POLAR NIGHT Marine Ecology

- life and light at the dead of night -

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Front cover: Work in the Arctic Polar Night North of Svalbard in January 2018. Photo Michael Snyder

Back cover: An iceberg illuminated from of the ship FF *Helmer Hanssen* January 2016 in Svalbard. Most of the work presented in this book have been conducted onboard this ship. Photo Geir Johnsen

Chapter 1

Introduction

Jørgen Berge, Geir Johnsen and Jonathan H. Cohen

Abstract

The current understanding of marine Arctic ecosystems is deeply rooted in the classical view of a bottom- up controlled system with strong physical forcing and seasonality in primary-production regimes. Consequently, the Arctic Polar Night has commonly been disregarded as a time of year when biological activities are reduced to a minimum due to a reduced food supply. Recently, based upon a multidisciplinary ecosystem-scale study from the Polar Night on Svalbard, an entirely different view has been presented. Instead of an ecosystem that has entered a resting state, we have documented a system in which activity levels and biological interactions across most trophic levels remain high. In some habitats, biological diversity and presence of juvenile stages were elevated in winter months (November-February) compared to the more productive and sunlit periods (March-October). The main ambition of this book is to present how key environmental variables, such as the light regime (intensity, colour and day length) are important cues for marine ecosystem dynamics, biodiversity, production and eco-physiology across different organism groups during the Polar Night. Ultimately, these results suggest a different perspective regarding ecosystem function that will be of importance for future environmental management and decision making, especially at a time when Arctic regions are experiencing accelerated environmental change due to human activity.

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1.1 Historical perspectives on Arctic Polar Night

This is a book about the Arctic marine ecosystem during Polar Night. We mainly focus on biological processes, but it is impossible to describe life in the Polar Night without also describing the Polar Night as a habitat and the technological platforms needed to observe biological processes in the dark. And, as our general perception of life in the Polar Night have radically changed during the last ten years, we also include a chapter on environmental monitoring and management in relation to the observed and projected increase in human activities in the high Arctic during the Polar Night. Ten years ago, this book would have been rather thin and easy to write, as common knowledge basically disregarded the Polar Night as void of any significant biological processes. Fortunately, using Svalbard as a field laboratory, we have been able to unravel a very different perspective about the marine ecosystem during the Polar Night. This book is intended to capture this new information and use it to understand natural ecosystem dynamics and how human activity rapidly can change the environmental conditions that organism may not be able to adjust to.

The Arctic has long captivated the public imagination and held a fascination for explorers. One of the first major scientific expeditions was Nansen's *Fram* expedition of 1893-1896. These early expeditions where, for obvious reasons, more focused on physical studies such as mapping the depth of the ocean, its hydrography and exploration of unchartered waters. Nansen allowed his ship to freeze into the ice north of eastern Siberia, from where it drifted across a previously unknown Arctic area before finally escaping the ice three years later between Greenland and Svalbard – a passage now known as the Fram Strait. A great deal of significant scientific information was gathered by this expedition, although relatively little concerning the cold and dark Polar Night. Later, several explorers attempted various expeditions into uncharted areas of the Arctic, including those of Admiral Peary in 1909, Stefansson in 1914, Storkerson in 1918, and Amundsen in the early 1920's. Then, in 1937, the former Soviet Union established their first Severnyi Poljus ("North Pole" in Russian) drift ice stations. This was the start of a series of remarkable years using scientific Arctic ice drift stations to enhance the understanding of marine physical, chemical and biological processes. However, while many did cover both the winter and the Polar Night periods, samples or measurements of biological activity were rarely secured, most likely because it was an accepted "truth" that the dark Polar Night contained no significant biological activity.

For a long time, ice-covered areas of the Arctic were presumed to be unproductive, and early scientific studies in the Arctic generally supported this paradigm (Nansen 1902). Evidence of human settlements and hunting activities in the high Arctic over several thousand years, however, conflicted with these early observations and constituted a paradox as to how human activities could subsist in regions considered to be biological deserts. Further investigations revealed the existence of productivity hot spots equal to some of the most productive places on earth, providing the first indications of complexity and the importance of the links between ice, ocean, and land in Arctic ecosystems. During the last 30 years, culminating in the 2019-2020 MOSAiC expedition during which an estimated 600 researchers and research technicians will participate, national and international research efforts in the Arctic sharply increased. Despite the fact that attention, awareness and research efforts have increased, there are still major and fundamental gaps in knowledge preventing a holistic understanding of the Arctic. Perhaps the most obvious and largest of these known gaps is centred around the still widely accepted view that Arctic marine ecosystems are best compared with a marine desert during the long and dark Polar Night. But just as the paradigm of the Arctic Ocean being an unproductive biotope was refuted a hundred years ago, the prevailing view of the Polar Night as devoid of biological activity has recently been challenged, initially by Weslawski et al. (1991) and more recently by Berge et al. (2015a,b).

All co-authors on the 11 chapters included in this book have taken an active part in developing the knowledge about the Polar Night that we present here. Many more have participated and played important parts, not the least all the MSc and PhD students who have taken part various campaigns on Svalbard. Since we published our first paper (Berge et al. 2009) documenting the presentence of synchronised diel vertical migration of zooplankton during the Polar Night, this broad cooperation has been instrumental to placing ourselves in the position where it is logical to write this book. It is, however, important to point out that our first discovery (Berge et al. 2009) was nothing more than an accident. Originally, we had absolutely no intention of studying the "dead" Polar Night. The first researchers to deliberately and actively study biological processes during the Polar Night was Jan Marcin Weslawski and colleges (Weslawski et al 1991) who spent two winters at the Polish research station in Hornsund, Svalbard (1981-2 and 1984-5). During these winters they made several key observations of biological activity during the winter period. This included presence of overwintering seabirds (common eider, Atlantic fulmars and black-legged kittiwakes), growth rates of selected zooplankton and benthic invertebrates and metabolism of living phytoplankton cells. However, at that time, they did not distinguish between Polar Night and winter (see Chapter 3 for further discussion). Rather, they used three different definitions of winter; in terms of climate (November-May), hydrology (January-March) and biology (November-March). One reason for this, as will be apparent as you read the book, may be that the Polar Night in Hornsund (77°N) is not a total darkness. In fact, even at winter solstice, the sun at noon is around 10° below the horizon, and the light climate characterized as "nautical twilight" (see Chapter 3). Hence, for the human eye, there is a difference between night and day, although at this latitude not comparable to e.g. Tromsø at 70°N. In fact, that the Polar Night is not a period of complete darkness is key to understanding the biology of the Polar Night (Fig. 1.1). In this book, we present different definitions of Polar Night which are complementary (see section 1.3 and Chapter 3), but we make a clear distinction between "winter" and "Polar Night" (see section 1.3 and Chapter 2).

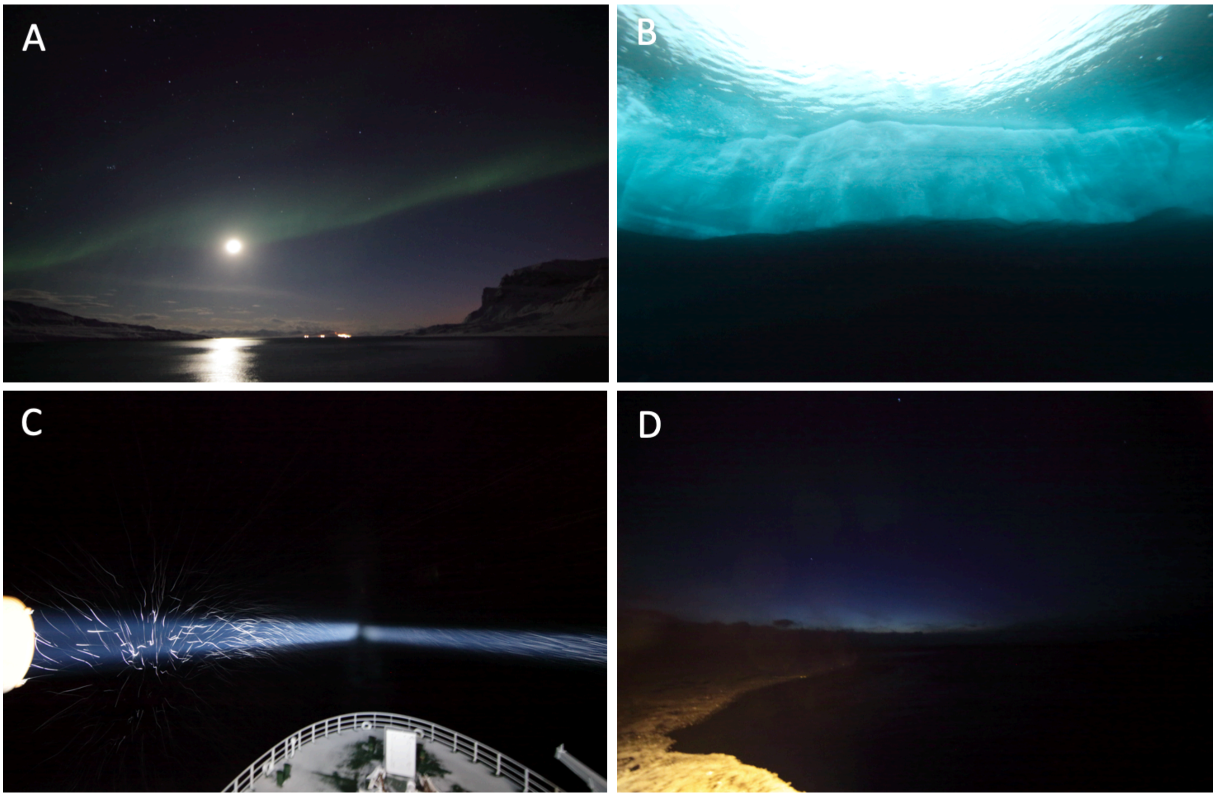

Fig 1.1 The different faces of "darkness". The Polar Night is not necessarily just a total darkness, but rather a complex composition of light from the moon, aurora borealis, background illumination from the sun and artificial light (A). Picture of Polar Night taken from the inner part of Trygghamna in Isfjorden at noon in January with ambient light from the sun which is below the horizon (bright horizon), the moon, northern light and artificial light from Barentsburg in Grønfjorden. (B) A bright day in spring do not necessarily need to be that bright underneath 1m thick sea-ice (N-Svalbard), the time when ice-algae blooms (see Chapter 4). (C) Noon at 81°N in January where, to the human eye, there is no difference between night and day. (D) The "ice-edge" north of Svalbard in January 2017. The diffuse light of the sun is seen to the south (brightest part of horizon). Artificial light from the RV *Helmer Hanssen* illuminates the edge of sea-ice. Photos: Geir Johnsen.

1.2 Rijpfjorden and the International Polar Year (2007-2008)

In 2006, in the run-up to the International Polar Year (IPY, 2007-2008), a project funded by the Norwegian Research Council was in its preparatory phase. The project was named *Cleopatra*: *Climate effects on planktonic food quality and trophic transfer in Arctic Marginal Ice Zones*. The project was one of the official Norwegian IPY projects, with a main aim of studying the effects of reduced ice cover on primary and secondary production in the Arctic. In other words, it was a project that focused on the importance of light, and how changing ice cover would affect the all-important primary production at the base of the food chain. Two fjords on Svalbard (Fig. 1.2) were chosen as model systems, one on the west coast of Spitsbergen (Kongsfjorden), and the other on the northern part of Nordaustlandet (Rijpfjorden). Kongsfjorden is strongly influenced by inflowing warm Atlantic water, and hence has a surprisingly short annual ice cover. Rijpfjorden, on the other hand, is a north-facing fjord with an ice cover that some years lasts for nearly 12 months. The central idea was then to use these two fjord systems, one without sea ice and the other with, to examine how primary and secondary production is defined by sea ice. Among the tools used were moored observatories capable of taking measurements throughout the water column during the entire productive season. But in order to do that, the moorings had to be deployed before the fjord froze over, hence during the previous autumn. When sampling commenced in the spring of 2007 (Fig. 1.3), the mooring had been in place for almost 6 months. As a consequence, or more precisely as a by-product, the moorings were in place and collected data not only in the spring when the sun returned, but in fact throughout the entire Polar Night and winter. Polar Night at that time was considered a totally uninteresting and "dead" period, so not much was expected to come of these measurements. We were, however, completely taken by surprise when we started examining the data after the mooring was recovered in 2007. The most striking discovery was that Arctic zooplankton conduct diel vertical migration both during the Polar Night and during early winter months underneath a thick cover of ice and snow. And as it turned out, this was in fact the start of a series of Polar Night campaigns, projects and publications aimed specifically at Polar Night ecology that have come out during the last 10 years, and which collectively are the basis for this book. With this book, and the studies conducted during the last 10 years as a springboard, we will focus on what we know today about the activities, processes and interactions that characterize the Arctic marine Polar Night. We will mainly use examples from Svalbard (Fig 1.2), but at the same time aim at placing these in a broader and more pan-Arctic context. In short, the research carried out during the last 10 years provides solid evidence that challenges the classical paradigm of biological quiescence during the Arctic Polar Night. Instead of an ecosystem that has entered a resting state, we now recognise a system in which high species diversity, activity levels, and biological interactions across most trophic levels and phyla remain high during the Polar Night.

Rijpfjorden also provides an excellent example on the importance of distinguishing between "winter" and "Polar Night". The fjord typically freezes in January-February and the water column has a temperature of -1.8°C (arguably a "winter" condition) between February and early July. However, during the darkest part of the Polar Night, water temperatures are well above the freezing point. Further, phytoplankton blooms often occur while temperatures are at yearly a minimum (see also Hodal et al. 2012) and close to the freezing point, demonstrating the relative importance of light rather than temperature as a regulating factor for primary production. This is also typical for spring blooms of phytoplankton along coastal N-Europe, occurring at the coldest water temperature in March-April. Limiting our focus to a period defined by available incident light, however, does not recognize that there may be large differences in available light depending on regional patterns in the attenuation of light by clouds, snow, ice cover, and by the water itself and its constituents such as phytoplankton, coloured dissolved organic matter (cDOM) and total suspended matter (e.g. Volent et al. 2007; Hovland et al. 2014). In areas characterized by thick snow and ice cover during winter, the water column beneath is often regarded as "dark" and the Polar Night might therefore be defined temporally and/or spatially beyond the limits of a solar angle alone (Sejr et al. 2009). This phenomenon is highly relevant for the timing of reproduction in the pan-arctic copepod *Calanus glacialis* (Daase et al. 2013) and is likely to play a major role in the timing of other ecological processes as well (Leu et al. 2015). However, based on both the spectral composition of ambient irradiance (Cohen et al. 2015) and low thresholds for detecting light intensity by key Arctic zooplankton (Båtnes et al. 2013), irradiance levels when the sun emerges above the horizon, but a thick ice and snow cover remains, might still resemble an early spring (rather than a Polar Night) situation.

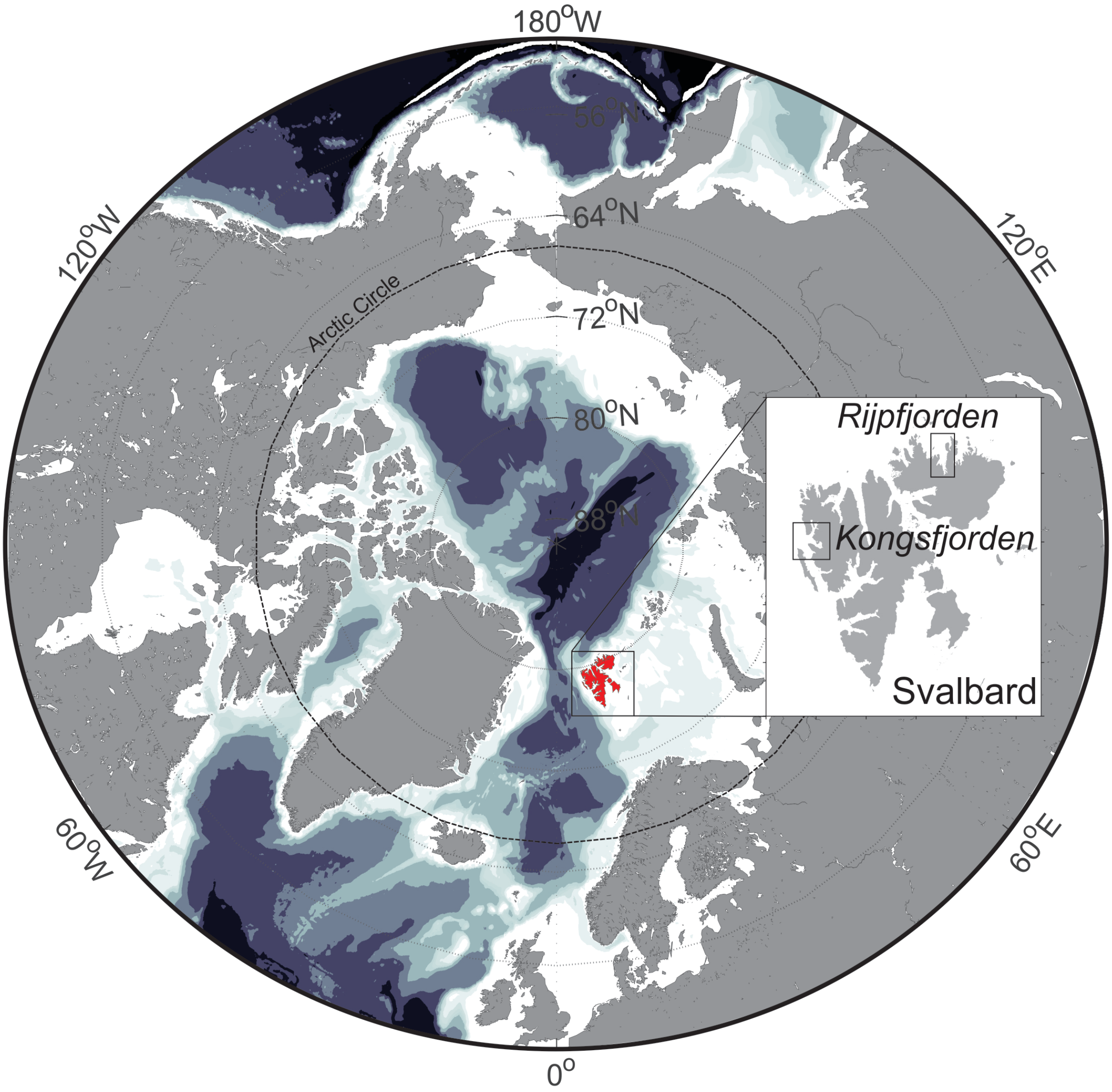

Fig 1.2 Map of the Arctic with Svalbard highlighted in red. Kongsfjorden on the west coast of Svalbard represent the main study area in which most of the knowledge presented in this book is based.

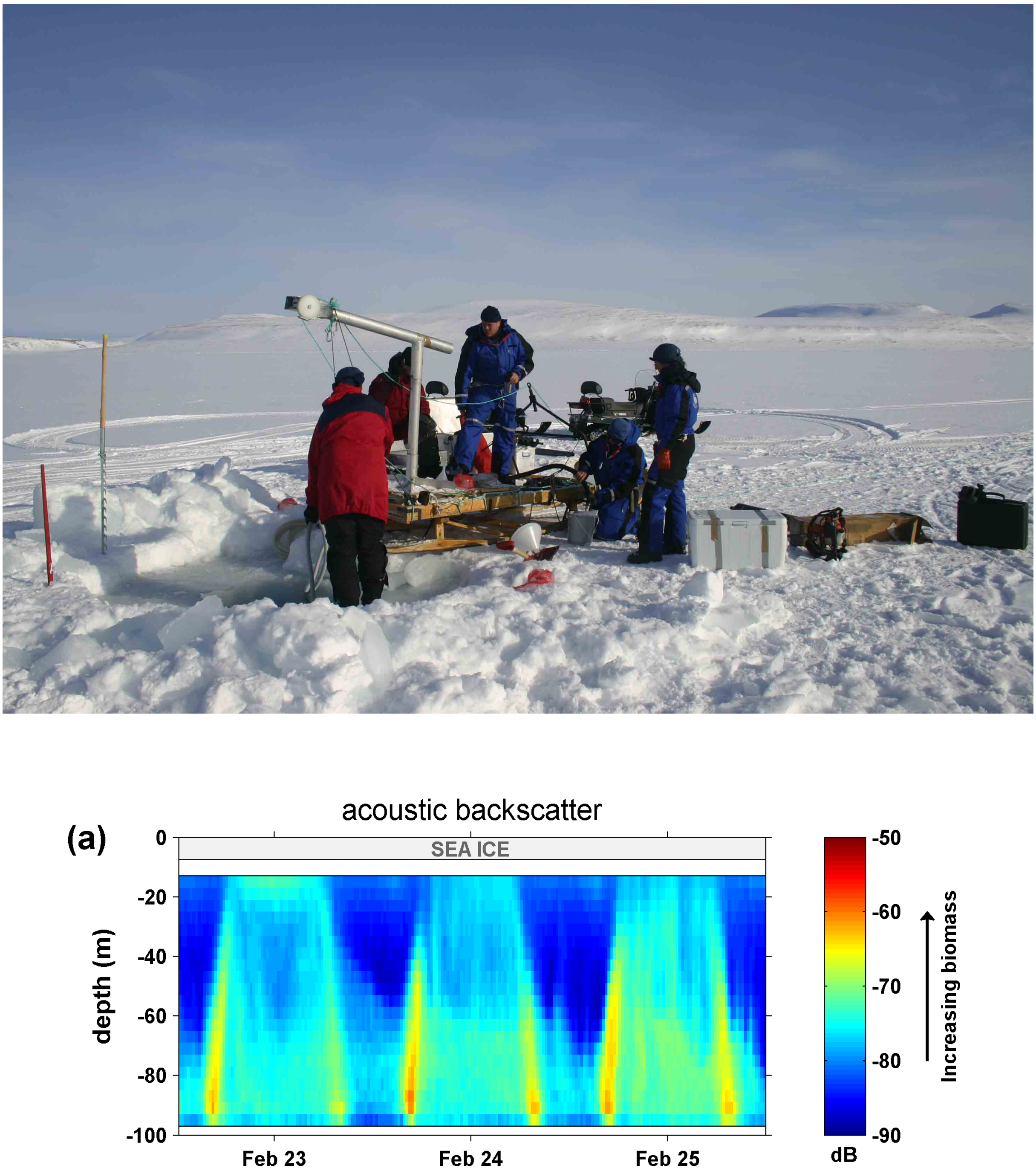

Fig 1.3 (**a**) Picture from Rijpfjorden in April 2007 in connection with fieldwork on a project that was aimed at the importance of light in an ice covered fjord on primary and secondary production. Samples were taken through a hole in the ice close to a fully autonomous moored platform that was deployed the previous autumn. (**b**) Data from this mooring was the first record of fully synchronised diel vertical migration of zooplankton in the early winter (Polar Night lasts until 20th of February at this location) and underneath a 1m thick ice cover (Berge et al. 2009). Photo: UNIS

1.3 The Polar Night and the *Novaya Zemlya effect*

The two terms "winter" and "Polar Night" are often used as partly synonymous, or at least as two periods with a clear overlap. Arguably, "winter" is often used in relation to temperature, whereas "Polar Night" is defined by the light regime (see Chapters 2 & 3). Here we concern ourselves primarily with the Polar Night, although it is impossible not also to consider the winter in many cases. What then is Polar Night? For most people, the term "Polar Night" is synonymous with "dark" – the sun stays below the horizon during the entire diel cycle. That is, solar elevation remains less than 0° with respect to the horizon over the 24-h day. When considering the number of days each year that this occurs, the duration of Polar Night theoretically increases by approximately 6 days for each degree of latitude (Fig. 3.1A). Thus, Polar Night lasts ~2 months at 70° N, 3.5 months at 78°N, and 5.5 months at 88°N, theoretically extending to a full 6 months at the North Pole. But in reality, the light climate of Polar Night is more complex. First, the apparent position of the sun relative to the horizon does not necessarily equal its actual vertical position. As the sun approaches the horizon (from above at sunset or below at sunrise), its light is refracted through the atmosphere. The phenomenon is called *atmospheric refraction* and causes what is commonly known as a "mirage". More importantly for understanding the Polar Night, however, it also causes light curving along the Earth's atmosphere to appear for an observer as though it travelled in a straight path from the sun (Fig. 1.4). Hence atmospheric refraction will cause astronomical objects (such as the sun) to appear higher in the sky than they are in reality. As closer to the horizon these objects are, the greater the effect. In relation to the Sun, the atmospheric refraction will be zero at zenith, but increases non-linearly as the angle between the Sun and the horizon decreases. At the horizon, the total refraction may be greater than the apparent diameter of the Sun. According to Young (2004), "for centuries, astronomers have known that atmospheric refraction … depends almost entirely on the temperature and pressure at the observer, and not on the detailed structure of the atmosphere" (Young 2004:3622). An important consequence of this is that the atmospheric refraction of light from the Sun at sunrise / sunset is not a constant, but dependent on local conditions at the point of observation. On Barents' last expedition in search of the Northeast passage in 1596-7, during which he discovered the Svalbard archipelago, members of Barents' expedition observed that the end of the Polar Night came 15 days earlier than what they could expect based on geometry alone. This observation caused quite a degree of controversy, both among the expedition members and later in the international scientific community. Barents, knowing the position where his expedition became icebound (76°15'N) off the Russian island Novaya Zemlya, at first refused to believe what his own members of the expedition had observed, but was of course convinced when he a few days later could see the phenomenon with his own eyes (Lehn & van der Werf 2005). Although the phenomenon was discussed already by Aristotle, the observations from the icebound expedition at Novaya Zemlya was the first report of this phenomenon in Western scientific literature. It is for this reason often referred to as the *Novaya Zemlya effect* in the literature today. There is, however, an important mistake in the original observations that we need to take into account. Originally, Barents reported the sun to rise above the horizon on the 24th of January 1597, a full 15 days earlier than expected. As this effect will be symmetrical across winter solstice, it would also mean the sun drops below the horizon 15 days later at the start of the Polar Night. This dramatic reduction of the Polar Night period is not in accordance with our current understanding of the start / stop date of the Polar Night at different latitudes (Fig. 1.4 and Chapter 3). How could they be so wrong? If Barents observations were correct, the total refraction of the sun would be no less than 5°26' in relation to the horizon. In fact, the observations by Barents is most likely highly accurate, but based on an outdated calendar (Lehn & van der Werf 2005)! In 1582, the Gregorian calendar had been proclaimed to correct the errors that were slowly accumulating in the old Julian calendar. The conversion introduced a correction of 10 days. While Barents claimed they had used the Gregorian calendar for every date, it is likely they were actually using the Julian calendar. If this is correct, their first observation of the Sun would have been only 5 days early, and in full coherence with contemporary measurements and observations regarding the onset and end of the Polar Night (Fig. 1.4 and Chapter 3).

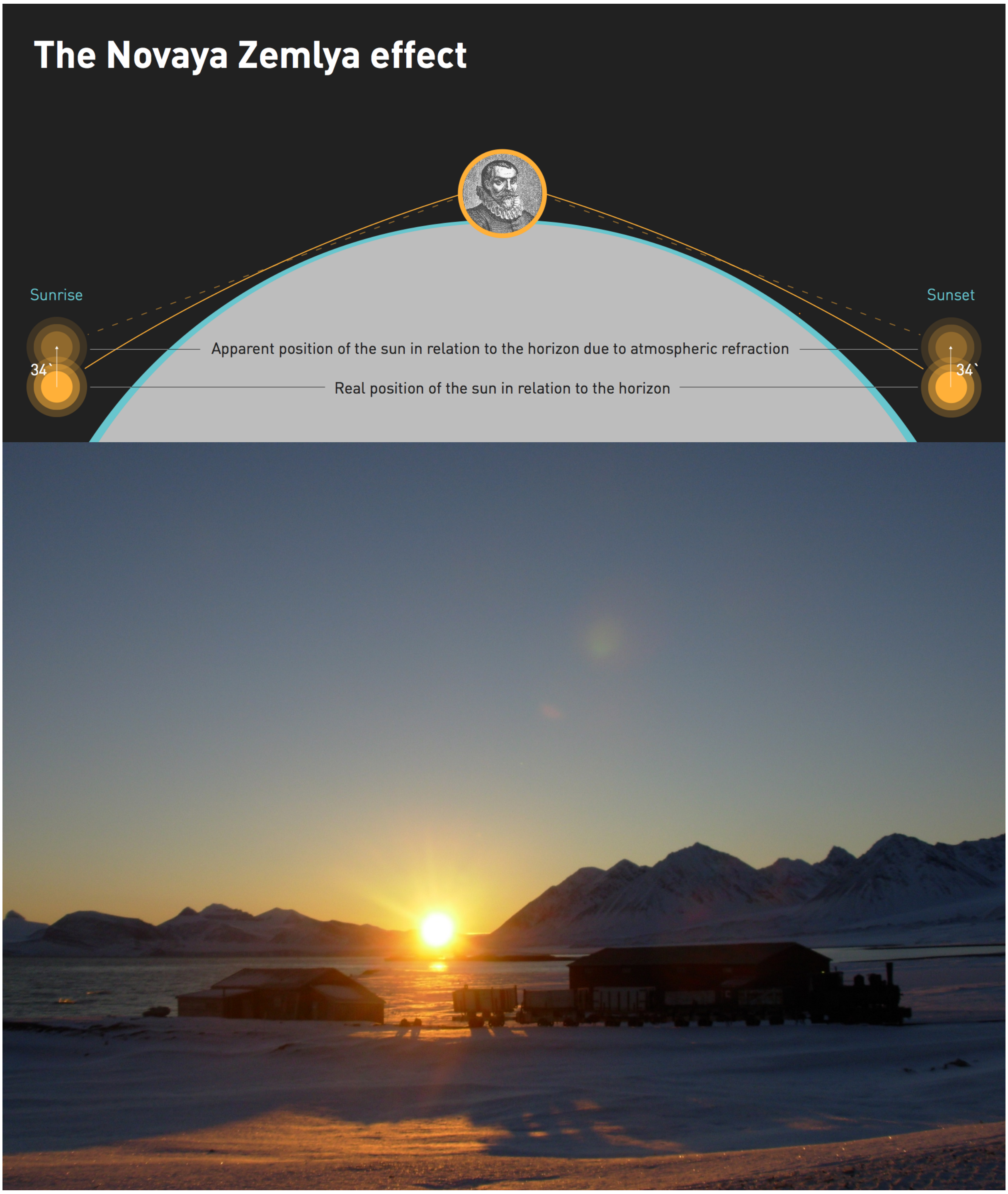

Fig 1.4 (**a**) Atmospheric refraction of the sun. On the 24th of January 1597, while trapped in the ice at 76°N close to Novaya Zemlya, members of the Willem Barents expedition noted that the first sunrise after the Polar Night occurred 15 days earlier than previously assumed. The effect became known as the *Novaya Zemlya* effect, but is in reality what we today refer to as atmospheric refraction. (**b**). Sunset in Ny-Ålesund, Svalbard. For the human eye or camera, the sun appear to be just above the horizon. In reality, and due to atmospheric refraction of light, its actual position will nominally be 34' arc minutes (i.e. 0.567 degrees) lower. The amount of atmospheric refraction is a function of temperature, humidity,

turbulence and air-pressure, hence the exact position of the sun may be more or less than the nominally 34'. A. Image by Eivind Reibo Jentoft, B. Photo by Jasmine Nahrgang-Berge.

The total effect of atmospheric refraction is a function of many factors, such as temperature, humidity and pressure. Hence it is never possible to give a universal and absolute value to the number of arc minutes (60th fractions of one degree – not to be mistaken by a latitudinal degree) for apparent position of the Sun in relation to its true position. In general, however, the effect is always that the apparent sunrise is earlier than the true sunrise and the apparent sunset is later than the true sunset. In polar regions, this has an important effect on the apparent duration of the midnight sun and Polar Night periods. This results in the disk of the sun (or moon) being visible for longer during twilight than otherwise predicted by geometry alone. This phenomenon of atmospheric refraction is dependent upon elevation and temperature. Additionally, Polar Night is not uniformly dark; nor is it a static event, akin to a switch being flipped and then darkness ensues. Rather, the Polar Night needs to be understood both in space and time in order to fully understand and describe the "darkness". Polar Night can better be thought of as having four different zones (Polar twilight, Civil Polar Night, Nautical Polar Night, and Astronomical Polar Night), with each zone defined by the sun's elevation at the winter solstice. The further below the horizon the sun appears to be, the darker the Polar Night. The exact zone of Polar Night at given location depends on latitude (Fig. 1.5). For the northern hemisphere, the lowest level is **Polar twilight** which occurs from 66° to 72° N when solar elevation remains between 0° and 6° below the horizon at the winter solstice. The entire duration of Polar Night at these latitudes is limited to Polar twilight. Further north in a band from 72° to 78° N, Polar Night begins with a period of Polar twilight which is followed by **Civil Polar Night** when solar elevation remains between 6° and 12° below the horizon at the winter solstice, and then again by Polar twilight. Still further north in a band from 78° to 84° N, Polar Night consists of Polar twilight and Civil Polar Night followed by **Nautical Polar Night** when solar elevation remains between 12° and 18° below the horizon at the winter solstice, and then again by Civil Polar Night and Polar twilight. And finally in a band from 84° to 90° N, the periods of Polar twilight, Civil Polar Night, and Nautical Polar Night are followed by **Astronomical Polar Night** when solar elevation remains 18° below the horizon at the winter solstice, and then again by the three lesser periods before the sun returns above the horizon. For the human eye, there is no difference between night and day within the Astronomical Polar Night. Geometrically, there is one day of Polar Night at the Arctic circle, and the Polar Night lasts for 183 days at the pole. However, due to atmospheric refraction of sunlight, at sea level there will appear to be direct sunlight at noon on winter solstice up to approximately 67.4°N. The Polar Night must also be understood as a temporal phenomenon. Just as the night anywhere on Earth will change in its characteristics of darkness from dusk to dawn, so will the Polar Night (see Chapter 3 and Fig. 11.3). The geographical extent of the four Polar Night zones illustrated in Fig. 1.5 is only as a symmetrical period across the winter solstice. The duration (number of days indicated in Fig.1.5) is the total duration of the Polar Night within four different latitudinal bands, whereas the definition of the light climate (polar twilight, civil polar night, nautical polar night and astronomical polar night) refers to the darkest type of polar night within each band.

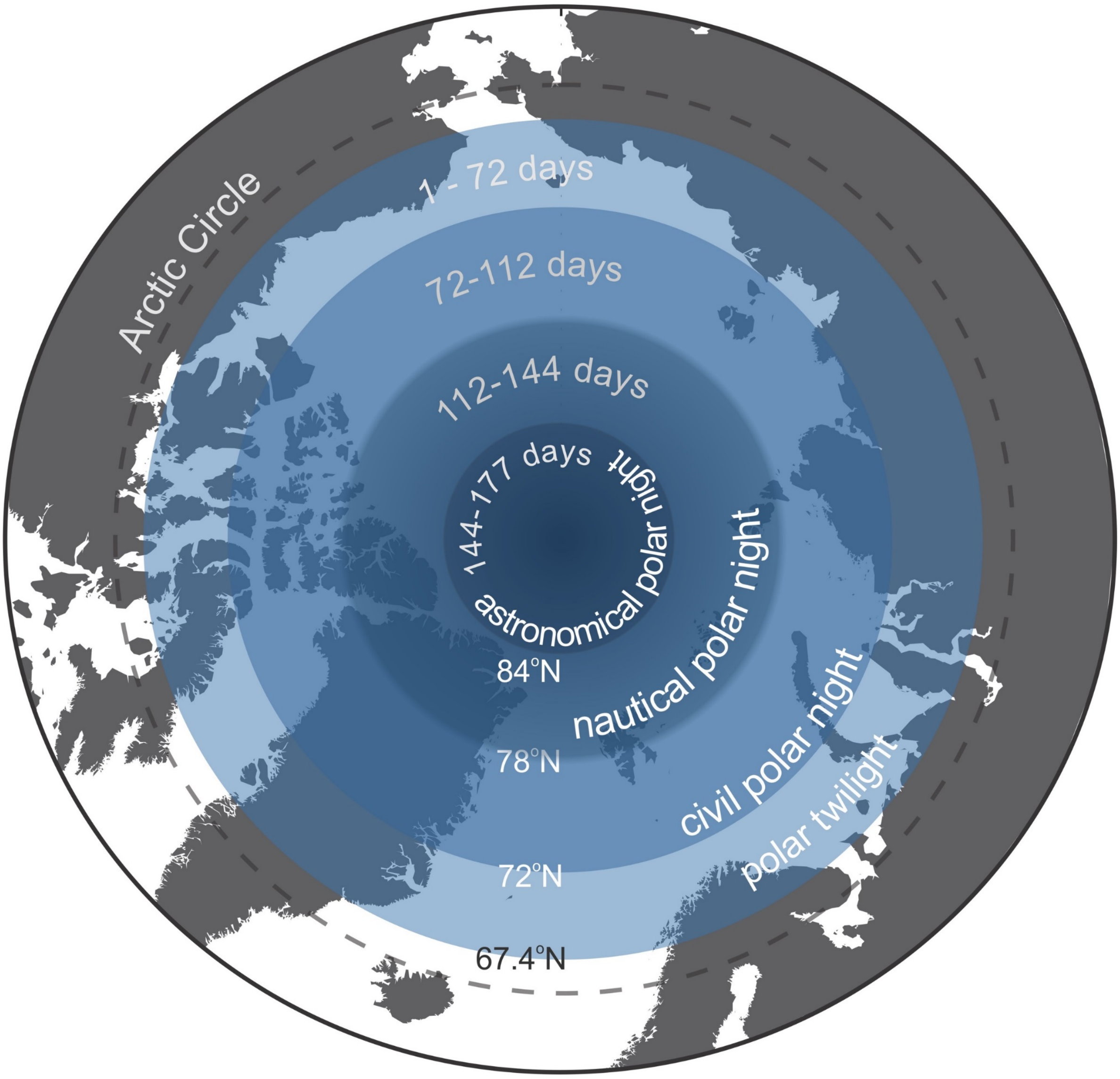

Fig 1.5 The geographical extent of the four zones of Polar Night at winter solstice. Optically, due to atmospheric refraction (deflection of light rays) and the way the sunlight is curved around the Earth's surface, the Polar Night does not start at the polar circle, but at around one degree further north (67.4°N). Geometrically, however, at the polar circle (66.3°N), the sun is below the horizon for one full diel cycle at winter solstice. Also, despite the fact that geometrically there is only one day and one night at the two poles, in terms of light the Polar Night is shorter (177 days) than the midnight sun period (189 days) at the poles. Both the duration and relative darkness of the Polar Night increases with latitude (Chapter 3). The duration indicated represent the duration of the Polar Night, defined as the number of days between the last sunset in the autumn and the first sunrise in the spring.

Marine ecosystem processes are direct consequences of the complex behaviours and interactions between organisms, many of which are driven by the physical environment. Accordingly, a classical paradigm in Arctic marine ecology suggests that most biological processes stop during the Polar Night at high latitudes due to low food availability and the lack of light. This assumption was first challenged by presenting evidence of diel vertical migration (DVM) of zooplankton during the Polar Night (Fig. 1.3). This discovery initiated a large range of diverse studies, most presenting unexpected new discoveries of a system in full operation and with high biological activity levels (reviewed in Berge et al. 2015a,b). Perhaps most striking is the documentation of seabirds actively foraging deep inside the Polar Night (Figs. 11.20-21). For seabirds such as Brünnich's guillemot (*Uria lomvia*) and little auks (*Alle alle*), both dependent on finding their zooplankton prey daily, surviving the high Arctic Polar Night is vivid and direct evidence that ecosystem interactions and processes are ongoing, even at 80°N. They are visual predators, searching for their prey in what to us appears to be total darkness – how is this possible? This, together with our growing realisation of how important moonlight, diffuse background illumination from the sun, and even bioluminescence is in the marine Arctic during the Polar Night, gave rise to the title of this book: *Life and light at the dead of night*.

This book has 11 chapters, each with a clear focus on the marine environment and with a majority of examples used from Svalbard (Fig 1.2). Although the main focus of the book is to document and explain how marine organisms remain active and are able to detect and respond to light throughout most of the Polar Night, it is not possible to do this without also considering the Polar Night as a habitat. Chapters 2 and 3 is dedicated towards describing to physical characteristics of the Polar Night, both in terms of oceanography (Chapter 2) and light (Chapter 3). Most people would assume that the Polar Night is a cold, ice covered and dark period. The reality is far from that simple. In fact, at least in the ocean, the Polar Night is usually a warmer period than the spring, and the annual minimal ice extent occurs when the Polar Night is initiated within the central Arctic Ocean. And in terms of light, the Polar Night is anything but a constant darkness! Chapters 4-7 take us through the main organismal groups, starting with marine algae, zooplankton, benthos, and fish. Chapter 8 focus on a special phenomenon that is very often characteristic of dark environments, so also in the Polar Night: biological clocks. Chapter 9 is an overview of current capabilities regarding technological platforms and sensor technology, both key issues when it comes to studying biological activity in the otherwise rather in-accessible Polar Night. In fact, a major contributor to many of the discoveries that have been made regarding biological activities during the Polar Night has been fully dependent on implementation of new enabling technologies. For this, our collaboration with the Centre for Autonomous Marine Operations and Systems (AMOS) at NTNU (Norway) have been essential, providing and co-developing functional platforms solutions to handle the challenging operations in the dark. Chapter 10 is intended as a summary of all previous chapters; using a real event that occurred north of Svalbard in December 2018 when a trawler ran ashore in Hinlopenstredet as an example, we want to highlight that the Polar Night can no longer be considered as a low-risk period when it comes to possible exposure of organisms to e.g. oil spills. In reality, it is most likely quite the opposite – knowing that the Polar Night is a key period for reproduction in many organismal groups, a potential oil spill in the Polar Night might have an even more detrimental effect than any other periods of the year. Finally, chapter 11 contains a series of exhibition posters made for a museum exhibition with the same name as the book.

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There are many people who should be thanked, not the least all the students and colleges that have participated in Polar Night campaigns, cruises and UNIS (University Centre in Svalbard) with MSc and PhD courses during the last 10 years. A special thanks to the staff in Ny-Ålesund who, during the three years we hosted a Polar Night course based at the marine laboratory (Marine Lab) there, made an incredible effort to reduce all possible sources of light pollution during the two-week periods we spent there. This included turning of street and quay lights and blinding off all windows facing the sea and not the least accepting that all outdoor lights were

turned off for two weeks before and two weeks during courses in the middle of the dark Polar Night to ensure that the marine organisms examined in situ or in the laboratory were not influenced by artificial light (light pollution)!

This work comprises several funding sources, with the Norwegian Research Council as the most important. Through a range of different projects, starting with the FriPro project in 2011, the NRC have funded five main research and infrastructure projects: *Circa* (project no 214271), *Marine Night* (project no 226417), *Arctic ABC* (project no 244319), *Arctic ABC Development* (project no 245923) and the Centre of Excellence *AMOS* (project no 223254) that have all had a significant contribution towards the development of Polar Night research. Without these projects, this book would not have been possible! Other funding sources have also been important, with National Geographic Society, Svalbard Miljøvernfond and NORUS project financed by Centre for higher education in Norway (SiU), a partnership in higher education between Norway and North America, "Technology development for marine monitoring and ocean observation". Finally, the Nansen Legacy Programme (NFR project no 27272) have provided financial support.

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Chapter 2

The Marine Physical Environment during the Polar Night

Finlo Cottier and Marie Porter

Abstract

The physical environment of the Arctic is captured in popular perception as being an isolated, frozen and intensely cold ocean. The reality is surprisingly different; an ocean system that supports warm inflow to the Arctic and exchange with the adjacent ocean basins, influenced by stormy weather systems that can originate in mid-latitudes, and having a sea-ice cover that is experiencing ongoing reduction in its extent and thickness. The Arctic environment of popular myth is probably derived from centuries of exploration where expeditions set out to map the coastlines and harvest resources, often being forced to endure long winter months under extreme conditions (Chapter 1). True, the human isolation still prevails in many regions of the Arctic, but the common conception of the Arctic experiencing atmospheric and oceanographic isolation needs to be clarified. Some of the key ideas presented in the chapter demonstrate that the Arctic can be a highly advective system, with the physical pathways of ocean currents and atmospheric storm tracks providing effective transport mechanisms and connectivity.

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2.1 The Ocean

2.1.1 Winter vs Polar Night in the physical environment

This chapter on the Physical Marine Environment will use the terms Polar Night and winter. In Chapter 1 the precise astronomical definition of the Polar Night was discussed and it was noted that deviations from that precise definition can occur due to optical phenomena. In contrast, the term winter is a more loosely defined and is used with a variety of meanings and interpretations. In this chapter we utilise the precise term Polar Night where possible, noting its variation with latitude. Most of the occurrences in this chapter of the more generic term 'winter' will refer to a calendar based approach which is invariant to geography and which will typically encompass December, January and February, for example Gjelten et al. (2016) and Park et al. (2015), occasionally also spanning the period December to March (Alexeev et al. 2017) and Onarheim et al. (2014) of which Polar Night might only be a subset of that winter period and not entirely bounded by it. This use of 'winter' is most common when authors of research papers are making statements about the physical environment of the Arctic, particularly climatology and meteorology. In these cases we also use the term 'winter months' to reinforce this particular use of the term. Within the Chapter we will also reemphasise the distinction that was made in Section 1.2 between Polar Night and winter with respect to water temperatures.

2.1.2 General characteristics

A common descriptor of the Arctic is that it is an "ocean surrounded by land", and critically for processes occurring in the Polar Night, the major proportion of that ocean is north of 72°N (the limit for Civil Polar Night, see Chapters 1 and 3) making it the highest latitude ocean in the world, and therefore also the darkest. In global terms the Arctic Ocean is relatively small; it constitutes only 1% of the world ocean volume and 3% of the world ocean surface area. Nevertheless, there are important inflows of water to the Arctic from the North Atlantic and the North Pacific and these oceanic fluxes are critical to the functioning of the Arctic (Cottier et al. 2017; Beszczynska-Möller et al. 2011). Although small by volume, the Arctic Ocean can claim some remarkable statistics (Wassmann 2015) and are produced in Table 0.1 below: The interactions between the land and the sea are very important to Arctic processes and the Arctic has 35% of the world coastline with the shallow coastal waters receiving more than 10% of global run-off.

Table 0.1 Key statistics about the Arctic Ocean (data extracted from Wassmann (2015))

World Ocean Volume	1%
Earth Surface	5%
World Ocean Area	3%
World Continental Shelf	25%
World Coastline	35%
Global River Runoff	11%
Global Population	0.05%

Away from the coast, half of the Arctic Ocean comprises relatively shallow (< 300m depth) continental shelf which itself is 25% of the world continental shelf area. These shallow and relatively productive waters extend out to 78°N (the limit of Nautical Polar Night) meaning that these important circumpolar shelf seas are exposed to a wide range of photoperiods. The shelf areas have been defined previously as being ‘inflow’, ‘interior’ or ‘outflow’ shelves depending on their relationship with the large scale oceanography (Carmack et al. 2006). At the Atlantic gateway is the Barents Sea, one of the two main inflow shelves, where nutrient rich, warm and saline Atlantic Water enters through the Barents Sea Opening providing the largest contribution of oceanic heat to the Arctic (Rudels et al. 2015). Another branch of Atlantic Water flows into the Arctic through the relatively deep Fram Strait. Observations over many years in the Atlantic inflow sector of the Arctic have shown an increased influence of Atlantic Water that has been termed “Atlantification” – see Box 0.1. The other main inflow shelf is the Chukchi Sea, which receives water from the Pacific Ocean through the Bering Strait. This relatively fresh inflow brings a third of the freshwater into the Arctic and is a significant source of inorganic nutrients (Beszczynska-Möller et al. 2011). The interior shelves are found north of the Russian coast on the Eurasian side of the Arctic and the Beaufort Sea on the North American side (Williams and Carmack 2015). The main outflow from the Arctic is through the shallow waters of the Canadian archipelago and along the East Greenland shelf in the Fram Strait.

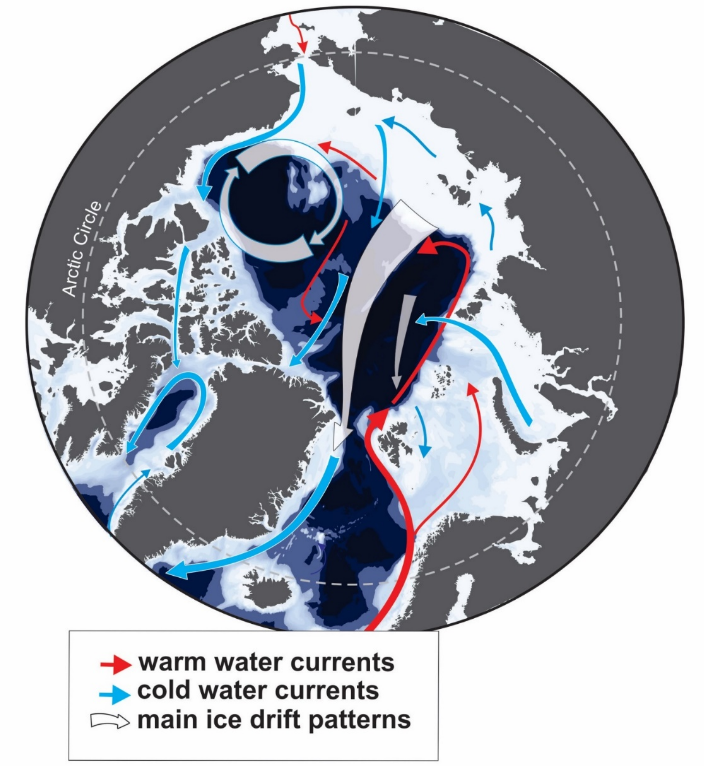

Fig 0.1 Sectional view of the Arctic Ocean basin showing the main inflow/outflow paths and the principle shelf seas.

Box 0.1: Atlantification of the Marine Arctic

Atlantic Water is relatively warm with a temperature greater than 0°C, but can be much warmer where it enters the Eurasian Basin of the Arctic through the Barents Sea or the Fram Strait, Fig 0.1. The term "Atlantification" was first used to describe the observed increase of Atlantic Water into the Barents Sea and sets the boundary of the ice-free region (Årthun et al. 2012). However, the extent of Atlantic Water influence goes well beyond the Barents Sea. Atlantic Water is present across much of the Arctic, but beyond the southern Barents Sea and the Fram Strait it is isolated from surface waters, and any overlying sea ice, by a density structure in the ocean called the Arctic Halocline (Box 0.2). The formation of the halocline in the Eurasian Basin is reliant on spring and summer sea ice melt as an input of buoyant low salinity water at the surface (Cottier et al. 2017). However, as atmospheric forcing drives reductions in sea ice cover and increases mixing in the surface layer, there is a reduction in the stratification of the upper ocean in the Eurasian Basin (Polyakov et al. 2017; Polyakov et al. 2018).

The Northern Barents Sea (Lind et al. 2018; Barton et al. 2018) and Eurasian Basin (Polyakov et al. 2017) are part of the seasonal ice zone, where fresher surface waters cause the saline Atlantic water to be subducted, isolating it from the overlying ice. As this seasonal ice zone has retreated northward, the lack of freshwater input has weakened the halocline (Lind et al. 2018). This is in contrast to other regions of the Arctic, notably the Amerasian Basin, where there is general freshening of the surface waters (Carmack et al. 2016) which leads to a strengthened halocline (Polyakov et al. 2018). With a reduced salinity contrast between the surface and Atlantic Water masses in the Eurasian Basin, the density gradient between the water masses is reduced and the warm Atlantic Water is able to shoal toward the surface. The shoaling of the Atlantic Water and erosion of the halocline is further encouraged as the loss of sea ice allows for greater turbulent mixing, with regular storms adding energy to the water column and mixing the surface waters (Polyakov et al. 2017).

The shoaling of warm Atlantic Water to the surface, driven by reduced sea ice cover, has a positive feedback for sea ice loss. The warmer water is not conducive to the local formation of sea ice further reducing sea ice cover and decreasing the stratification of the water column (Barton et al. 2018). The resulting well-mixed, largely ice-free water column is predominantly Atlantic Water and reflects the structure of the Atlantic dominated southern Barents Sea and western Eurasian Basin. This progression from a stratified system with intermediate depth Atlantic Water overlain by fresher, surface waters to a mixed system, with full depth Atlantic Water and a weakened halocline is described as "Atlantification".

Beyond the limit of the shelves, extending into the highest latitudes and darkest period of Polar Night, are the deep basins of the Arctic (Bluhm et al. 2015). These deep basins are the regions where the thicker, perennial sea ice cover is found (Stroeve and Notz 2018), making them the most extreme in terms of light climate. The basins descend to depths of around 4000m and are separated by well-defined sub-sea ridges that facilitate a connection to the surface by steering currents in the upper waters. Two major basins are the Amerasian and Eurasian, separated by the Lomonosov Ridge and each of these basins is further sub-divided; the Amerasian in to the Makarov and Canada Basins and the Eurasian into the Nansen and Amundsen Basins. At the margin of the shelves and the deep basin are found the cyclonic boundary currents that are topographically trapped to the shelf slopes. These provide effective transport pathways through the Arctic basins with the potential to advect species to high-latitudes with different photoperiods (see Chapter 8).

There are two dominating wind-driven surface currents in the Arctic. The Transpolar Drift acts as a pathway that crosses perhaps the greatest range of latitudes, and therefore light conditions, during the transit from the East Siberian Sea (~ 73°N) across the North Pole (90°N) toward the exit at Fram Strait, the east coast of Greenland and the Arctic Circle. Over the Amerasian Basin is the anticyclonic Beaufort Gyre, with a circulation pathway that extends from approximately 75°N to the 90°N. The overall picture is one of a relatively small, advective and highly connected ocean that shows considerable variability in its physical characteristics.

2.1.3 Coastal conditions

Biological activity during the Polar Night has been carefully documented in coastal waters (Berge et al. 2015; Berge et al. 2009) and at sites in the deep Arctic Ocean (Last et al. 2016). Observations of oceanographic conditions from the deep Arctic basins during the Polar Night have come from traditional profiling techniques deployed from drifting ships e.g. Nansen (1897) or more recently Granskog et al. (2016), from ice camps and automatically recorded by moorings in deep water (McPhee et al. 2003) or profiling technologies (Timmermans et al. 2008). Our appreciation is that the Polar Night ecosystem is relatively more active in shelf and coastal waters and so it is important to understand the ice and oceanographic conditions in these shallower waters and the changes that are occurring. As discussed in Section **Error! Reference source not found.**, the shallow Arctic shelves are a dominating feature and these are arguably the most accessible areas for deployment of automatic sensors for measuring conditions in the Polar Night (Renner et al. 2018; Cottier et al. 2007; Hop et al. 2019).

One of the primary processes occurring in coastal or fjordic regions during autumn is the release of heat from the water column to the atmosphere. This has the effect of increasing the water density, reducing the stability of the water and promoting vertical mixing. This tends to bring warmer water to the surface and thus sustain the seasonal cooling. Vertical mixing is enhanced by strong wind events and gradually the thermal stratification in the water column is eroded with the upper water column gradually cooling to freezing point (Søreide et al. 2010; Cottier et al. 2007; Tverberg et al. 2019). The rate of cooling is such that at the time of the Polar Night, the surface waters may be approaching freezing temperatures but the mean water column temperature is still well above freezing, with heat remaining in the deeper water, Fig 0.2. This has important consequences for both ice formation, which can be delayed (Muckenhuber et al. 2016), but also to the biological process rates of benthic organisms which are found to remain active during Polar Night (Berge et al. 2015).

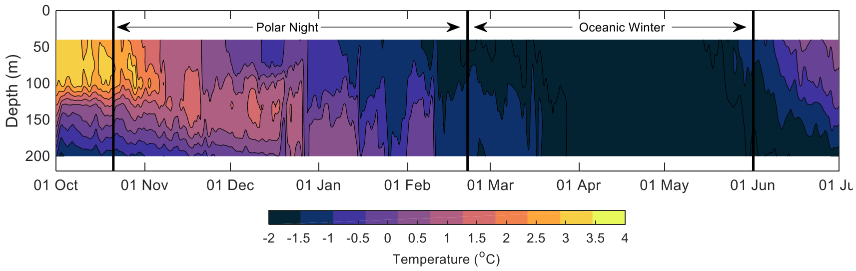

Fig 0.2 Cooling of the water column in Rijpfjorden (80.2°N) showing the gradual cooling throughout the Polar Night period but only attaining homogeneous temperature close to freezing well after the Polar Night in what might be termed the 'Oceanic Winter'. Data from the Rijpfjorden Marine Observatory (Cottier et al. 2019) during the period 2015 to 2016.

We see in Fig 0.2 that at the time of Polar Night the water is typically not at its minimum temperature, this is a key aspect of Polar Night oceanography. Heat is still being lost from the water, particularly in Atlantic-influenced regions where there can be large volumes of warm water masses present (Cottier et al. 2007). Using the depth mean temperature of the water column as a guide we see in Figure 2Fig *0.3* that in both Kongsfjorden (Atlantic influenced) and Rijpfjorden (Arctic influenced) the temperature minimum for the fjord is found in April, well after the period of Polar Night has ended. Further, the depth mean temperature maximum is found in both fjords at the start of the Polar Night. Consequently, Polar Night in coastal locations should not be characterised oceanographically as the period of coldest temperatures, rather it is a period of relatively warm waters which undergo cooling. Nevertheless, we see that the surface waters will approach freezing point as the Polar Night advances.

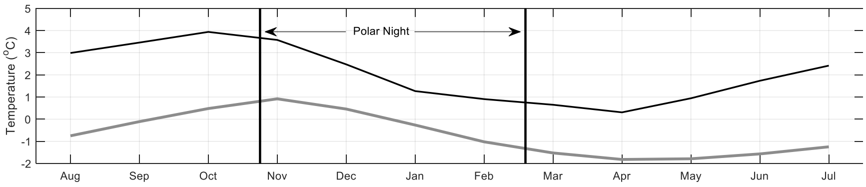

Fig 0.3 Depth averaged monthly mean temperature for Kongsfjorden (black line) and Rijpfjorden (grey line) showing the mismatch between the period of Polar Night and the time of minimum temperature in April. Data from the Kongsfjorden and Rijpfjorden Marine Observatories (Cottier et al. 2019; Hop et al. 2019).

In the western areas of Svalbard, the coastal and fjordic waters are gradually warming year on year (Goszczko et al. 2018) due to a greater influence of Atlantic Water and favourable wind forcing (Nilsen et al. 2016). The impact of this on the Polar Night oceanography over the last decades is that water temperatures have gradually warmed. In Fig 0.4 we see the depth mean temperatures of the water in Kongsfjorden. We note that whilst there is interannual variation there is also a clear warming signal of around 2°C per decade. This has been implicated in the ability for species to overwinter (Geoffroy et al. 2018; Berge et al. 2015), making for new viable life strategies.

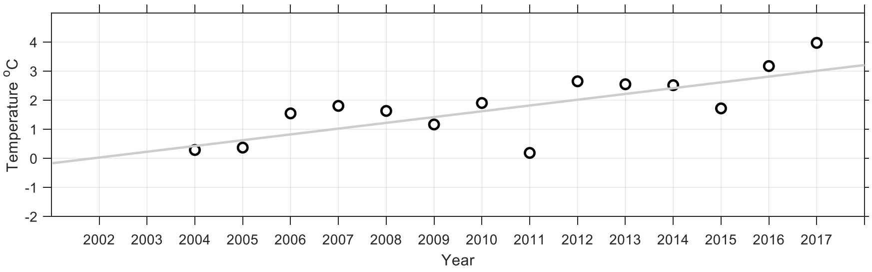

Fig 0.4 Depth averaged water temperature for Kongsfjorden for the months of November to February, corresponding to the period of Polar Night. The water is warming at a rate of around 2°C per decade.

2.2 The Atmosphere

Arctic air temperatures have been increasing twice as fast as the global average and are one of the key indicators of modern climate change. Seasonally, the most rapid warming has been recorded during winter months. In Svalbard, for example, warming during the Polar Night has been particularly strong over recent decades (Fig 0.55), with an increase in temperatures of 2°–3°C decade^{-1} (Førland et al. 2011; Gjelten et al. 2016). The warming seen between the decades in Fig 0.5 has been attributed to the loss of sea ice along the West Spitsbergen coast (Gjelten et al. 2016) and we discuss further the close coupling between ocean, ice and atmosphere within this section.

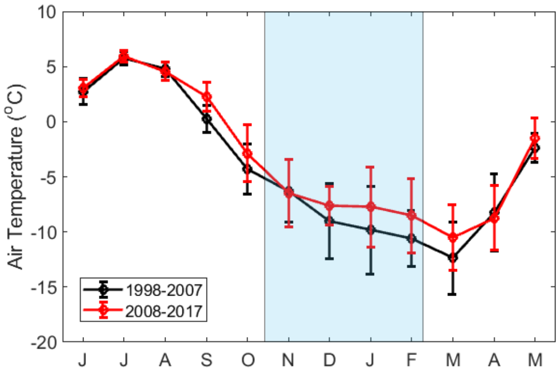

Fig 0.5 The mean monthly surface air temperature at Ny Ålesund (79°N), World Meteorological Observation station number 01007. The bars show one standard deviation either side from the decadal mean. The blue sector highlights the period of Polar Night.

The highest latitudes in the Arctic will typically experience the coldest, almost continental climate, having an amalgam of multi-year ice, seasonal ice and open water. Further south, sea ice in the circumpolar shelf seas is mainly seasonal or largely absent and the ocean then becomes highly coupled with the atmosphere. The role of the ocean and ice in modifying the atmosphere is well illustrated in the Barents Sea (Fig 0.1) where there is an oceanic transition from warm and well mixed Atlantic origin waters in the south and west to cold, stratified Arctic dominated waters in the north and east. The inflow of warm Atlantic Water to the western Barents Sea ensures that the climate in this region and particularly around western Svalbard is unusually mild given its latitude. In contrast the north eastern Barents Sea is capped with Arctic surface water and is often ice-covered during the Polar Night giving a cold and drier climate to areas east and north of Svalbard compared to the west. Since the 1970s there has been an observed reduction in the sea ice cover, which combined with increasing transport of Atlantic Water into the Barents region gives rise to a gradual poleward progression of a warmer, damp, Atlantic dominated maritime atmosphere.

In particular the observed warming during winter months is governed by the large-scale transfer of heat and moisture from mid latitudes by storms, leading to an increasing frequency of warm events[1] (Graham et al. 2017a; Alexeev et al. 2017). These events originate as storm systems that develop in the adjacent Atlantic or Pacific Oceans and propagate into the Arctic. The winter warming events from the Pacific and the Atlantic affect the Arctic to different extents. Storms emanating from the Pacific tend not to penetrate as far north as those from the Atlantic giving rise to an asymmetry in the average maximum winter temperature – typically -4°C at 85°N in the Atlantic sector compared to -11°C at 85°N in the Pacific sector (Graham et al. 2017a). The impact of these more frequent warm events on sea ice formation is to reduce the number of freezing degree days available for ice growth (Stroeve and Notz 2018).

The atmosphere in the Polar Night is neither uniformly cold nor stormy. Measurements from field campaigns occurring in the Polar Night have revealed two distinct atmospheric states; either cold, with clear skies or much warmer and cloudier (Graham et al. 2017b). The latter is triggered by the storm events that enter the Arctic from the adjacent oceans causing a positive flux of heat and moisture As a consequence of these two distinct states winter surface temperatures have a bimodal distribution being either significantly above or below (± 10°C) the seasonal mean temperature at most times and locations (Graham et al. 2017a)

Ocean-atmosphere heat fluxes are a key property that control the physical dynamics of the Arctic Polar Night. Across the Atlantic sectors of the Barents Sea, the surface water during the Polar Night is substantially warmer (~3°C) than the colder overlying air temperature (~ -10°C). This leads to significant heat fluxes with annual means of 56-83 Wm^{-2}, depending on local ice cover (Smedsrud et al. 2013). These conditions give rise to local atmospheric instabilities and convection which can build into Polar lows – intense, sub-mesoscale low pressure systems that are a feature of the Polar Night. These Polar lows require heat from the ocean for their formation and are become short-lived if they move over land, but they can produce heavy precipitation and hurricane force winds at sea and in coastal regions. In addition to Polar lows, the region around Svalbard is subject to large low pressure systems from the North Atlantic, spurned from the jet stream. These systems are associated with precipitation, wind and warm temperatures and are significant in driving exchange processes between the ocean and adjacent shelves (Nilsen et al. 2016; Goszczko et al. 2018; Tverberg et al. 2019).

The passage of large low pressure systems during the Polar Night brings increased atmospheric heat, moisture and wind to the Arctic by transferring energy from the warm North Atlantic (Førland et al. 2011; Alexeev et al. 2017). These storms also mix the water column which is a critical process during the Polar Night as it can resupply the surface with warm water from depth, further increasing the heat flux from the sea into the atmosphere. The heat that storms transport, associated with the increased cloud cover can cause periodic increases in heat flux to the ocean and ice. This can result in delayed onset of ice formation in the period of Polar Night, or reduced ice growth rate or enhanced sea-ice melt (Alexeev et al. 2017). Ocean and ice conditions through the winter months, encompassing the period of Polar Night, are therefore highly correlated with the frequency and severity of these storms. As the sea ice cover begins to advance in spring to reach its annual maximum extent (Section 2.3), the ocean-atmosphere heat fluxes are reduced bringing significantly colder air temperatures and less frequent low pressure events.

Atmospheric models indicate that in general, the frequency of storms occurring across the Arctic during the winter months, and therefore in the Polar Night, will reduce (Day et al.

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[1] Defined as atmospheric events where the air temperatures exceed -5°C

2018). This is due to a reduced temperature gradient between mid- and high-latitudes during winter. However, as is usual for the Arctic, the picture is highly regional. Analyses of data from Ny-Ålesund has shown that the number of storm events in the early part of the Polar Night (Nov-Dec) has increased by more than 5 events per decade in the period 1979-2015 (Rinke et al. 2017). The increased occurrence of these cyclones during the last decade has been attributed to stronger atmospheric blocking (Häkkinen et al. 2011), especially during January–February; but increased heat fluxes and reduced sea-ice cover are also contributory factors (Rinke et al. 2017).

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The seasonal patterns of elevated air temperature and low winds from June to October and low air temperature and high winds from December to April (with the lowest temperatures and highest wind speeds around March) are not unique to Atlantic influenced regions of the Arctic. Stations of comparable latitude Ittoqqortoormiit, Greenland (Scoresbysund) at 70.2°N and Tromsø at 69.4°N and Danmarkshavn, Greenland at 76.5°N and Hornsund, Svalbard (Polish research station) at 76.6°N show that the same seasonal pattern is found in eastern Greenland where the nearby ocean surface currents are cold Polar Waters (Fig. 2.6). These cold water bounded coastal meteorological stations are in the lee of the prevailing wind direction in the North Atlantic, in contrast to the Norwegian stations and as such they experience more extreme seasonal air temperature variability and lower wind speed variability. Nevertheless, in all locations the coldest air temperatures and highest wind speeds are found at the limit of, or outside, the period of Polar Night. In conclusion we can say that the Polar Night is not simply characterised by being the coldest and windiest period of the year as we might instinctively perceive it to be.

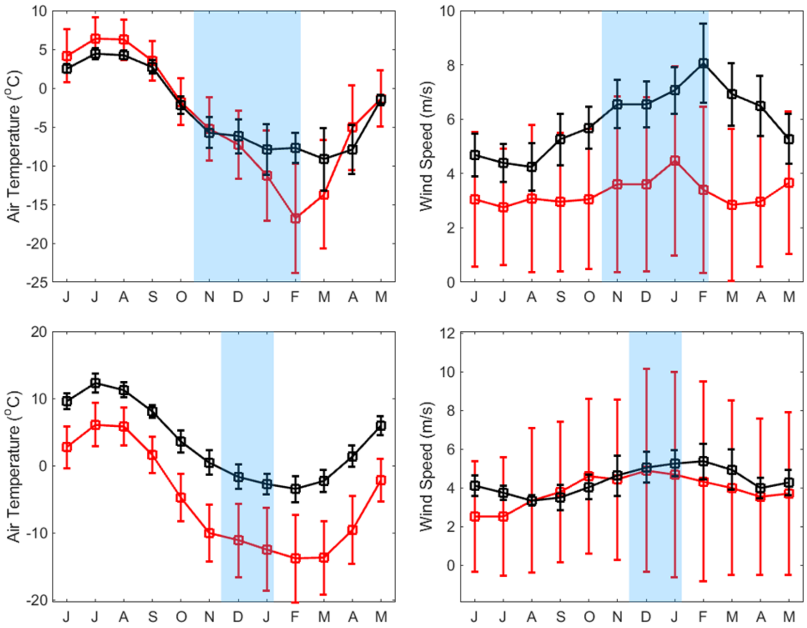

Fig 0.6 The mean monthly surface air temperature (a, c) and 10 m wind speed (b, d). For Panel a and b: Danmarkshavn, Greenland at 76.5°N (WMO station 04230, red) and Hornsund, Svalbard at 76.6°N (WMO station 01003, black). For Panel c and d: Ittoqqortoormiit, Greenland at 70.2°N (WMO station 04339, red) and Tromsø at 69.4°N (WMO station 01025, black). The central points for each plot represent the monthly mean between 1997 and 2013, the bars show one standard deviation from this mean. The blue sector highlights the period of Polar Night, the duration of which is seen to vary with latitude.

2.3 The Ice

A defining feature of the Arctic is its sea ice cover, the frozen ocean, forming a solid lid on the marine domain. The ice is fundamental to many upper ocean processes (Cottier et al. 2017) and plays a leading order role in moderating the exchange of heat and the transfer of solar energy into the ocean (Katlein et al. 2015; Perovich 2017). But the ice cover is undergoing exceptional changes in both its extent, its thickness and its age (Stroeve and Notz 2018); generating intense public awareness of the reduction in Arctic sea ice and presenting us with the prospect of a future ice-free Arctic (Onarheim et al. 2018).

Presence and absence of sea ice is highly regional with some locations in the southern marginal seas of the Arctic experiencing just a brief ice cover in spring, whilst other locations north of Greenland, for example, are recognised as having a more persistent. Ice thickness also shows wide geographic variation, ranging from relatively thin (< 1.0 m) ice in marginal and coastal waters whilst the areas of perennial ice may experience thicknesses of 2-3 m of undeformed ice increasing to >6 m in areas of ice with ridges caused by deformation of the ice floes (Haas 2017). Presence of open water, even at maximum ice extent also shows great variation with the presence of semi-permanent openings in the ice offering a window of light to the underlying ocean.

The seasonal formation and retreat of sea ice across the Arctic follows a relatively consistent cycle. During the growth-melt cycle the ice and the ocean are closely coupled (Vinje 2009; Cottier et al. 2017); where ice growth results in a release of saline brine which promotes mixing and minimises stratification whilst ice melt releases freshwater into the surface promoting stratification and inhibiting vertical mixing. Sea ice will typically begin to form during the late fall and early winter to reach a maximum extent[2] in March with an area of around 15 million km^2 before melt and export of ice cause it to diminish and retreat to a current minimum extent of around 5 million km^2 in September. Superimposed on this annual cycle is the recent decline in extent in all seasons (Onarheim et al. 2018). The trend of decreasing summer sea ice is generally pan-Arctic with an average rate of decrease in ice extent of around 14% per decade.

Whilst many projections exist about an ice-free summer, is there potential for some peripheral regions in the Arctic to become increasingly ice-free during the Polar Night? During the period of Polar Night, ice extent is decreasing at around 4% per decade (see Fig 0.7) and the most significant changes are occurring in seas at the southern boundary of the Arctic, e.g. Barents Sea, Sea of Okhotsk, Greenland Sea and Baffin Bay (Onarheim et al. 2018). Decline of sea ice in the Atlantic sector during the winter months has been partly attributed to enhanced downward infra-red radiation (Park et al. 2015) driven by atmospheric fluxes of moist, warm air described in Section 0. However, in the Barents Sea particularly, there is also strong evidence that the winter ice extent and variability is controlled to a large extent by variations in Atlantic inflow and the oceanic heat content (Årthun et al. 2019; Onarheim and Årthun 2017; Onarheim et al. 2014). Projections from a Community Earth System Model show that the Barents Sea may become ice free in March within the time period 2061–2088. (Onarheim and Årthun 2017)

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[2] Extent is typically defined as the areal coverage of sea ice with at least 15% concentration

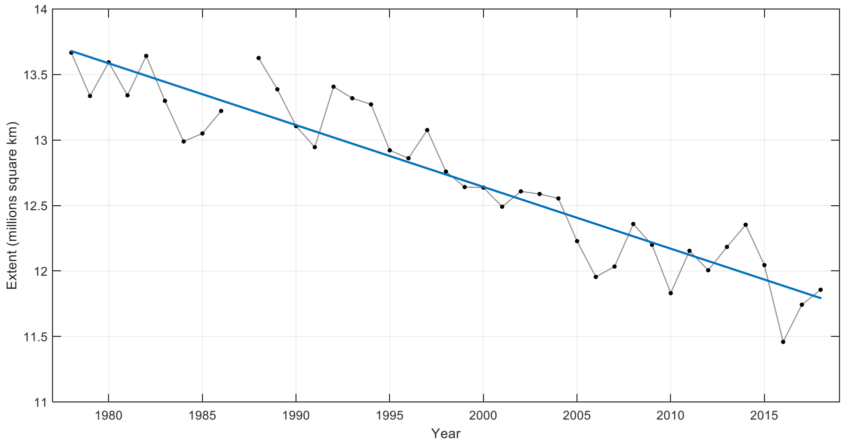

Fig 0.7 December mean sea ice extent in the Arctic between 1978-2018. Data from National Snow and Ice Data Centre [nsidc.org].

A reduced, or absent, sea ice cover during the period of Polar Night becomes highly relevant when considering any processes linked to vestigial light sources. It has been suggested that if some areas of the Arctic that are currently frozen during winter months were to become and remain ice-free then there would be quite considerable impact on the local ecosystem function (Carmack et al. 2006). In effect, the annual cycle of ice formation, growth, melt and retreat is an overlay onto the latitudinally and seasonally varying light climate.

Overlaying these long term changes, the distribution of sea ice is also highly variable on relatively short length and time scales. For example, ice that has persisted through the winter and spring in coastal areas can be lost in just a few hours due to sudden changes in wind direction. Further, the open and dynamic arrangement of floes in the marginal ice zone mean that the ocean is either open or ice-covered at a scale of 10s of meters. This creates highly variable environment in the water below and the Polar Night ice conditions, particularly in marginal seas, can be highly heterogeneous.

The observed northward retreat of the ice and the resulting increase in open water during the summer impacts on ice extent in the Polar Night through oceanic coupling and the memory in the system. Early retreat of the ice in summer exposes large areas of open water for longer periods of time. This sets up a very effective positive feedback mechanism that further accelerates the loss of ice and the subsequent gain in heat during summer (Stroeve et al. 2012). Greater areas of open water lead to increased fetch and wave action causing mechanical break-up of the ice and exposure of open ocean (Asplin et al. 2014). Earlier melt and longer duration of open water leads to greater warming of the surface and increased heat content of the surface water (Stroeve et al. 2014; Serreze and Stroeve 2015).

This excess heat must be released to the atmosphere through surface heat fluxes before freezing can start. Yet warming in all seasons has reduced the likelihood of especially cold winters. In recent decades careful observation of Arctic sea ice has shown that the timings associated with the seasonal cycle of ice have begun to shift. The timing of onset of ice freeze up has become later by around 2 weeks per decade (Johnson and Eicken 2016). Warmer air temperatures during the Polar Night play a role by reducing the number of freezing degree days (Stroeve and Notz 2018) but in the Barents Sea the duration of the freezing period is determined primarily by the variation in Atlantic Water inflow to the region (Onarheim et al. 2015; Årthun et al. 2012).

The impact of summer ice retreat therefore is to push the date of freeze-up in the Arctic later in the season so that that during the Polar Night, waters may only experience a thin ice cover or still be ice-free. This is counter to the popular perception that a dark, cold Arctic will be dominated by sea ice. This effect can be further exacerbated through the more frequent and intense storms which have the capacity to support deep mixing and bring relatively warm water to the surface. The delay in onset of freezing reduces the overall freezing period such that by spring and maximum sea ice extent, the ice will be thinner and more susceptible to break up, exposing the ocean surface to further solar heating during that summer.

Delayed onset of freezing, reduced period of thermodynamic growth and a more mobile ice cover, susceptible to advection, means that the fraction of old sea ice has reduced from 20% in the 1980s to only 5% in the current decade (Serreze and Stroeve 2015). The ice is therefore necessarily thinner and the mean sea ice thickness is estimated to have reduced by at least 40% over the last 30 years (Meier et al. 2014). The overall situation for ice cover during the Polar Night is for a thin, fragile, young ice that is susceptible to break up by storms and providing minimal shading of light.

It is clear that the Polar Night ice cover is increasingly vulnerable to loss. It is particularly sensitive to the flux of heat from the ocean (Onarheim et al. 2018; Onarheim et al. 2014) and this will persist as the Arctic experiences greater “Atlantification” (Box 0.1). During the Polar Night the ocean heat flux to the underside of sea ice can be enhanced. Brine released during ice formation can force convection to bring heat from the upper layers of the Atlantic Water into the surface mixed layer and storms can support enhanced shear and mixing to increase the ocean heat flux to the ice (Polyakov et al. 2013). These effects are further enhanced due to a reduced halocline which reduces the density contrast between the surface mixed layer and the Atlantic Water. The increased heat flux to the underside of sea ice is more than sufficient to cause considerable thinning or to decrease the rate of ice growth (Polyakov et al. 2010).

Some areas of open water during the Polar Night can be semi-permanent and are linked to local meteorological or oceanographic phenomena. These areas are called polynyas, a Russian word meaning “ice hole” and can be tens or thousands of square kilometres in size. The occurrence of polynyas during the Polar Night is due to two possible mechanisms. The first is through enhanced ocean heat flux causing melting (sensible heat polynya) and the second is through the action of strong winds pushing the ice to create open water (latent heat polynya). The wind effects are often enhanced by topography such that latent heat polynyas are typically found in coastal regions where offshore winds can push ice away and maintain areas of open water. It is likely that the increased storminess described in this chapter may result in more extensive and persistent coastal polynyas in the Polar Night.

The sea ice cover also acts as a platform on which snow can accumulate. Snow reduces both the exchange of heat and the propagation of light through the ice. The timing of snow fall relative to ice formation is important, particularly with respect to conditions experienced in the Polar Night. Snow fall in autumn will tend to accumulate on thin ice, reducing ice growth and resulting in a thinner ice cover. If ice formation is delayed due to warming surface waters then the snow will fall onto open water, such that the accumulation of snow will be reduced giving a thinner overall snow cover during the Polar Night and into the spring . The impact of delayed onset of freezing is being seen in reduced mean snow depths (Webster et al. 2014). The impact of snow cover on light transmission is very significant with snow covered sea ice having extinction coefficients for light that are more than an order of magnitude greater than for bare ice (Sturm and Massom 2017).

Box 0.2: Sea Ice Formation

Sea ice will only form in water at its freezing point, about -1.8°C for seawater. As the water is cooled during the autumn and into the winter months, heat is being extracted from the upper part of the water until it is isothermal and then freezing can commence. The initial ice formation is as small fragile crystals that accumulate at the surface and form a thin uniform sheet (during calm periods of weak winds) or as an icy slush some meters thick (during periods of strong winds and waves). The different formation conditions give rise to different crystal textures; in calm conditions we get congelation ice with large, elongated vertically oriented crystals and in windy conditions we get frazil ice with small, randomly oriented crystals. As ice begins to form, the salt in the seawater becomes partitioned between the ice and the ocean; about half is retained in the ice, making it slightly salty (salinity value 15-20) and the rest is released into the ocean as a saline brine.

The sea ice cover continues to grow through thermodynamic processes whereby heat is removed from the upper ocean by conduction through the ice. The growth occurs at the interface between the ice and the ocean in a porous, fragile layer of ice called the skeletal layer. As the ice consolidates and thickens, vertical channels being to form which allow the brine trapped within the ice to gradually drain into the ocean. These brine channels make the ice a relatively open and permeable structure allowing it so support biological communities through the exchange of oxygen and nutrients. Sea ice can also increase in thickness through dynamic growth. This is the process of rafting and ridging caused by currents and wind where the sheets of sea ice can ride up on top of each other (effectively doubling the thickness) or crumple at the edges leading to a random arrangement of ice blocks in thick structures called ‘ridges’.

To sustain an ice cover, the ocean heat flux to the underside of the ice must be minimal, otherwise melting of the bottom surface would occur. The biggest reservoir of oceanic heat in the Arctic is the Atlantic Water that enters through the Fram Strait and Barents Sea where extensive areas of open water persist. Once the Atlantic Water has become subducted below the surface waters it can become isolated through the action of an oceanographic structure called the Arctic Halocline which provides a density barrier between the colder, fresher surface water and the warm and saline Atlantic Waters. The halocline is typically found at depths between 50 and 200 m and limits the extent to which heat from the deeper Atlantic layer can penetrate to the surface leading to ice melt. The interaction between ice and ocean is exemplified in the existence of the halocline because ice growth and release of cold and dense brine is critical to halocline formation.

2.4 Knowledge Gaps

Data from the Arctic is patchy both by season and by location. Some places and some seasons are relatively data rich, whilst few observations have been made in other locations. In particular, the Polar Night is a period that is relatively data sparse, though automatic and robotic measurement systems (Chapter 9) are starting to change this. As a consequence our understanding about physical processes in the Polar Night is based on relatively few observations and so we are also reliant on appropriate application of modelling techniques to close the gaps between measurement and understanding.

A clear uncertainty is how ocean temperatures during the Polar Night will evolve in the future. This is critically important for both physical processes linked to weather and sea ice but also biological process linked to respiration, growth and overwintering strategies. Future ecosystem function in the Polar Night will be highly dependent upon water temperature as a primary control on biochemistry, affecting growth rates, development and respiration. Future projections of ocean temperature are of course important but rather limited without projections of ocean transport so that the overall flux of heat through the Arctic can be quantified. Tools exist to do this and thus relate future Arctic oceanic state with changes occurring further upstream in the mid-latitude ocean basins (Årthun et al. 2019).

A key aspect of ocean warming is the temperature of the surface waters. This is important with respect to the regional meteorology and the formation of Polar lows (Section 2.2) but also important for biological processes occurring at the surface. Longer periods of ice-free water in the summer will allow the uptake of heat, leading to increased surface temperatures. With warmer air temperatures the rate at which this heat is lost from the surface is reduced. The result is more heat required to be removed before ice formation can start leading to Polar Night conditions with increasingly warm surface waters and no ice cover.

In the Arctic the seasonal cycle of sea surface temperature tends to be rather weak. There a various reasons for this, not least the presence of sea ice moderating the surfaces fluxes that warm the ocean and the annual melt/freeze cycles of the ice. Excess heat in surface water goes into melting sea ice in summer (latent heat of fusion) and this heat is returned to the surface mixed layer during the freeze up process in the Polar Night. Those regions with relatively minimal ice concentrations such as the Nordic Seas and the Southern Barents Sea currently experience the largest seasonal variations in sea surface temperature. In the coming centuries, projections show that the strength of the seasonal cycle in air temperature will reduce yet the amplitude of the seasonal cycle of sea surface temperature is expected to double (Carton et al. 2015). The primary reason for this is the loss of the moderating effect of the heat loss/gain to the surface layer during ice melt/growth. This in turn will have considerable impact on the sea surface salinity and the stratification and stability of the water column. Mixing in the upper water column and the process of nutrient regeneration are important processes during the Polar Night. Future widespread modification of the seasonal cycles in temperature, salinity and stratification in the Polar Night is an area of understanding that we need to progress to fully appreciate the impact of reduced sea ice cover in the Arctic.

Whilst there remains active discussion about the prospects of a future ice-free Arctic in summer, there is also the potential for an ice-free Polar Night. Climate models are showing that this transition could occur much more rapidly than loss of summer sea ice for the same rate of warming (Bathiany et al. 2016). This is linked to the realisation that following an ice-free summer, it only requires that the water cannot be cooled to freezing point through the winter months to prevent large-scale ice-free conditions. However, the precise timing of this transition to an ice-free state may fall outside the period of Polar Night such that an ice-free Polar Night is merely the prelude to a fully ice-free Arctic with no winter formation of sea ice. The detail of the timing and implications on water column structure through such projections of sea ice cover are important to appreciate the physical characterisation of future Polar Night conditions. As more regions in the Arctic become seasonally ice free, sea ice loss during the Polar Night will being to dominate (Onarheim et al. 2018).

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Chapter 3

Light in the Polar Night

Jonathan H. Cohen, Jørgen Berge, Mark A. Moline, Geir Johnsen and Artur P. Zolich

Abstract

How much light is available for biological processes during Polar Night? This question appears simple enough. But the reality is that conventional light sensors for measuring visible light (~350 to ~700 nm) have not been sensitive enough to answer it. Beyond this technical challenge, "light" is a general term that must be qualified in terms of "light climate" before it has meaning for biological systems. In this chapter, we provide an answer to the question posed above, and explore aspects of light climate during Polar Night with relevance to biology. Specifically, how Polar Night is defined by solar elevation; atmospheric light in Polar Night and its propagation underwater; bioluminescence in Polar Night and the concept of Polar Night as a deep-sea analogue; light pollution; and future perspectives. This chapter focuses on the quantity and quality of light present during Polar Night, while subsequent chapters in this volume focus on specific biological effects of this light for algae (Chapter 4), zooplankton (Chapters 5, 8), and fish (Chapter 7).

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3.1 What is Light Climate?

There are several excellent reviews on light and its biological relevance in general (Land and Nilsson 2012; Johnsen 2012; Cronin et al. 2014), and in the polar environment specifically (Sakshaug et al. 2009; Pavlov et al. 2019), and we refer you to these for further details on physical aspects of light, and how organisms detect and use it. Here, we highlight the concept of light climate, as it includes the key elements needed to understand light during Polar Night.

Specifically, light climate comprises the *intensity*, *spectrum*, and *duration* of light for a given location. Each of these parameters can be considered in a variety of units, and crucially for their biological relevance, each are species-dependent (see Box 3.1). We briefly discuss some fundamental considerations for each parameter concerning measurement and units.

3.1.1 Intensity

Light intensity can be measured as radiance (L) or irradiance (E) (Fig. 3.1A). Radiance refers to photons emitted per unit area per second, while irradiance refers to photons received per unit area. The angle of the sensor is variable for either quantity, but typically in biological studies directional measurements concern downwelling light (L_d, E_d) or upwelling light (L_u, E_u). Irradiance is typically measured in "hemispheres" where the collector may either be cosine-weighted to favor photons normal to the collector face (cosine), or equally capture photons from all angles of the 180° hemisphere (2π). Alternatively, scalar irradiance (E_o) measurements can be made with a 4π collector which encompass both downwelling and upwelling light over 360°, mimicking the absorption surface of an algal cell in the water column. Irradiance is commonly measured in energy units ($W\ m^{-2}$) or quantal units (photons $s^{-1}\ m^{-2}$ or μmol photons $s^{-1}\ m^{-2}$), with the latter particularly useful for studies of photosynthesis and vision. A common confusion concerning intensity measurements involves photometry versus radiometry. Radiometry concerns measurements of radiance and irradiance. Photometry concerns measurements of luminance and illuminance, which are analogous, but involve weighting the measurement by photopic human visual sensitivity and are expressed in terms of lumens. Photometric measurements are not directly relevant to biological processes apart from human vision.

3.1.2 Spectrum

No matter how intensity is measured, the spectral composition of the ambient light and the spectral window of the sensor must be considered (Fig. 3.1B). One way to do this is to measure both intensity and spectrum simultaneously with a hyperspectral light sensor, providing measurements of L, E, and E_o per nanometer across the spectral window of the sensor. However, a common approach to light measurement in biological studies is to report a value for "Photosynthetically Active Radiation" or PAR, which is light intensity integrated from 400-700 nm. While this light range encompasses wavelengths responsible for many biological processes (e.g., photosynthesis, vision, entrainment of endogenous rhythms), it must be remembered that "PAR" only denotes the spectral range of the measurements, so radiance or irradiance as described above could both be measured as PAR. For an irradiance measurement, clearly defining a measurement as, for example, $E_{o,PAR}$, resolves this issue.

3.1.3 Duration

The diel (24h) cycle of light can be considered in terms of its photoperiod (Fig. 3.1C). In this way, the light portion of the 24h cycle is denoted as "day" or "photophase", and the dark portion as "night" or "scotophase". Photoperiod then is expressed as [hours day]:[hours dark]. For some biological processes, such as photosynthesis, day represents the active period (i.e., actinic light providing photosynthesis) while night represents the inactive period (see Chapter 4). However, the active phase may occur at night for other processes, such as nocturnal diel vertical migration (Chapter 5). Photoperiod can entrain biological clocks, providing information on time of year needed to control patterns of physiology and behavior (Chapter 8). An open question concerning measurement of photoperiod is what light level to consider as the break between "day" and "night". This will ultimately depend on the light sensing ability of the organism in question (see Box 3.1 and section 3.7 below).

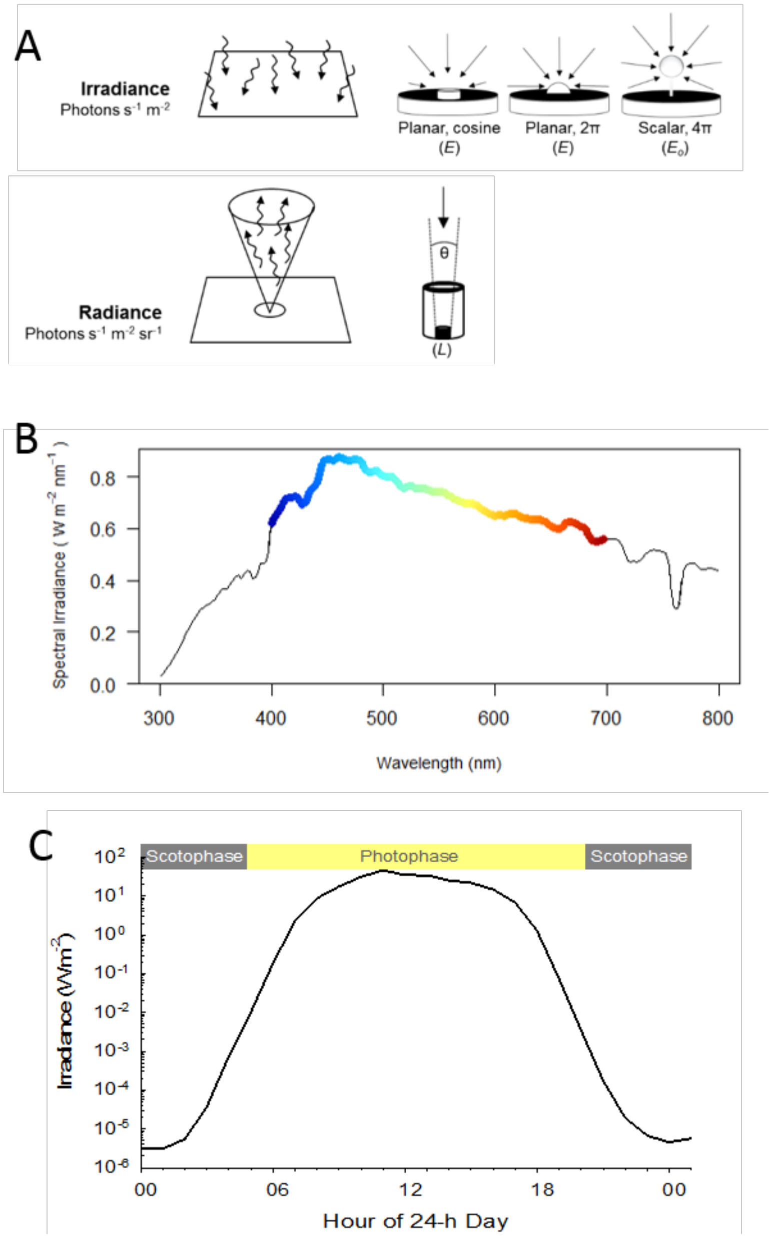
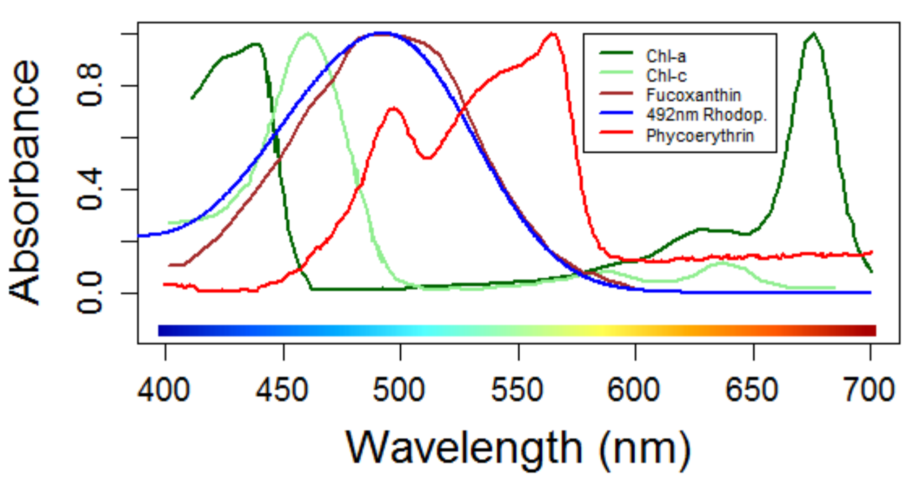


Fig 3.1 Measurement considerations for light climate. (**a**) Irradiance and radiance provide different, yet complementary ways to quantify environmental light. (**b**) Spectral irradiance at Ny-Ålesund, replotted from Hisdal (1986). These are global radiation values (direct solar radiation and diffuse radiation from reflected/scattered sunlight). Colored points indicated the spectral range for Photosynthetically Active Radiation (PAR, 400-700 nm), with colors at these wavelength as they appear to the human visual system. Note that spectral irradiance is not flat over this region, and there is incident light outside of the PAR region. (**c**) An example of photoperiod where irradiance changes over the 24-h day. Periods of scotophase (night) and photophase (day) are indicated. The duration of these periods is variable, depending on e.g. location and light source

Box 3.1 Biological utilization of light in polar night

According to the First Law of Photochemistry (Albini 2016), light must be absorbed for photochemistry to occur. This implies that if the photochemical capacity for absorbing light of a particular wavelength is not present in an organism, then photobiology (e.g., photosynthesis, vision, light-directed movement, etc.) will not take place, irrespective of the intensity or duration of exposure. It is critical then to consider the spectral absorbance of the molecules responsible for absorbing light and initiating downstream biological processes, and what the resulting spectral sensitivities might mean for light-mediated biology during polar night (Chapters 4-8).



Ice algae, planktonic algae, and benthic macroalgae possess a wide range of light-absorbing pigments (see Chapter 4), which can include chlorophylls absorbing in the blue (400-500nm) and red (600-700nm) regions, carotenoids (e.g., fucoxanthin) absorbing mostly at 400-530 nm and phycobiliproteins (e.g., phycoerythrin) as example) with high absorption in the green-orange region (500-570nm). Collectively, these pigments provide broad spectral coverage, but information in specific spectral channels may be used by the organism in different ways. For example, high energy blue light can selectively upregulate genes responsible for photoprotection, while lower energy red light selectively affects photosynthetic efficiency (Valle et al. 2014). However, there does not appear to be enough light at necessary wavelengths during polar night to allow for algal photosynthesis (Chapter 4).

Animals, including planktonic and benthic invertebrates and fish, possess both visual and non-visual light-sensitive pigments. Among marine animals, rhodopsin is the visual pigment, which contains a chromophore *retinal* derived from vitamin-A1, and a protein moiety *opsin* which determines the spectral sensitivity of the pigment. Some species have a single rhodopsin spectral class and thus a relatively narrow spectral sensitivity (e.g., krill with a 492nm Rhodop.; Cohen et al. 2015), while other species have multiple spectral classes and a broader spectral sensitivity (e.g., Atlantic cod with 490 and 550 nm Rhodop.; Anthony and Hawkins 1983). Marine animal visual systems (and likely their non-visual light-sensing pigments as well) have sufficient sensitivity for light-mediated processes during polar night (copepods, Båtnes et al. 2013; krill, Cohen et al. 2015; scallops, Tran et al. 2016; fish, Vollset et al. 2011) (Chapters 5, 7, 8). Scattering layers of zooplankton and fish clearly exhibit diel vertical migration (Ludvigsen et al. 2018) and lunar vertical migration during polar night (Last et al. 2016). The extent to which spectral cues resulting from solar and lunar elevation (e.g., Chappuis Effect) may be involved in DVM and LVM (Chapter 5), or in seasonal timekeeping (Chapter 8), remain unknown.

3.2 Polar Night as defined by solar elevation

In its most simple definition, ***Polar Night*** (or *perpetual night*; The Norwegian Arctic Pilot, 2018) occurs when the sun remains below the horizon throughout a full diel cycle. That is, solar elevation remains less than 0° over the 24-h day. When considering the number of days each year that this occurs, the duration of Polar Night increases by approximately 6 days for each degree of latitude (Fig 3.2A). Thus, Polar Night lasts ~1 month at 68° N, 3.5 months at 78° N, and 5.5 months at 88° N, extending to a full 6 months at the North Pole. At the southern hemisphere, the Polar Night can be defined in exactly the same terms. However, with a focus on the marine system, the two hemispheres are "poles apart" in more than one respect – while the marine Arctic cover nearly the entire region north of 80°N, the Southern Ocean does not go beyond 80°S. Hence, we will in this chapter not focus on the Antarctic and Southern Ocean, although all definitions, parameters and processes that are defined by the sun's elevation relative to the horizon are also valid for the Southern Hemisphere.

As introduced in Chapter 1, the above definition assumes that Polar Night is a static event. However, the Polar Night is anything but static. Rather, it can better be thought of as an annual process with four different levels of light (Polar twilight, Civil Polar Night, Nautical Polar Night, and Astronomical Polar Night), with each level defined by the sun's elevation relative to the horizon. Hence, the exact level of Polar Night at any given location depends not only on latitude (Fig 1.5), but also have a temporal component. While these definitions adequately describe Polar Night in an annual context, solar elevation is constantly changing over the diel cycle, whether the sun is visible or not. So understanding light climate during any of the four levels of Polar Night also requires further consideration of solar elevation in terms of the gradation of ***twilight***. Twilight is defined based on the sun's elevation below the horizon at any moment (Fig 3.2B). **Civil twilight** occurs when solar elevations are between the horizon and 6° below it. **Nautical twilight** occurs when solar elevations are 6° to 12° below the horizon. **Astronomical twilight** occurs when solar elevations are 12° to 18° below the horizon. Beyond this is "darkness" (Table 3.1). These definitions are useful for understanding light during Polar Night in two ways. First, at any point in the diel (24 h) cycle during Polar Night, the gradation of twilight can be identified, which then provides a measure of light intensity at that time (Fig 3.2B). Second, any given day during Polar Night can be categorized according to the level of twilight occurring at solar noon. This provides a useful way to think about Polar Night at a given latitude.

Table 3.1 Definitions of Polar Night and twilight based on solar elevation. Polar Night definitions are for solar elevation at the winter solstice, while for twilight the definitions apply at any point in the solar day (see Urban and Seidelmann, 2013). Note that "darkness" does not necessarily mean the total absence of light. Relevant latit2udes are based on geometric positions of the sun (see Chapter 1 for further details). Note that the notations of twilight and Polar Night are different.

Solar Elevation (°)	**Polar Night Definition**	**Twilight Definition**	**Relevant latitude (N and S) at noon on winter solstice**
0 to -6	polar twilight	civil twilight	66-72°
-6 to -12	civil polar night	nautical twilight	72-78°
-12 to -18	nautical polar night	astronomical twilight	78-84°
less than -18	astronomical polar night	darkness	84-90°

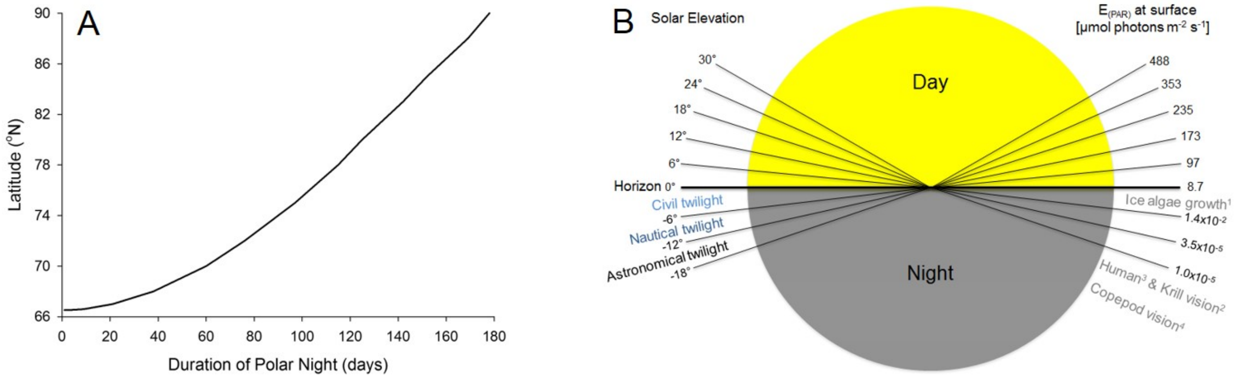


Fig 3.2 Polar light environment with respect to solar elevation. (**a**) Duration of Polar Night as a function of latitude, where Polar Night is defined as the sun remaining below the horizon throughout the 24-hour day. These durations are based on apparent solar elevation (see Chapter 1). (**b**) Gradations of twilight. Solar elevations (left labels) are shown with corresponding atmospheric light intensities (right labels) taken as the median measured E_{PAR} (400-700nm, Photosynthetically Active Radiation) for a given solar elevation (± 1°) measured at the light observatory, Ny-Ålesund, Svalbard. Solar elevations corresponding to Civil twilight (-0° to -6°), Nautical twilight (-6° to -12°), and Atmospheric twilight (-12° to -18°) are indicated on the left scale, while irradiance thresholds for select biological processes are indicated on the right scale. [1]Hancke et al. 2018; [2]Myslinski & Frank 2005; [3]Rieke & Baylor 1998; [4]Båtnes et al. 2013

3.3 Atmospheric light in the Polar Night

The seasonal cycle of sunlight drives annual patterns in polar ecosystems, most notably primary productivity (Chapter 4). While a characteristic lack of the sun above the horizon defines Polar Night, it does not mean that light from the sun is completely absent from the sky at this time of year. Rather, diffuse light from the sun below the horizon is a distinctive part of the light field during Polar Night, as it is at lower latitudes during twilight. Moonlight, which is reflected sunlight, likewise can play an important biological role during Polar Night. In fact, during periods characterized by nautical or astronomical twilight, lunar illumination during the full moon becomes the dominant ambient illuminator. In addition, the solar winds causing atmospheric molecules to emit light as the aurora borealis (northern lights) will also be a contributor to the ambient light during Polar Night. Therefore, the orb of the sun itself may not be an obvious feature of the Polar Night sky at first glance, but the sun plays a major role in the atmospheric light field of the Polar Night. Beyond the sun, starlight represents another light source of potential relevance during Polar Night. Each of these light sources has a characteristic intensity and spectrum, which we explore below, as well as photoperiod (see section 3.7).

3.3.1 Intensity

Arguably, the most complete record of the annual light intensity cycle in the Arctic comes from observations made at Ny-Ålesund, Svalbard (78.9° N, 11.9° E). Since 1992, the Alfred Wegener Institute for Polar and Marine Research (AWI) has made surface radiation measurements (pyrheliometer, pyranometer, pyrgeometer) through the Baseline Surface Radiation Network (BSRN) (Maturilli et al. 2015). At this location, Polar Night occurs 24 October - 18 February, while Polar Day (i.e., Midnight Sun) occurs 18 April - 24 August, with direct sunlight reaching

Ny-Ålesund 8 March - 8 October given the surrounding mountains. The Ny-Ålesund BSRN data are extremely valuable for satellite observations and climate models, but the sensor suite lacks instruments optimized for light measurements relevant to biology. The most relevant detector in this time series is a pyranometer for diffuse shortwave radiation (200 - 3,600 nm), which is too spectrally broad in its sensitivity to relate to biological processes. For example, PAR is used as a proxy for biologically available light (e.g. photosynthesis and vision), and these are only a fraction of the wavelengths contributing to the diffuse shortwave radiation measurement (e.g., Fig. 3.1B). Additionally, the BSRN shortwave pyranometer is only sensitive enough to detect light during sunlit portions of the year (February-October), so no data from the Ny-Ålesund BSRN pyranometer are available for Polar Night.

To address this gap, a light observatory was established in January 2017 at the new Geodesy station at Brandalspynten, Kongsfjorden (Zolich 2018) 4km away from the settlement itself. This location was chosen to provide infrastructure and access, while minimizing light pollution from the settlement at Ny Ålesund. This light observatory (*ArcLight*) was put into operation providing data with high (1 hour) temporal resolution throughout the year, including during Polar Night. It is located in heated hut with a transparent plexiglas dome on the roof providing a 180° view towards the atmosphere. The *ArcLight* observatory consists of three sensors (Fig 3.3): (1) a spectroradiometer provides cosine-corrected downwelling spectral irradiance ($E_{d\lambda}$) at 1 nm spectral resolution from 350-800 nm; (2) a digital camera (full size sensor) with an 8 mm lens providing a 180° "fish eye" view of the sky (mimicking a planar cosine corrected irradiance light collector; Fig. 3.1A), and calibrated to deliver irradiance in red, green and blue channels; and (3) a custom irradiance sensor provides a high dynamic sensitivity range from bright summer to dark winter values. All sensors are remotely controlled, acquiring data at user specified intervals. The spectroradiometer and camera are calibrated for units of energy [$W\ m^{-2}\ nm^{-1}$] or quanta [$\mu mol\ photons\ m^{-2}\ s^{-1}\ nm^{-1}$]. The suite of sensors provides sufficient data to extract a range of light regime parameters, including spectral irradiance (E_λ), irradiance in the visible spectral range (E_{PAR}), irradiance in RGB channels (600-700nm, 500-600nm, 400-500nm, respectively), day length, cloud cover, light pollution, sun phase, moon phase, northern light dynamics, starlight, rain and snow conditions.

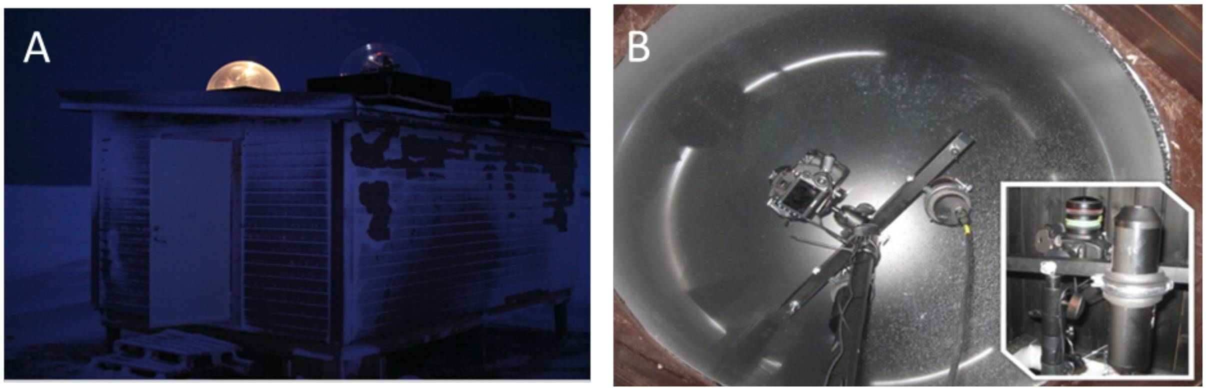


Fig 3.3 ***ArcLight* Observatory and sensors outside Ny-Ålesund**. (**a**) ArcLight observatory during Polar Night, with dome illuminated during service of sensors. (**b**) InSitu Marine Optics Ussimo spectroradiometer and Cannon 5D Mark III digital camera with fish eye lens pointing upwards through the plexiglass dome. Inset shows the spectroradiometer and camera laterally. Photos: Geir Johnsen

Not only is the annual cycle of light intensity into and out of the midnight sun resolved in *ArcLight* observatory camera-based measurements (Fig 3.2, 3.4A), but biologically relevant irradiance throughout Polar Night is reliably measured and quantified (Fig 3.4B). This effectively covers a seasonal quantal range of 8-9 orders of magnitude (Zolich 2018, Pavlov et al. 2019). From these data measured at sea level at 79° N, maximum E_{PAR} around 1200 μmol photons m^{-2} s^{-1} is typically found during mid-summer in June at solar noon. In contrast, the maximum E_{PAR} at solar noon (brightest time of day) during the darkest part of Polar Night at this latitude (nautical Polar Night, astronomical twilight) ranged between 1–1.5 x 10^{-5} μmol photons m^{-2} s^{-1} in clear weather conditions and with the moon below the horizon. Hence, values reflect not only diffuse solar illumination, but also potentially light pollution from Ny-Ålesund. Cohen et al. (2015) likewise reported E_{PAR} at solar noon in Ny-Ålesund during mid-January to be ~1x10^{-5} μmol photons m^{-2} s^{-1}, which is consistent with the *ArcLight* time series. Measurements reported in Cohen et al. (2015) were made with the moon below the horizon, whereas the *ArcLight* time series provides the opportunity to see irradiance changes over the lunar cycle. Indeed, the full moon is a striking feature during Polar Night, and its 29-day period is evident in this light record. E_{PAR} is ~100-fold higher during the full moon as compared to the new moon period (Fig 3.4B,C; Fig 3.5B,C). Thus, the full moon increases light intensity during astronomical twilight to levels occurring between civil and nautical twilight. This is consistent with measurements made during dusk at 36° N by Palmer and Johnsen (2015) who reported moonlight affecting downwelling irradiance when solar elevations exceeded -8°. It is important to note that during the new moon, any "ambient" irradiance recorded at this location could include (1) diffuse light from the sun, (2) a range of other natural atmospheric sources (integrated starlight, zodiacal light, airglow and aurora; see Johnsen 2012, Cronin et al. 2014), and (3) light pollution from Ny-Ålesund. Indeed, Ludvigsen et al. (2018) reported diffuse skylight irradiance (350-730nm) as low as 10^{-8} μmol photons m^{-2} s^{-1} in Kongfjorden away from Ny-Ålesund, but these measurements were likely influenced by occlusion of the sky by surrounding mountains. Further work is needed to determine ambient light values during Polar Night absent of light pollution.

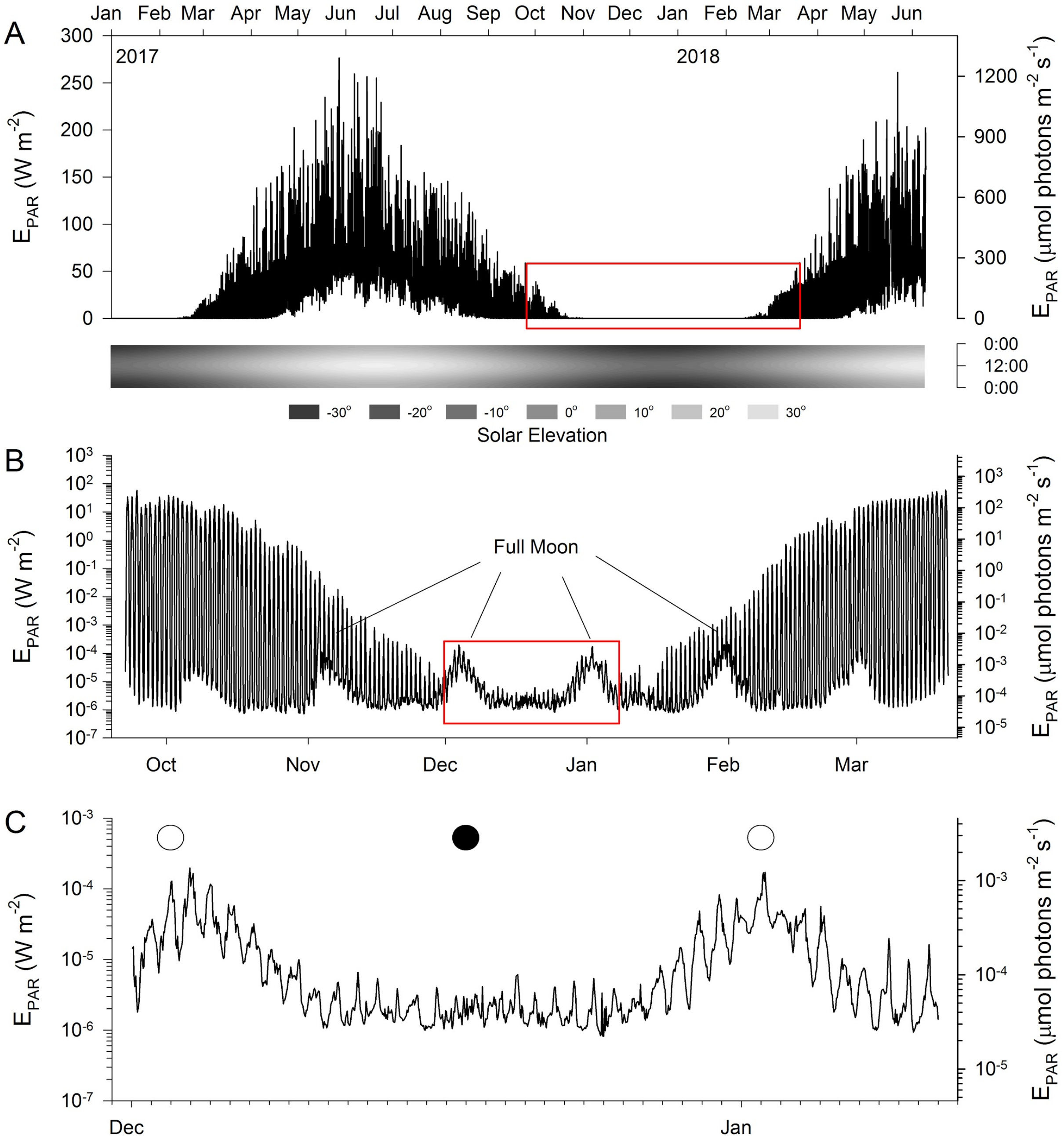


Fig 3.4 Atmospheric irradiance (E_{PAR} recorded at the *ArcLight* Observatory 4 km away from Ny-Ålesund. (**a**) Annual cycle of E_{PAR} from January 2017 - June 2018. Corresponding solar elevation across the 24-h day is plotted below the panel. (**b**) Light data for the Polar Night period falling between the autumn and spring equinox (red box in panel A). (**c**) Light data for December 1, 2017 - January 11, 2018 and centered on the winter solstice (December 21). Open and closed circles show the days of the full and new moons, respectively. E_{PAR} measured during the new moon represents darkest "ambient" light lowest annual polar night irradiance) at Ny-Ålesund, which likely includes both natural and anthropogenic sources. Data are re-plotted from Zolich (2018)

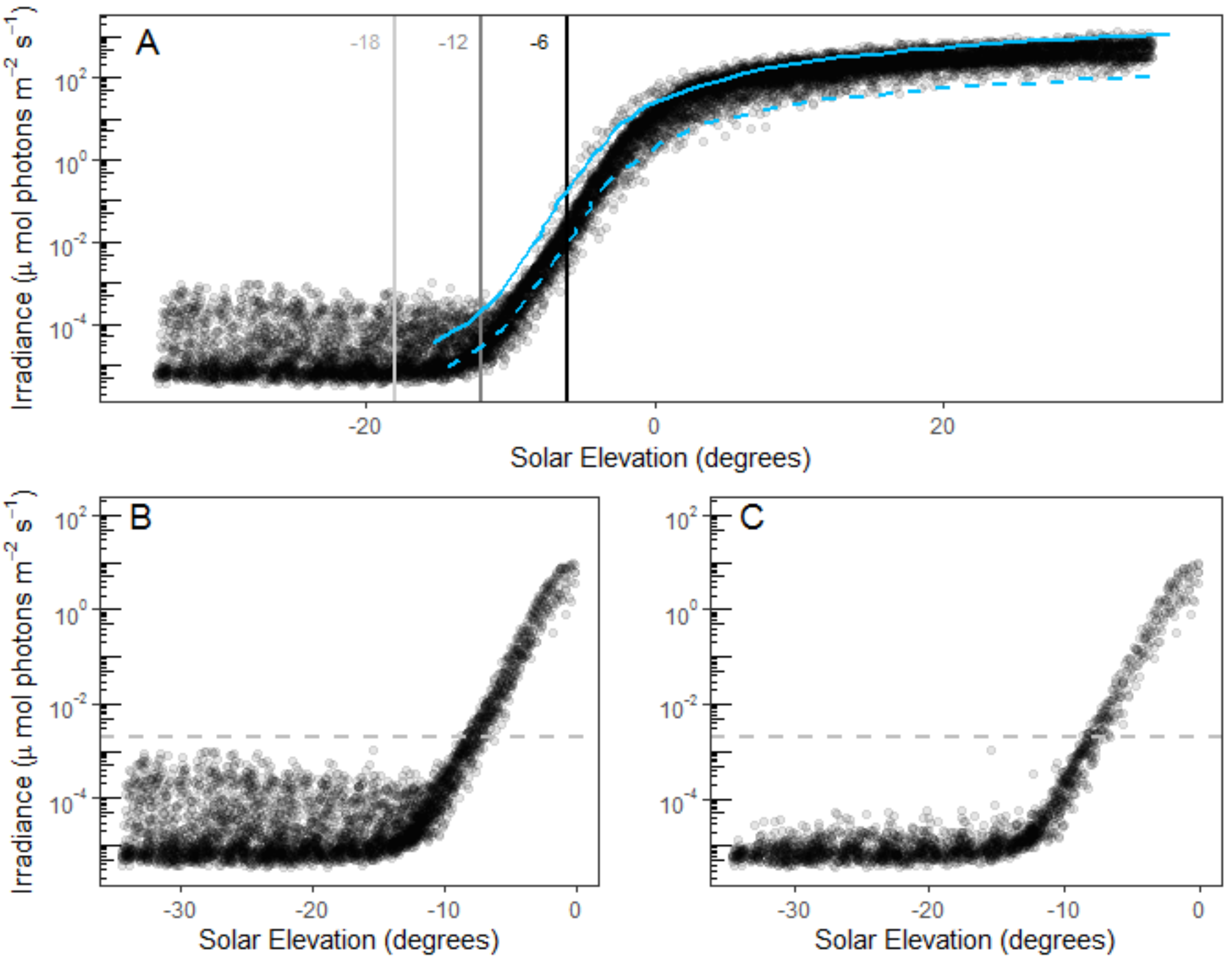


Fig 3.5 Variation in atmospheric light with changes in solar elevation and lunar stage. (**a**) Light data from Fig 3 are plotted here as a function of solar elevation. Vertical lines at -18°, -12°, and -6° indicate lower limits of atmospheric, nautical, and civil twilight. Blue lines are based on data from Bond and Henderson (1963) for clear sky (solid line) and overcast sky (dashed line), converted from illuminance using a conversion factor of 0.0185. (**b**) Light data for only Polar Night (days with elevation at solar noon <0°). The dashed horizontal line denotes irradiance of a full moon at 32° elevation (from Bond and Henderson (1963)), corresponding to the maximum lunar elevation during this time series. (**c**) Data as for panel B, except only for days where the lunar disk was <50% full

3.3.2 Spectrum

The spectral (wavelength) composition of light is fundamental to its biological impact. For sunlight, its spectral composition is dependent on solar elevation. Solar elevations at midday during Polar Night are comparable to twilight periods occurring during dawn and dusk at lower latitudes (Fig. 3.2 and Table 3.1). This means that the spectral composition of diffuse skylight during Polar Night is quite similar to the spectral composition during dawn/dusk periods at lower latitudes. For the sun at elevations just below the horizon during civil twilight (0 to -6°), this involves an increase at blue wavelengths transitioning to a combination of blue and red (Figs. 3.6, 3.7B). This appears magenta to the human eye, and results from a reduction at yellow wavelengths selectively absorbed by atmospheric ozone as the path-length of solar light through the atmosphere increases during nautical twilight (-6 to -12°), a phenomenon termed the *Chappuis Effect*. Skylight then reddens during astronomical twilight (-12 to -18°) due to airglow and integrated starlight (see Johnsen 2012 for details).

These characteristic shifts in the spectral composition of skylight with solar elevation can be further influenced by the presence of the moon (Palmer and Johnsen 2015). Moonlight is reflected sunlight, thus when either of these celestial objects is well above the horizon their spectral compositions are similar, with a peak at blue wavelengths gradually reducing through red wavelengths (Fig. 3.7). Accordingly, the general effect of moonlight on skylight spectral composition during Polar Night will be to increase longer-wavelength visible light (yellows and reds). This is evident in a 24-h spectral time series from Ny-Ålesund (Fig. 3.6), where the increase in E_λ at solar noon shows a characteristic "twilight" spectrum with blue and red peaks which then transitions into a blue-dominated spectrum as the lunar elevation increases well-above the horizon. This is also evident when comparing normalized spectral composition of skylight for early May (sun above the horizon, moon below; Fig. 3.7A) and early February (moon above the horizon, sun below; Fig. 3.7B) at Ny-Ålesund. When the sun is above the horizon and its elevation decreases to minimum around midnight (May), loss of yellow wavelengths is observed at that point. However, when the moon is above the horizon and its elevation increases to a maximum around midnight, a gain of yellow wavelengths is apparent.

Ultimately, the elevation of the sun and moon is critical to the spectral composition of the light produced at any given point during the 24-h day. Above this background "solar" spectrum, however, aurora provides a distinct light feature during Polar Night (Fig. 3.6). This light is spectrally narrow, with portions at several discrete wavelengths (e.g., 391 nm, 557 nm, and 630 nm). Accordingly, while aurora is clearly distinguished above solar/lunar light at these wavelengths, its overall contribution to biologically relevant light appears limited.

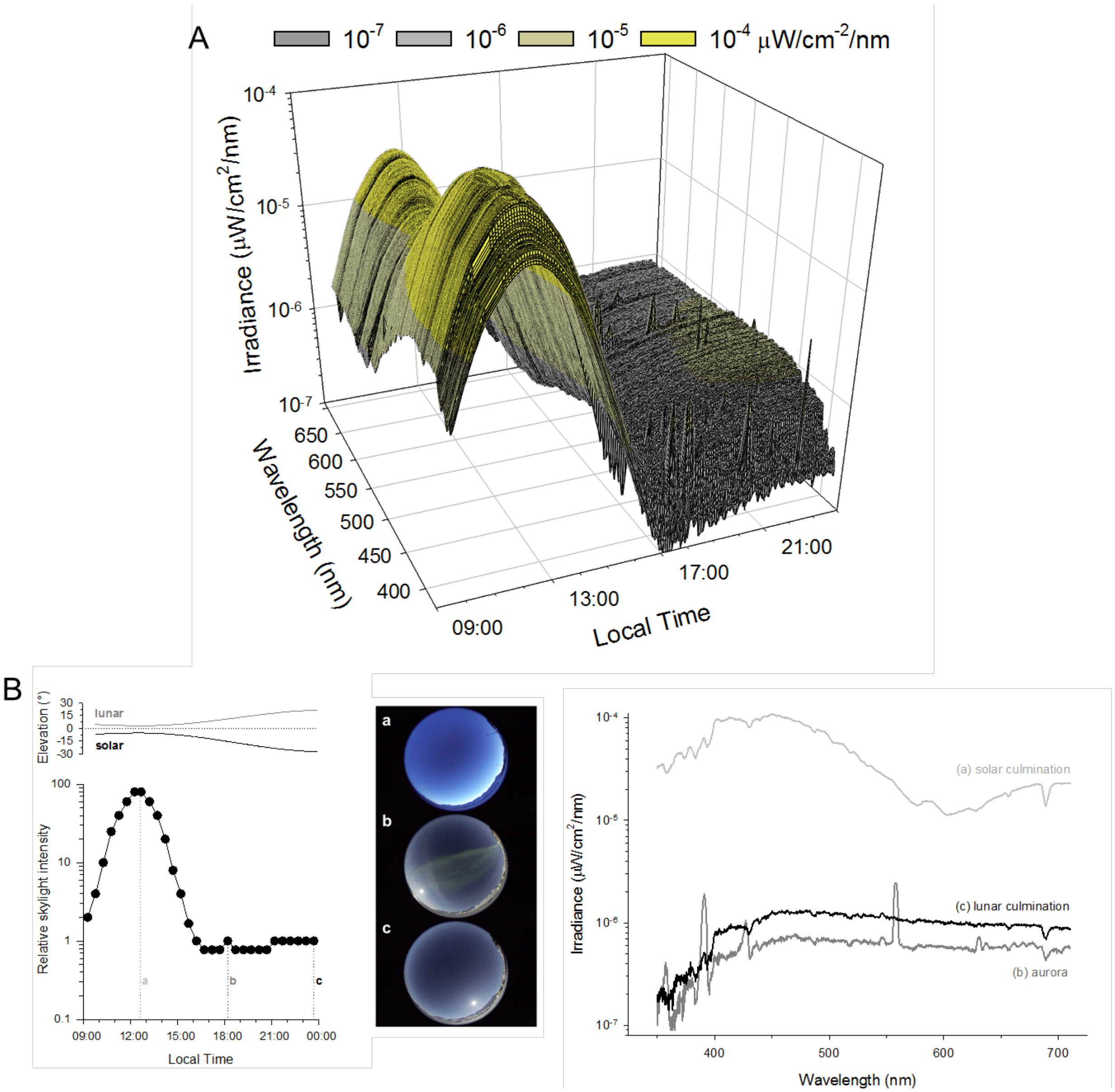


Fig 3.6 Spectral composition of the diel atmospheric light cycle at Ny-Ålesund during Polar Night. (**a**, upper panel) Spectroradiometric measurements of diffuse skylight irradiance at 5 min intervals (see Cohen et al. 2015 for collection details) show a distinct spectral composition as the nears the horizon (blue and red wavelengths dominate with loss of yellows) which then changes to a flatter spectrum as solar elevation becomes more negative and moonlight dominates. At culmination (i.e., maximum elevation), solar and lunar elevations were -6° and 25.2° respectively. (**b**, two lower panels) All-sky camera images were taken at 30 min intervals coincident with the spectroradiometric data. Inverse shutter speed was used to generate a relative skylight intensity value. Images for three time points are shown (a, b, c), along with their spectral irradiance, highlighting the spectral change as solar influence yields to lunar influence. Note the distinct aurora signature at time point b.

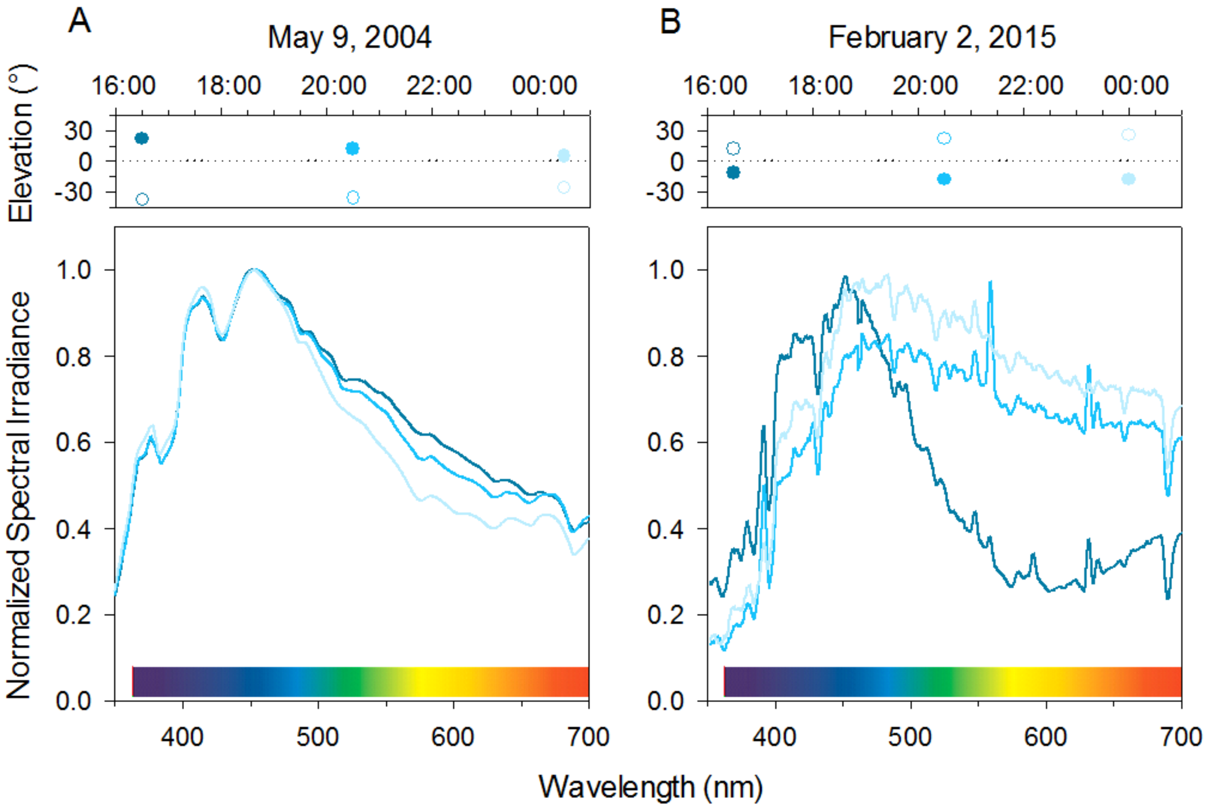


Fig 3.7 Changes in spectral irradiance when the sun or moon near the horizon. Data are irradiance ($E_{d\lambda}$) at sea level in Ny-Ålesund. (**a**, upper and lower panels) Midnight sun in May, when the sun (filled circles, upper panel) is always above the horizon and the moon (open circles circles) is always below the horizon. The sun contributes most to $E_{d\lambda}$ at this time. (**b**, upper and lower panels) Polar Night in February, when the moon is always above the horizon and the sun is always below the horizon. The moon contributes most to $E_{d\lambda}$ at this time. Colors associated with the visible spectrum are provided with each panel. For both midnight sun and Polar Night, the spectra are reduced at yellow wavelengths during the times when the dominant light source (sun during midnight sun, or moon during Polar Night) is near the horizon, and accordingly the path length for its light is the longest at that point of the diel cycle

3.4 Underwater light in the Polar Night

The underwater light climate is dependent upon (1) atmospheric light sources, such as the sun and moon, (2) any in-water light sources, primarily bioluminescence, and (3) the optical properties of the water that influence propagation of these light sources. We have already described atmospheric light during Polar Night (section 3.3), and focus here on the latter two aspects.

3.4.1 Propagation of atmospheric light through the water column

Measuring the underwater light field during Polar Night is challenging due to the detection limits of commercially available light sensors. This will no doubt change as sensor technology develops. For now, our understanding of underwater light during the Polar Night comes primarily from radiative transfer models incorporating observations of atmospheric light (i.e., diffuse sky irradiation) and the inherent optical properties (IOPs) of fjordic waters in Svalbard. These models yield predictions of the underwater spectral irradiance during Polar Night (Fig. 3.8). Overall, this work suggests the optically clear water present during Polar Night is similar to that of early spring, prior to the spring bloom and extensive freshwater runoff. Downwelling irradiance ($E_{d\lambda}$) in the water column has a spectral transmission maximum in the blue spectral region, with a broad peak at ~455 nm in shallow waters transitioning to a narrower peak at ~495 nm by 100 m depth.

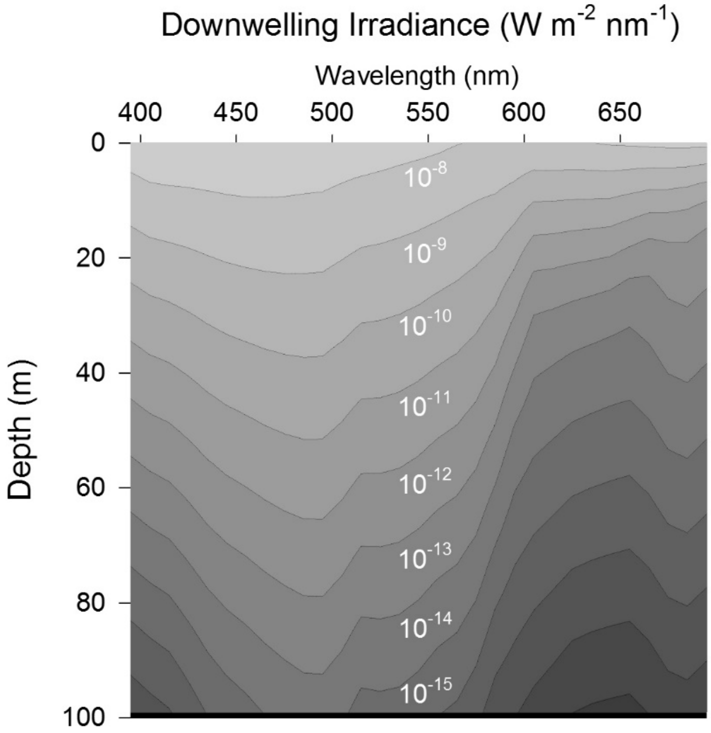


Fig 3.8 Modelled underwater spectral light field in Kongsfjorden at midday under clear sky conditions. Contours show the ambient underwater light as downwelling spectral irradiance ($E_{d\lambda}$, µmol photons m^{-2} s^{-1} nm^{-1}) derived from the radiative transfer model HydroLight. Data were replotted from Cronin et al. (2016)

The bulk optical properties of seawater determine what happens to photons as they travel through the water column, and in turn generate the spectral attenuation described above. Photons can be absorbed or scattered by water molecules and the particulate and/or dissolved constituents in water, and it is these absorption and scattering properties that are termed Inherent Optical Properties, or IOPs (Johnsen et al. 2009). IOPs are independent of the ambient light field and will not change with changes in incident light, as compared to apparent optical properties, described below, which are dependent on solar intensity, angle, etc. IOPs are commonly described in terms of light absorption, $a(\lambda)$ and scattering, $b(\lambda)$ coefficients. Light beam attenuation, $c(\lambda)$ is therefore defined by $a(\lambda) + b(\lambda)$. As particulate and dissolved substances in a parcel of seawater change with time and/or depth, so will its IOPs. For example, fjord and coastal waters of Svalbard vary seasonally in terms of phytoplankton (using [chl a] as a measure of biomass), coloured dissolved organic matter (cDOM), and total suspended matter (TSM) (Johnsen et al. 2009, Leu et al. 2011, Hovland et al. 2014, Hancke et al. 2014) which will each increase IOPs and light attenuation. Interestingly, little cDOM is locally produced as top soil is limited on Svalbard (Johnsen et al. 2009; see Chapter 4), leaving primary production and suspended material as primary factors affecting IOPs in this region.

While *in situ* observations of IOPs are available for a range of Arctic locations, these tend to focus on spring and summer periods. This timing reflects a goal of understanding biological impacts of optical conditions with seasonal sea ice cover and melt, the spring bloom, and suspended sediment from glacial freshwater runoff (e.g., Pegau 2002, Granskog et al. 2015, Hancke et al. 2014, Hovland et al. 2014, Pavlov et al. 2015, 2016, Sagan and Darecki 2018). Comparable IOP measurements during Polar Night are limited to Kongsfjorden, Svalbard (Cohen et al. 2015). These data suggest low IOP values that are homogeneous with depth below the upper ~10 m, reflecting a well-mixed water column. For comparison, Sagan and Darecki (2018) measured IOPs for specific water masses in Kongsfjorden (e.g., Cottier et al. 2005; see Chapter 2) during late July post-bloom conditions with high runoff in surface water. Polar Night IOPs align with Atlantic Water from this study. Atlantic Water in Kongsfjorden has lower overall absorption, scattering, and attenuation than other water masses in the fjord (Fig 3.9A,B); these other water masses are more influenced by local biological production, cDOM and TSM from freshwater runoff. Consistent with this, Polar Night IOPs are comparable to those measured by Pavlov et al. (2015) prior to the spring bloom in Atlantic Water of the West Spitsbergen Current off Kongsfjorden.

Another common way to quantify the underwater light field is through the Apparent Optical Properties of seawater, or AOPs, which depend on both IOPs and the ambient radiance distribution. AOPs include the diffuse attenuation coefficients for radiance and irradiance (e.g., K_d PAR). Because AOPs vary with both IOPs and the ambient light field, they are altered and regulated by factors such as: sun angle (affecting light intensity and spectral composition), albedo, surface waves, dynamic changes in cloud cover, rain, snow and air humidity (Sakshaug et al. 2009). Regardless, AOPs are relatively straightforward to measure and provide a valuable metric for describing the underwater light field, and light attenuation through snow/ice/water (e.g., Light et al. 2015). Hanelt et al. (2001) reported K_d PAR in Kongsfjorden from May through September, encapsulating the spring bloom (Fig. 3.9C). The lowest diffuse attenuation coefficients from that study correspond to those determined from radiative transfer models for underwater light during

Polar Night (K_d PAR = 0.18 m^{-1}; Cronin et al. 2016). These values are also comparable to AOPs measured in Kongsfjorden during pre-bloom spring conditions in May 2004 (Volent et al. 2007).

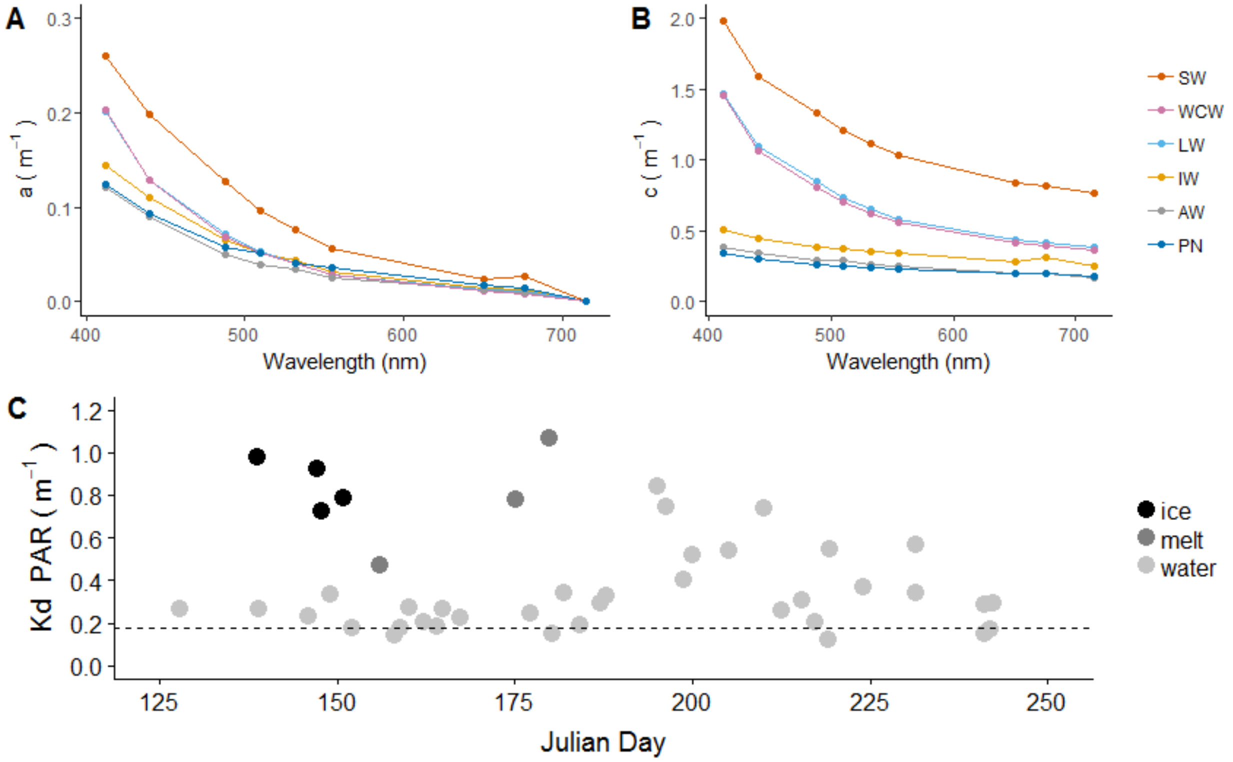


Fig 3.9 Optical properties of Kongsfjorden during Polar Night compared to other times of year. (A, B) Inherent Optical Properties (IOPs) measured during Polar Night (Cohen et al. 2015) and summer (Sagan and Darecki 2018). Panel shows absorption ($a(\lambda)$) and panel B shows beam attenuation ($c(\lambda)$) for Polar Night (PN), along with summer measurements for Surface Water (SW), Winter Cooled Water (WCW), Local Water (LW), Intermediate Water (IW), Atlantic Water (AW). (C) Apparent Optical Properties (AOPs) represented by $K_{d,\mathrm{PAR}}$ plotted as a function of Julian Day, replotted from Hanelt et al. (2001). $K_{d,\mathrm{PAR}}$ was calculated from vertical radiometric profiles in 1995-1998, including: four from rare "ice" periods when sea ice was present in the fjord in early spring (black circles); three from "melt" periods when turbid melt water influenced the upper water column (dark grey circles); and the remainder (n=36) from "water" periods with open water. Dashed line represents $K_{d,\mathrm{PAR}}$ for Polar Night calculated from a modelled light field (Cronin et al. 2016)

3.5 Bioluminescence contributes to the underwater light field

3.5.1 Bioluminescence as a phenomenon

In addition to atmospheric ambient light sources, biologically produced light represents another source of photons to the underwater light environment during Polar Night. Bioluminescence is a ubiquitous phenomenon in the world's oceans and plays significant roles in animal behavior. Bioluminescence is used in marine organisms for an array of specific defensive purposes using the light generated to startle, avoid, misdirect, and camouflage (see Chapter 11, Fig. 11.18). Offensive uses of bioluminescence include luring prey, stunning prey with light, and illuminating potential prey. Finally, bioluminescence functions in intra-species communication for mate attraction/recognition. Haddock et al. (2010) fully summarized and reviewed these behavioral adaptations and the diversity of luminous taxa. Given the prevalence of bioluminescence it is also not surprising that the spectral peak of bioluminescence (470- 490 nm; Widder 2010) is near the maximum transmission wavelength in clear ocean water (e.g., Fig. 3.8), as well as the highest sensitivity for vision in many fish and zooplankton (Turner et al. 2009, Warrant and Lockett 2004).

For the behavioral adaptations listed above to be effective, one would assume bioluminescence intensity must be higher than the ambient background light. These conditions would exist during periods and locations controlled by the periodicity of atmospheric light and a dynamic depth where functional light (for vision/detection) transitions exponentially to darkness. In addition to direct differences between intensities of bioluminescent and ambient light, there are endogenous rhythms of bioluminescent potential in organisms, which modulate bioluminescence intensity and is often synchronous with the ambient light environment (Batchelder et al. 1992). These conditions restrict the study of bioluminescence in the field to night hours and to the deep sea, an environment inherently difficult to study.

3.5.2 Bioluminescent taxa during Polar Night

Spectral irradiance during Polar Night is comparable to light at mesopelagic depths (e.g., Kaartvedt et al. 2019), where prolonged low solar/lunar irradiance results in the depth of transition to "darkness" in the water column occurring in shallow water (<50 m) (Fig. 3.10). Until recently, however, only a few studies had quantified bioluminescent organisms and the bioluminescence potential (potential maximum light intensity per organism) in Polar regions, and none during Polar Night. Buskey (1992) examined bioluminescence distributions and community structure during the spring in the Greenland Sea off Svalbard with the goal of developing methodology to use bioluminescence as a way to measure total biomass and light budgets of a given water mass. The majority of epipelagic bioluminescence was correlated with zooplankton. Specifically, it was produced by copepods (*Metridia* spp.), larvaceans (*Oikopleura* spp.), euphausiids (*Thysanoeassa* spp.) and ostracods (*Conchoecia* spp.). The contribution of bioluminescent organisms was found to vary significantly over that two-month study (Buskey 1992). Bioluminescent dinoflagellates (*Protoperidinium* spp.) were rare and did not contribute significantly to bioluminescence. Lapota et al. (1989, 1992) conducted studies in the Beaufort Sea during the autumn and in summer in Vestfjorden, northern Norway, respectively. In those studies, *Protoperidinium* spp. was abundant and accounted for between 20 and 90% of the total light budget in the upper 100 m in the Beaufort Sea and up to 96% of the total light budget in Vestfjorden, respectively. Vestfjorden had zooplankton assemblages similar to those in the Greenland Sea (*Metridia longa*, *M. lucens*, *Conchoecia* spp., and the euphausiid *Thysanoessa* spp.). In the Beaufort Sea, *M. longa* produced 80% of the bioluminescence potential, with *Protoperidinium* spp. producing the remaining 20%. Work on bioluminescence is even scarcer in the Southern Ocean, with one study associating bioluminescence with new species, many benthic (Raymond and DeVries 1976), and looking at the contribution of bioluminescence to elephant seal foraging (Vacquié-Garcia et al. 2012).

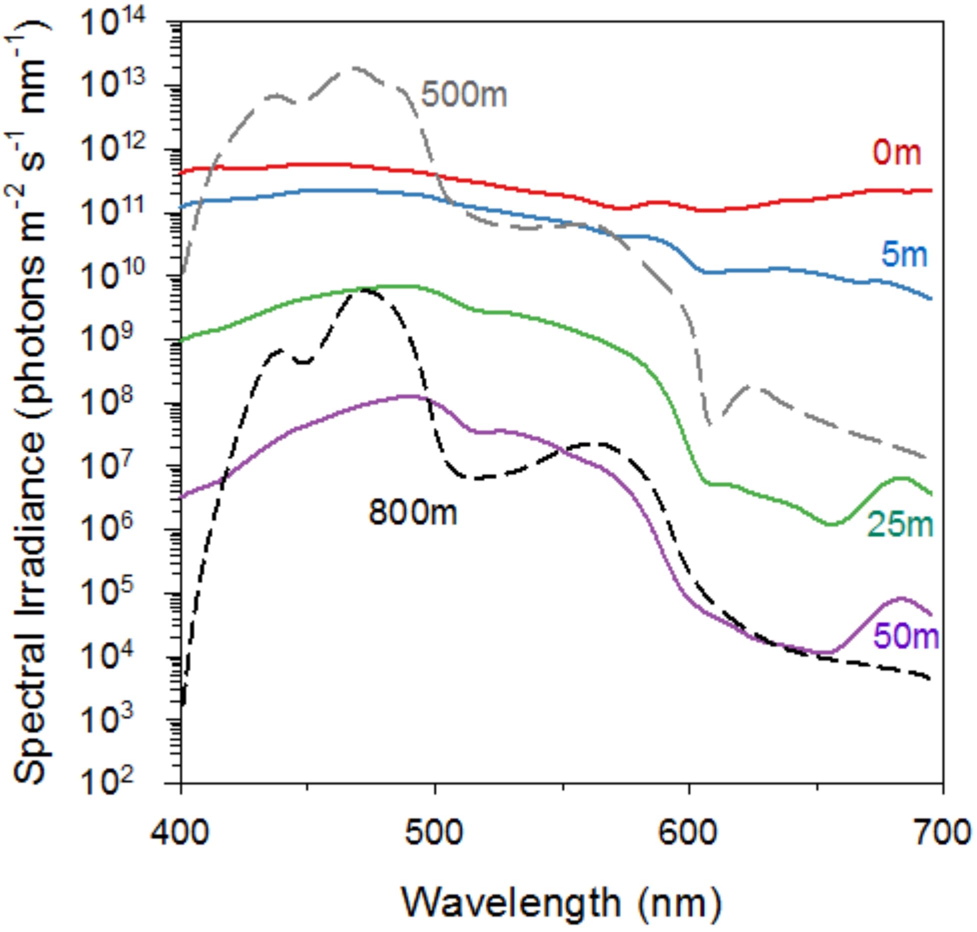


Fig 3.10 Comparison of Polar Night and deep-sea light. Data are modelled spectral irradiance for Kongsfjorden (solide lines) and the mesopelagic (dashed lines), replotted from Cronin et al. (2016) and Li et al. (2014), respectively. Both maximally transmit blue-green light, and spectral irradiance is similar between the upper 50m of Kongsfjorden and the mesopelagic.

With a general paucity of bioluminescent measurements made in high latitude regions during Polar Night, there has been a concerted effort over the last decade to expand our understanding of bioluminescent organisms, starting with an accounting of taxonomic representation. In mid-January, Berge et al. (2012) found the distribution of bioluminescent organism to be similar to previous studies (Buskey 1992, Lapota et al. 1989, 1992) with the addition of moderate numbers of *Oncaea borealis*, *Heterorhabdus noregicus*, and *Appendicularia*. While 180 µm depth-stratified nets were used in this study, an autonomous underwater vehicle (AUV) equipped with a bioluminescence bathyphotometer with 20 µm nets in the exhaust ports (Moline et al. 2004) was also employed in the same field to better understand the distributions and flash intensities of organisms. The nets on the AUV were able to capture both non-bioluminescent and bioluminescent zooplankton in Kongsfjorden in January equivalent to those caught by traditional net sampling (Berge et al. 2012). Because of the decreased mesh size, the AUV nets were also able to collect phytoplankton and showed that dinoflagellates comprised over 90% of the phytoplankton numbers and half were luminescent *Protoperidinium* spp. The most important result in Berge et al. (2012) was the distribution of bioluminescent organisms obtained by the targeted AUV sampling. Sampling around noon and near midnight, the distribution of bioluminescence at three depths showed significant differences with higher intensities at the shallow depth at “night” and higher intensities at the deeper depth around solar noon. Bioluminescent organisms were in low abundance, spatially distributed and varied four orders of magnitude in intensity.

Like previous studies that examined only the light intensities generated from bioluminescent organisms, Johnsen et al. (2014) followed this study up by examining the flash kinetics of individual flashes, which are known to be unique to each taxa (Nealson et al. 1986) (Fig. 3.11). By collection, measurement and parameterization of the dominant luminescent organisms (*Protoperidinium* spp., *M. longa*, *Mertensia ovum*, *Beröe cucumis*, and *Meganyctiphanes norvegica*), over 80% of the bioluminescent flashes were taxonomically identified (Johnsen et al. 2014). This is a powerful tool in that bioluminescent taxa can now be mapped on the time and space information collected by the bathyphotometers (both profiling, and on AUVs). This approach was demonstrated by Cronin et al. (2016) for the upper 120 m of the water column off Svalbard. The bioluminescent community were in this study were similarly represented by *Protoperidinium* spp., *Beröe cucumis*, *Mertensia ovum*, *Metridia* spp., *Meganyctiphanes norvegica*, *Thysanoessa inermis*, and *Boroecia* spp. These data show the species depth separation and highlight the limitations of net sampling to reveal depth distributions, which is critical when evaluating vertical migration (Chapter 5) and rhythmicity (Chapter 8) of bioluminescence in the Polar Night.

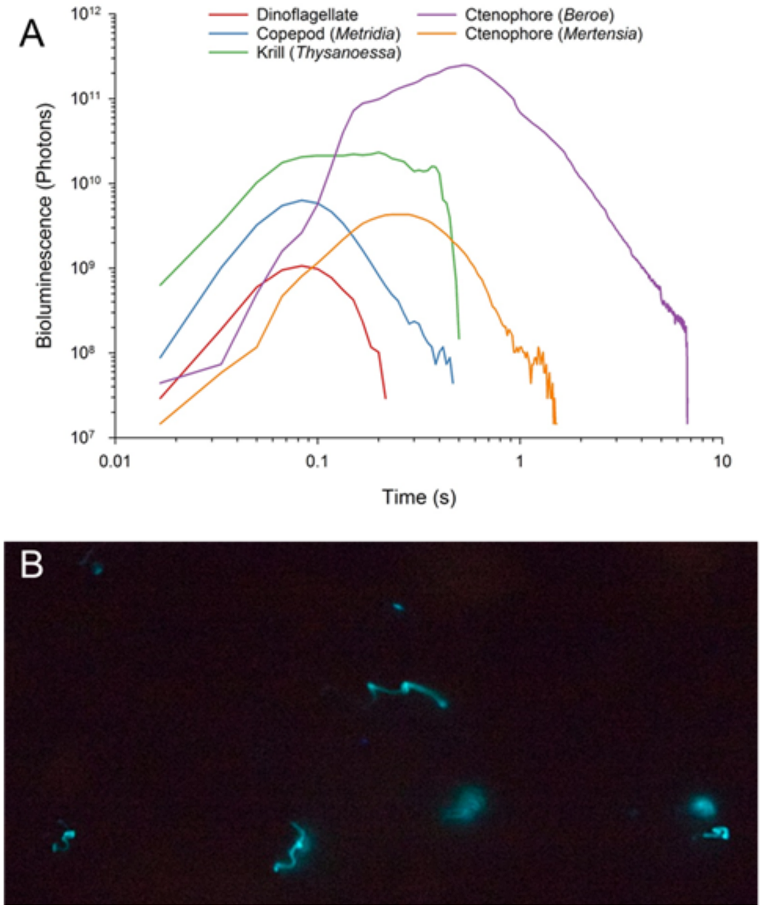


Fig 3.11 Bioluminescence of Arctic plankton common during Polar Night. (**a**) Luminescent emissions of each taxa as recorded by an *in situ* bathyphotometer (Underwater Bioluminescence Assessment Tool; UBAT) are distinguishable from one another. (**b**) A photograph taken from the Ny-Ålesund pier looking down into the water during Polar Night. Most likely, bioluminescent trails are the copepod *Metridia*, while more diffuse luminescence are from ctenophores. Photo: Geir Johnsen.

3.5.3 Rhythms in bioluminesence during Polar Night

Rhythmicity in bioluminescence has primary been examined in phytoplankton communities, with photoinhibition being the identified mechanism for measured decreases during midday (Kelly and Katona 1966, Batchelder et al. 1992). Whether this holds in zooplankton and during transition to Polar Night was the subject of recent studies. Berge et al. (2012) demonstrated that the bioluminescent community did not show variation over the day at the surface during the polar night. Similarly, Johnsen et al. (2014) showed there were no significant changes in flash intensities from individual taxa (including dinoflagellates) over a three-day period in mid-January from a fixed station continuously pumping at 20 m. Unlike these two short-term studies conducted in the middle of the Polar Night, longer-term bioluminescent data were collected from surface waters continuously over the transition period into Polar Night from September to December. Importantly, this study was conducted at the surface in shallow water as to avoid changes in bioluminescence due to vertical migration, which have been shown to continue during the Polar Night (Chapters 5 and 8). Data revealed that there was a diel pattern at the beginning of the study, but that this rhythmicity was lost in mid-November, corresponding to the start of civil polar night at this location (Fig. 3.12). Results of this time series also reveal that the loss of rhythmicity not only apply to dinoflagellates but also within the zooplankton community.

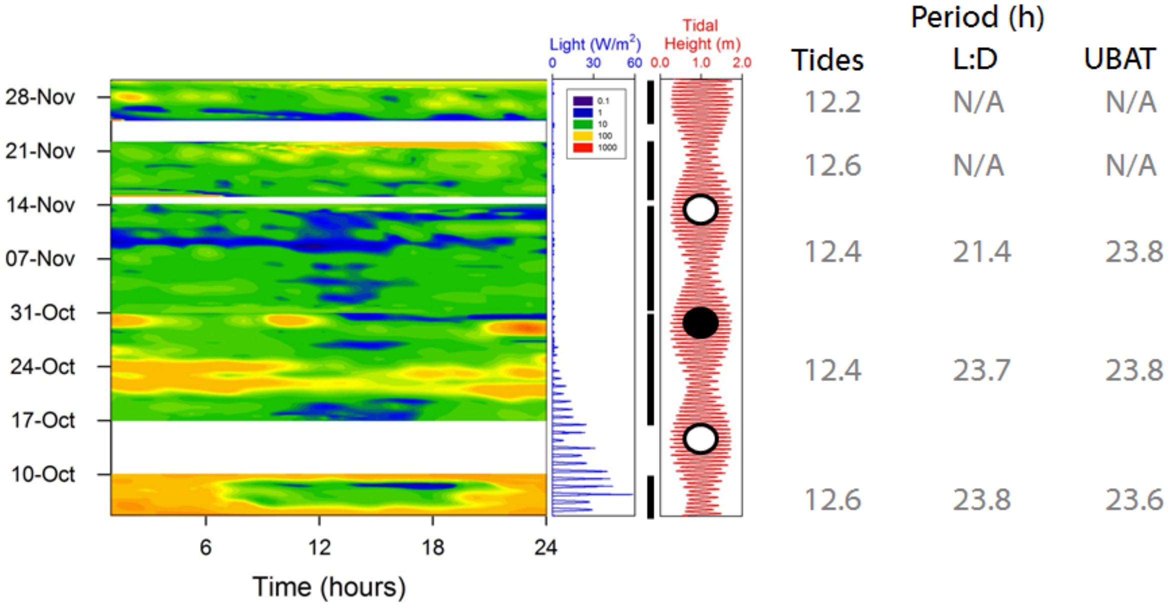


Fig 3.12 Rhythmic bioluminescence patterns decay into Polar Night. UBAT deployment at ~0.5m depth from a floating dock in Adventfjorden, Svalbard, during October - November 2011. Left panel is bioluminescence (log photons h^{-1}) with white sections indicating data gaps. Corresponding light (BSRN shortwave pyranometer, Ny-Ålesund) and tides (Longyearbyen) are plotted in right panels. Black lines indicate five separate sections for which the time series were analyzed for period with Maximum Entropy Spectral Analysis (numbers on right). While tides remain periodic throughout the time series, light decreases below detection with this sensor and becomes arrhythmic by mid-November, as does the UBAT signal

3.5.4 Spatial distribution of bioluminescence during Polar Night

In addition to these focused studies on taxonomy, flash kinetics, and rhythmicity, the larger scale distributions of bioluminescence in the Polar Night have been evaluated. In January 2012, a series of stations were occupied along a transect from mainland Norway to 82° N north of Svalbard. Profiles of bioluminescence were measured at these stations along with standard oceanographic variables (temperature, salinity, fluorescence). For the portion of this transect stretching between Rijpfjorden to the Marginal Ice Zone (Fig 3.13A), the distribution of bioluminescence was not correlated to any of these variables or derived variables of the physical structure of the water column (density, buoyancy frequency). Taken together, there was an inverse relationship between bioluminescence and depth (Fig. 3.13B), similar to findings of Buskey (1992) during spring in the same region. While profiles taken along a transect are able to capture the broad scale distributions, interpretation is problematic as they do not capture the time-dependent variability of vertical migration and response to the day length which are known to influence the vertical distribution of organisms as well as bioluminescence intensity by 2-3 orders of magnitude. Ideally, daily stations would be occupied along a latitudinal gradient to elucidate the response and importance of organismal bioluminescence in the water column to the gradient in atmospheric light when approaching the pole.

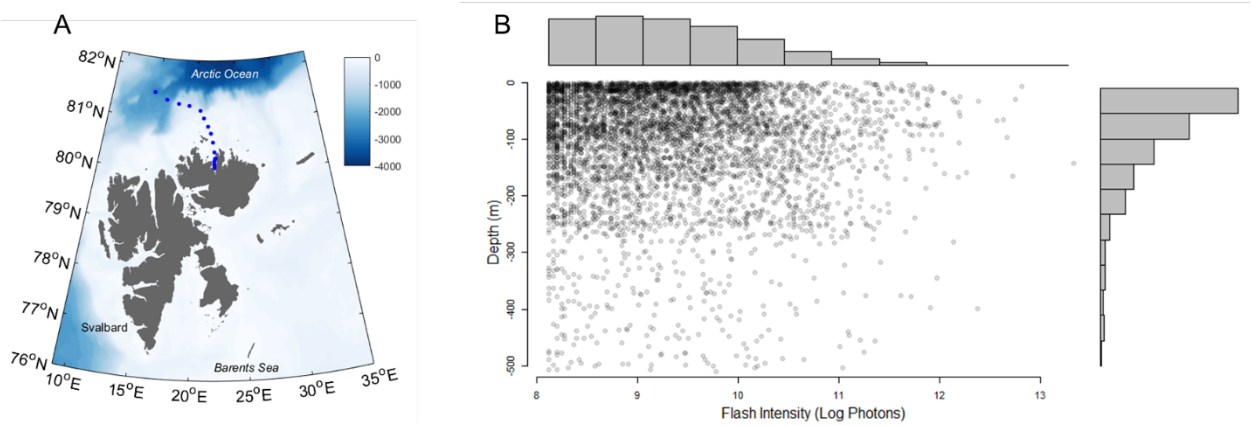


Fig 3.13 Bioluminescence transect from Rijpfjorden (Svalbard) into the Marginal Ice Zone during January 2012. (A) Stations (blue circles) where bioluminescence profiles were conducted. (B) Intensity (log photons) of each bioluminescence flash captured during these profiles. Histograms show the distributions of flash intensity (x-axis) and depth (y-axis). Median bottom depth among these stations was 273m

3.5.4 Bioluminescence and predator-prey interactions during Polar Night

The complexity and roles that bioluminescence plays in predator-prey interactions has been a challenging topic to understand. Visual cues for predators and prey alike are a combination of available light, which originates either from the atmosphere (see 3.4.1) or internally within the water column through bioluminescence, and the visual sensitivities of the organisms involved (Box 3.1). Cronin et al. (2016) mapped the vertical photon budget and the depth of transition from atmospheric light to that dominated by bioluminescence (Fig. 3.13). Over a relatively small depth range of 20 m, bioluminescent light transitioned from contributing less than 3% of the pelagic photon budget to over 85%, and below 60 m bioluminescence contributed over 98% of the pelagic photon budget. Interestingly, Cronin et al. (2016) also documented a change in the bioluminescent community in that depth range which is suggestive that this transition may play a functional role of bioluminescence in predator-prey interactions.

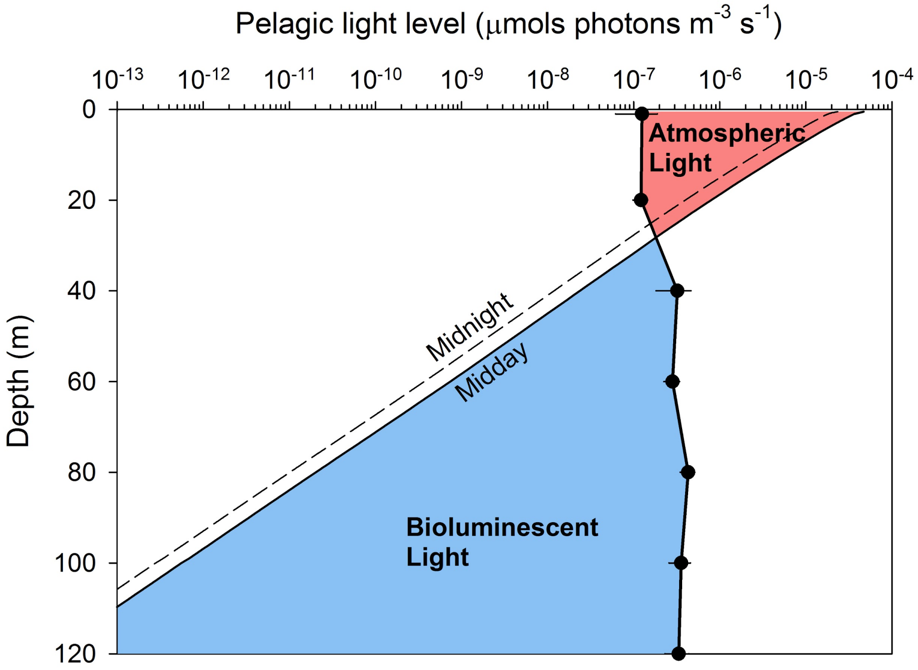


Fig 3.13 Photon budget for biological and atmospheric light sources in Kongsfjorden during Polar Night. The two components of the underwater light field in Kongsfjorden are plotted as a function of depth in equivalent volumetric units (μmol photons m^{-3} s^{-1}). Atmospheric light is scalar irradiance (solid line; 400-700 nm, $E_{o,PAR}$) modeled from diffuse atmospheric irradiance measured at midday (solid line) and midnight (dashed line) in January. Bioluminescence is mean bioluminescence potential (± SE, black dots). The colors represent photic zones dominated by atmospheric light (red shading) and bioluminescent light (blue shading). Data are replotted from Cronin et al. (2016)

3.6 Artificial light in Polar Night

As detailed above and in subsequent chapters (e.g., Chapters 4-8), low levels of ambient illumination are important for regulating biological processes during Polar Night. However, in "dark" habitats such as this, with organisms exhibiting capabilities of detecting and responding to extreme low levels of light, additional light can become a problem. At least artificial light, which becomes *light pollution*.

The area affected by artificial illumination at night is increasing by 6% per year on average, thus becoming one of the fastest-spreading environmental challenges of the Anthropocene (Hölker et al. 2010). An estimated 23% of all land masses between 75°N and 60°S are now believed to be exposed to scattered artificial light that is reflected back to the ground from the atmosphere (Falchi et al. 2016). Few pristine dark habitats above ground remain, and artificial lights from cities, coastlines, roads and marine infrastructures are visible from outer space. The Arctic Polar Night is, arguably, one of the last undisturbed dark habitats on the planet. However, with increased human presence in the Arctic, this may be about to change.

Pollution and other anthropogenic disturbances of biological systems are widespread across the planet, with rising CO_2 levels causing global warming being one of the most important. Even in sparsely populated areas of the Arctic, footprints of human activities are noticeable (Wassmann et al. 2011). However, while changing temperature, pH, ice cover, and CO_2 levels are all factors that naturally have affected biological communities throughout evolutionary history, anthropogenic light pollution is an unprecedented phenomenon starting by the end of 1800 century. Hence, while some taxa have adaptations that have evolved in relation to, for example, changing pH levels (Kelly et al. 2013) or ice cover (Berge et al. 2012), none have had the opportunity to evolve in relation to light pollution. Rather, the harmonic movements of the earth, moon and sun provide reliable cues to which many biological events are now highly attuned (Chapter 8). For polar regions, the intensities of these cues have, arguably, changed with changing ice cover over time, but not the periodicity and harmonic cyclic events. Although light pollution is globally widespread and expanding, we know very little about its potential effects at high latitudes. Arguably, the lack of attention towards light pollution in the Arctic is due to two factors: First, the Arctic is still sparsely populated, with vast regions unaffected by human settlements. Second, as described above, the light climate that governs polar regions is unique and extreme, with most of the biological activity assumed to occur outside of the darkest portions of the year (see Chapter 1 for historical discussion). Ambient darkness can be defined both in space (e.g., deep sea, polar versus temperate regions) and in time (night versus day). The Arctic polar night is a combination of both. However, while the deep sea is likely to remain largely unaffected by light pollution, the Arctic Polar Night is seeing an increase in human activity (Chapter 10) – and hence light pollution.

While not well-studied, light pollution in polar habitats at night, and during Polar Night, has been documented. Euphausiids (krill) on the Nova Scotia continental shelf during nighttime avoid artificial light from ships (Sameoto et al. 1985). Furthermore, artificial light is known to affect the distribution of fish, either by attracting or repulsing them (Marchesan et al. 2005, Nightingale et al. 2006). In work done during Polar Night, Ludvigsen et al. (2018) demonstrated that quick and consistent avoidance responses occur for the entire zooplankton and pelagic fish community when presented with artificial light from research vessels. These data show how even reduced and indirect artificial light from a ship biases measurements of abundance, distribution and behaviour of both zooplankton and fish. The potential implication of this study related to stock assessments and acoustic surveys carried out not only in the Arctic, but also in the dark more generally, are significant. Norwegian vessels conduct sampling "24/7" during stock assessment cruises, not considering if the acoustics or trawl hauls are carried out at day or night. A comparable review from Fisheries and Oceans Canada indicate that at least 25% of all assessments using bioacoustics are carried out at night.

3.7 Future perspectives and knowledge gaps

While observations and modeling of light during Polar Night are growing, numerous gaps remain. We review several key ones here.

1. Observational capacity. Conventional radiative transfer models are limited at low solar elevations, making observations essential. Existing data on light during Polar Night is limited to a few locations (e.g., Svalbard). Numerous factors contribute to this, including instrumentation available for low-level spectroradiometric measurements, and infrastructure for sustained observations throughout polar night. Camera-based measurements (e.g., Zolich 2018, Jechow et al. 2019) hold promise, and commercially available fiber-optic spectroradiometers are increasingly more sensitive (Johnsen 2012), addressing the former issue. Regarding infrastructure, a combination of fixed observatories (e.g., *ArcLight*) and autonomous platforms (Chapter 9) will both be essential to make sustained light measurements over the course of the year at high latitudes.
2. Environmental change. Polar environments are changing – atmospheric conditions and precipitation, the quantity and quality of Arctic sea ice, extent and influence of glacial meltwater, and location of marine water masses. All of these examples have the potential to alter the Arctic light environment during Polar Night, either through direct changes in the spectral irradiance entering the water, or indirect changes in IOPs which then influence the underwater light field. Changes to the underwater light field will affect primary productivity (Chapter 4) and predator/prey dynamics (Langbehn and Varpe 2017, Varpe et al. 2018).
3. Light pollution. Recent decades have seen increasing levels of light pollution globally, changing the intensity, spectral composition and photoperiod of night light. This makes it difficult to quantify "natural" light during Polar Night, even at remote locations (e.g., Jechow et al. 2019). We currently lack an understanding of the artificial light signal during polar night, and what effect it has on biology. However, we do know that light pollution can impact behavior of pelagic marine life during Polar Night (Ludvigsen et al. 2018). Beyond ecological effects of artificial light, the potential for vessel light pollution related to stock assessments and acoustic surveys carried out not only in the Arctic, but also in the dark in general, are immense.
4. Photoperiod. While the duration of day and night seems like a simple concept, it is complex when considering that for biological systems the spectral composition of the light field and the spectral responsivity of the light detector must be aligned. This applies to both marine

and terrestrial organisms. It is further complicated by the changing spectral conditions over the course of the year, most notably during polar night. To quantify "photoperiod" for a given organism we need to understand both the light environment at the location and perspective of the organism, as well as its ability to detect both the wavelength and intensity. Given the role photoperiod plays in biology during Polar Night (Chapters 4-8), quantifying this aspect of light is a priority.

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Chapter 4

Marine micro- and macroalgae in the Polar Night

Geir Johnsen, Eva Leu and Rolf Gradinger

Abstract Microalgae have unique adaptions including low metabolic activity, utilization of lipid storage, and resting stage formation to survive the Polar Night. Some species are mixotrophic or heterotrophic, and do survive periods that are not favourable for photosynthetic (autotrophic) growth, such as the Polar Night. In addition, the autotrophic and mixotrophic species seem to maintain the key components of the photosynthetic apparatus intact during the dark period, which allows them to resume growth rapidly once light comes back in spring. In contrast, some macroalgal species may act as "season anticipators" and utilize the winter darkness or early spring period as their major growth seasons. 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 seasonal development of the different groups of microalgae is described in section 4.3, comprising phytoplankton, microphytobenthos and sea-ice algae. Section 4.4 introduces the three classes of macroalgae (phaeo-, rhodo- and chlorophytes) with information about biological variables, seasonal processes and habitats. Section 4.5 sheds light on the ecophysiology of microalgae and macroalgae in the Polar Night, using selected examples. The last section 4.6 summarizes our current state of knowledge and provides some conclusions derived from it.

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4.1 Introduction

Marine primary production convert inorganic C (CO_2) to organic C, mainly by 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. 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). 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.

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).

Macroalgae 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; Grzymski et al. 1995; Estebar et al 2009. Table abbreviations: PPC: diadino- and diatoxanthin (DD), zeaxanthin (Zea). LHP: Chlorophyll b (Chlb), Chlorophyll c (Chl c1, Chlc2, Chlc3), Magnesium 2,4-divinyl phaeoporhyrin a$_5$ 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.

		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

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. *CO_2 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 (E) of irradiance in the visible part of the solar electromagnetic spectrum (E_{PAR}, 400-700 nm, often termed photosynthetic active radiance, PAR) and E(λ) (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 climate (light regime), comprising E_{PAR}, E(λ) 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 (Grzymski et al. 1997), see review in Johnsen et al. 2011). The photoperiod is a major driver for growth for both micro- and macroalgae and will 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 alga 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 1000 µmol photons m^{-2} 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 µmol photons m^{-2} 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 CO_2-limitation, due to photosynthetically CO_2-uptake rising the sea water pH > 9, indicating inorganic C limitation for photosynthesis (Olsen et al. 2006). The pH and [CO_2] are highly light regulated through the effect of photosynthesis (CO_2 uptake and O_2 release) and respiration (CO_2 release and O_2 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 CO_2 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). The biotic variables important for macroalgae and their impact on algal eco-physiology are discussed in section 4.4.1.

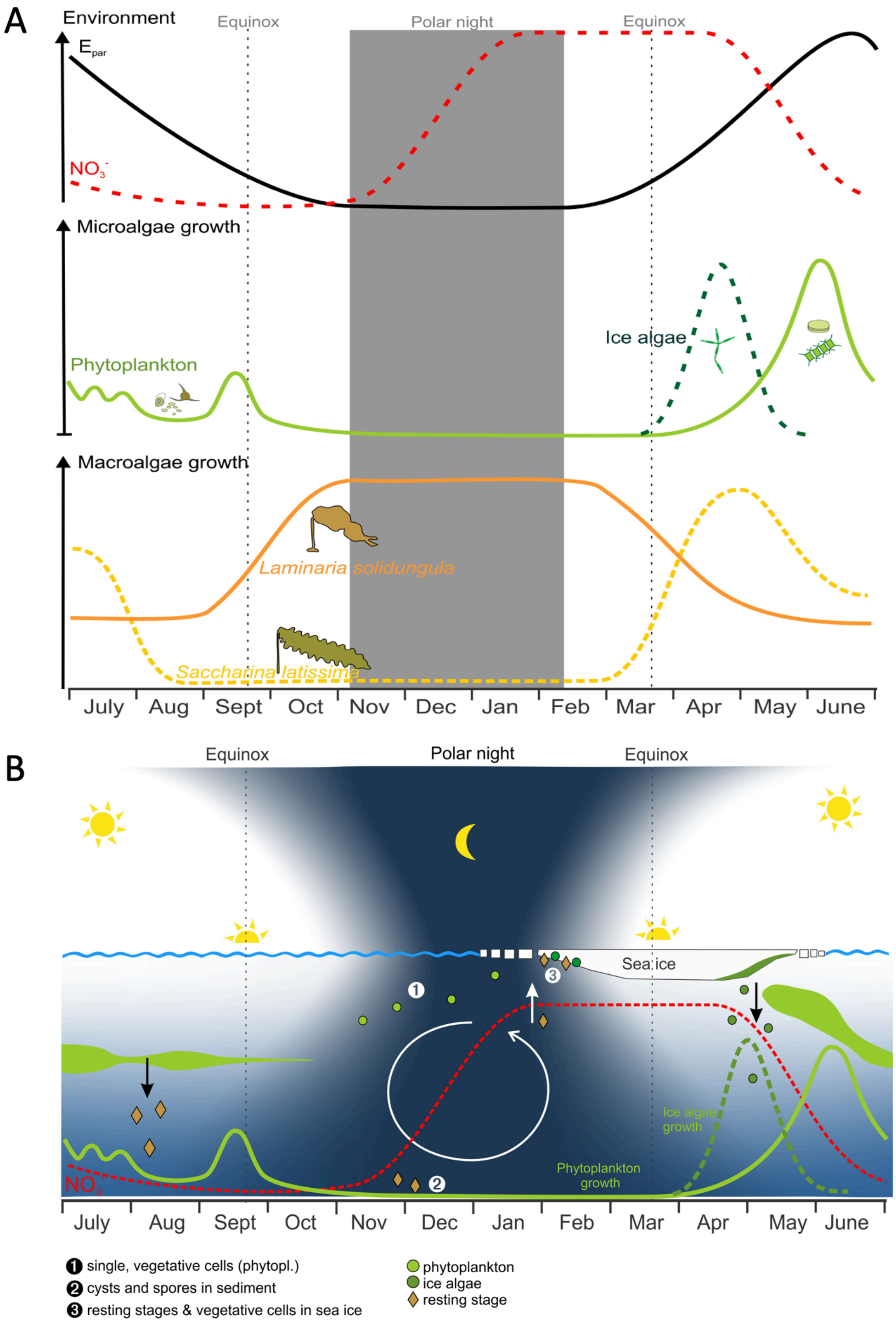


Fig. 4.1 (**a**) Seasonal variability of the limiting nutrient concentration (illustrated by nitrate, NO_3 in upper panel) and irradiance (E_{PAR}) for algal growth (upper panel). Idealized seasonal growth curves for typical representatives of sea ice algae and phytoplankton (middle panel), and for two 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 Daase.

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 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 seeding population for the production of the following year (Fig. 4.4). 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, Box 4.6; 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. Low numbers of vegetative cells stay in the water column throughout the dark period of the year as well. During the civil Polar Night (Chapter 3), low abundances of small pelagic photosynthetic pico- and nano-eukaryotes are found, even if solar irradiance is well below the detection limit of standard light measuring instruments. During the civil Polar Night Cohen et al. (2015) and Ludvigsen et al. (2018) detected peak surface irradiances (E_{PAR}) $<<15x10^{-6}$ μmol photons m^{-2} 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 (Table 4.2; 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 *Protoperidinium, 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 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). There are indications for osmotrophy found in diatoms as well (Lavoie et al. 2018, Horner&Alexander 1972). 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* (Table 4.2). 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 in 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 frequently neglected, 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 most detailed Arctic study was conducted in the high Arctic Young Sound, in Greenland (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 productivity rates for microphytobenthos that were similar to those of 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.

They survive the dark season 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), however, with 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. Their survival was based on 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 reseeding part of the phytoplankton bloom, but also their 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; Box 4.6). 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% (Gosselin et al. 1997). 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 with multiyear ice disappearing fast, and ice-free summers probably becoming 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 ≈ 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. Self-contained underwater breathing apparatus (SCUBA) 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) comprised most species 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 km^2) 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 photoperiod 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 (Johnsen and Berge 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), so also 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.) 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 a 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 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, *Cladophor*a, *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°83´N, 20°35´E), the northernmost island of "Sjuøyane" in the Svalbard archipelago, is characterized with barren areas from the surface to 2-3 meters water depth in which 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*, which is smaller than the other kelp species, 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 larger 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).

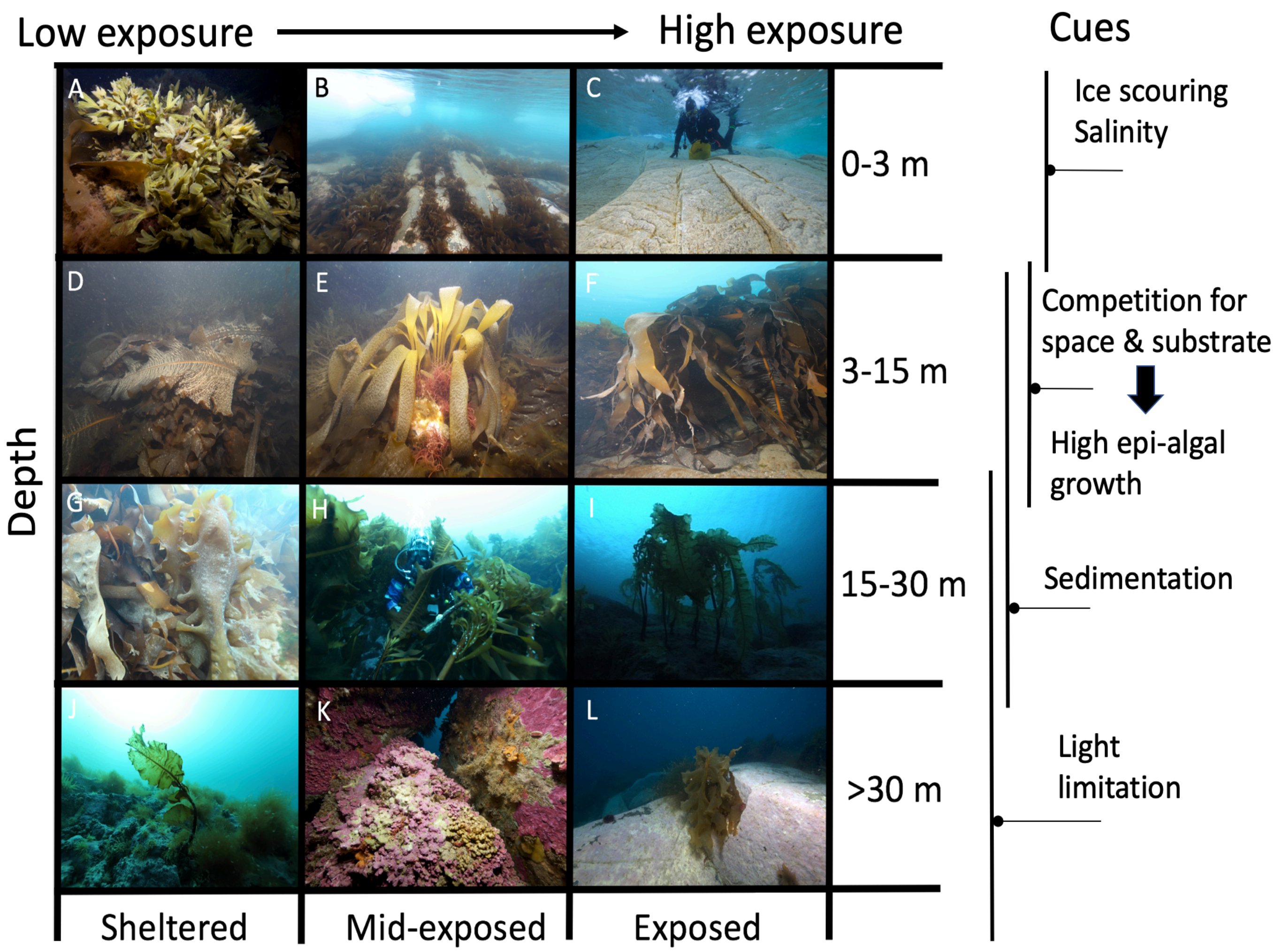


Fig. 4.2 Svalbard kelp forest dominated by perennial brown algae as a function of habitat exposure (X-axis) and depth (Y-axis, 0-30 m depth).

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 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 dived 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 µm 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 g $CaCO_3$ m^2 year^{-1} in North Atlantic rhodolith beds (Bosence 1980; Freiwald and Henrich 1994).

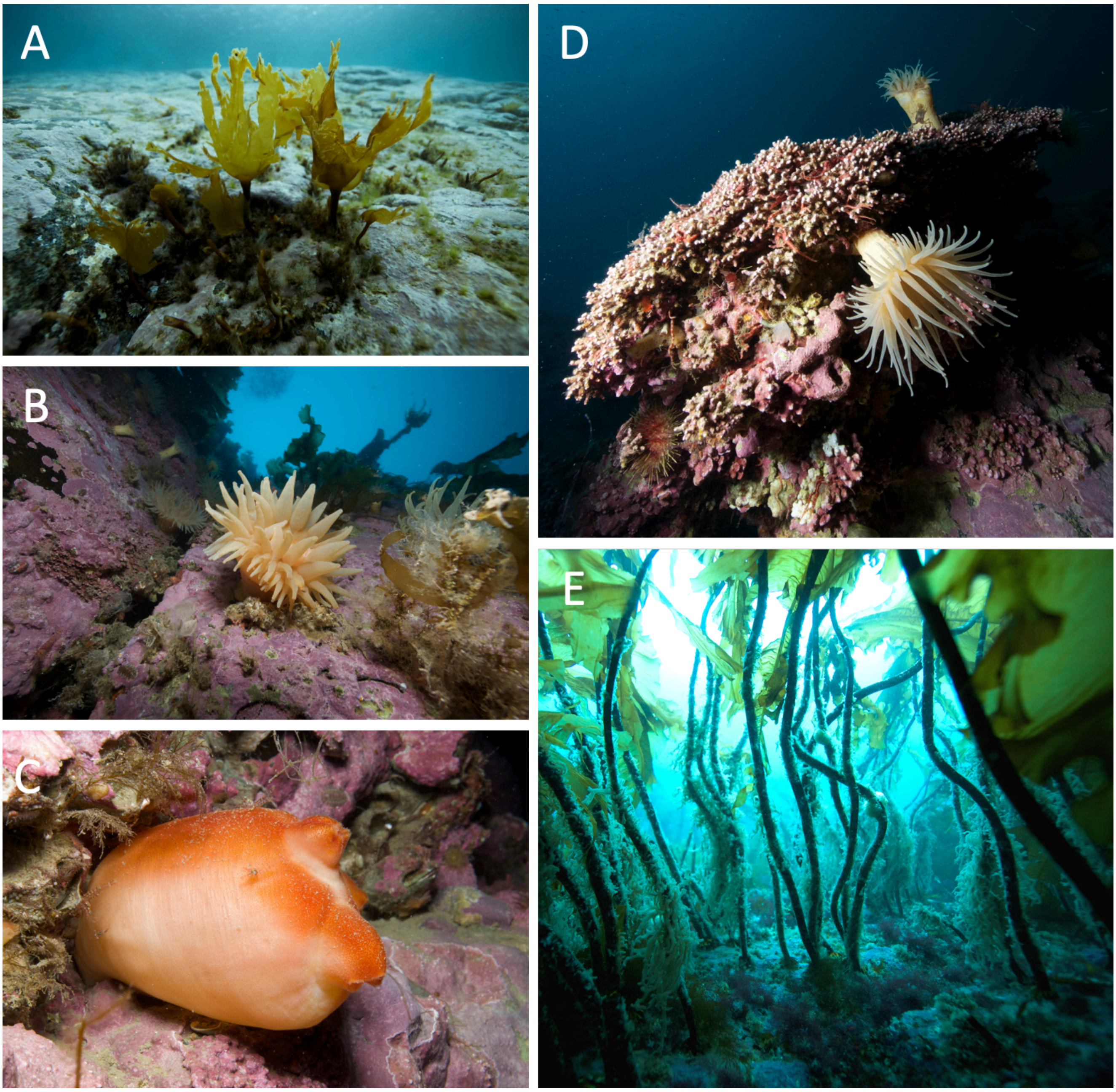


Fig. 4.3 Red calcareous algae habitats. (**a**) Typical crustose eu-littoral seascape (type 2 habitat by red calcareous algae) with shallow growing *Saccharina nigripes*. Picture from Tommelen, 4 m depth, Hinlopenstredet. (**b**) Large areas covered by crustose red calcareous algae, creating seascape 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 (type 1 habitat), 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*). Rijpfjorden, 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), based on 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 which are frequently 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. 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 extended time periods 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.

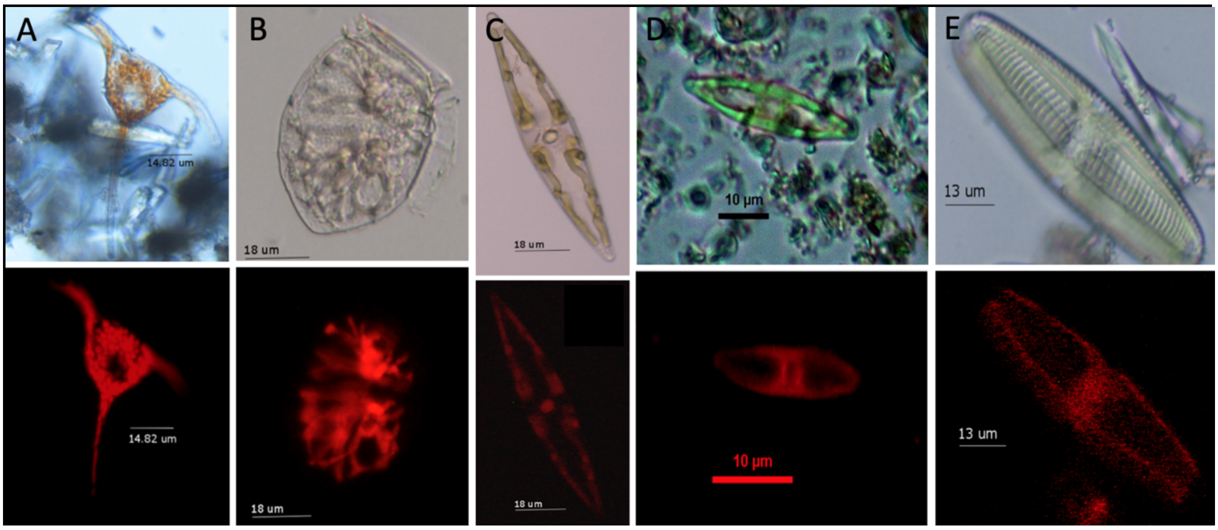


Fig. 4.4 Light micrographs of microalgae collected January 2015 in Kongsfjorden. Upper panel: White light images. Lower panel, the corresponding *in vivo* Chl a fluorescence images. Phytoplankton from surface waters: **(a)** *Ceratium arcticum*, **(b)** *Dinophysis* sp. and **(c)** *Pleurosigma* cf. *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 4.3).

Ice algal cultures that were maintained for months in complete darkness responded very rapidly and resumed growth shortly after re-exposure to light (Zhang et al. 1998). However, 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 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). Results from this study suggest the maintenance of an (almost) fully intact photosynthetic machinery during the dark winter period. Lacour et al. (2019) studied physiological processes in an Arctic diatom culture exposed to one month of darkness, finding very similar results, and postulated that the successful survival was based on extremely low expenditure of metabolic energy. 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, a 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 other groups of pelagic microalgae (see below). 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	x			Rijpfjorden, Sofiadjupet	LM	1,2
		Cylindrotheca closterium	x			Sofiadjupet	LM	2
		Entomoneis sp.	x			Sofiadjupet	LM	2
		Gyrosigma fasciola	x			Rijpfjorden	LM	2
		Nitzschia sp.	x			Sofiadjupet	LM	2
		Pseudonitzschia sp.	x			Rijpfjorden	LM	2
		Pseudonitzschia pseudodelicatissima	x			Sofiadjupet	LM	2
		Thalassiosira sp.	x			Rijpfjorden, Sofiadjupet	LM	2
		Thalassiosira sp. cf. *angulata*	x			Sofiadjupet	LM	2
		Actinocyclus sp.	x			Adventfjorden	LM	3
		Pleurosigma cf. *stuxbergii*	x			Adventfjorden, Kongsfjorden	LM	3
		Thalassiosira antarctica	x			Adventfjorden	LM	3
		Thalassiosira sp.	x			Adventfjorden, Kongsfjorden	LM	3
	Dinoflagellates	*Neoceratium arcticum*	x			Rijpfjorden, Sofiadjupet	LM	2
		Neoceratium fusus	x			Sofiadjupet	LM	2
		Polarella glacialis	x			Rijpfjorden	LM	1
		Naked dinoflagellates	x	x	x?	Rijpfjorden	LM	1
		Thecate peridinea	x			Rijpfjorden	LM	2
		Torodinium robustum	x			Sofiadjupet	LM	2
		Gymnodinium sp. cf. *wulfii*		x		Rijpfjorden, Sofiadjupet	LM	2
		Gymnodinium wulfii		x		Rijpfjorden	LM	2
		Pronoctiluca pelagica		x		Sofiadjupet	LM	2
		Protoperidinium cerasus		x		Rijpfjorden	LM	2
		Protoperidinium pellucidum		x		Sofiadjupet	LM	2
		Gymnodiales	x	x	x	Rijpfjorden	LM	2
		Gymnodinium galeatum			x	Rijpfjorden, Sofiadjupet	LM	2
		Gymnodinium ssp.			x	Rijpfjorden, Adventfjorden	LM	2
		Peridinea cysts		x		Rijpfjorden, Sofiadjupet		
		Gyrodinium helveticum				Adventfjorden	DNA	4
		Gyrodinium fusiforme		x		Adventfjorden	DNA	4
		Glenodinium sp				Adventfjorden	DNA	4
		Dinophysis cf. *acuminata*			x	Adventfjorden	LM	3
		Phalacroma rotundata		x		Kongsfjorden	LM	3
		Podolampas palmipes		x		Adventfjorden, Kongsfjorden	LM	3
		Protoperidinium brevipes		x		Adventfjorden, Kongsfjorden	LM	3
		Protoperidinium sp.		x		Kongsfjorden	LM	3
	Ciliophora	*Parafavella* sp.			x	Adventfjorden, Kongsfjorden	LM	3
		Tintinnida unident.			x	Adventfjorden, Kongsfjorden	LM	3
	Dictyophytes	*Dictyocha speculum*	x			Rijpfjorden, Sofiadjupet	LM	2
	Picoflagellates	*Micromonas pusilla*			x	Billefjorden, Tempelfjorden, Isfjorden, Rijpfjorden, Sofiadjupet, Adventfjorden	PCR	4,5
	Prymnesiophytes	*Phaeocystis pouchetii*	x			Billefjorden, Tempelfjorden, Isfjorden, Rijpfjorden, Sofiadjupet	PCR	4,5
		Coccolithus pelagicus	x			Sofiadjupet	LM	2
Sediment	Diatoms	*Porosira glacialis*	x			Rijpfjorden	Cult	1
		Attheya septentrionalis	x			Rijpfjorden	Cult	1
		Nitzschia frigida	x			Rijpfjorden	Cult	1
		Pleurosigma sp.	x			Rijpfjorden	Cult	1
		Entomoneis sp.	x			Rijpfjorden	Cult	1
		Navicula transitans	x			Rijpfjorden	Cult	1
		Thalassiosira antarctica	x			Rijpfjorden	Cult	1
		T. hyalina	x			Rijpfjorden	Cult	1
		Chaetoceros furcellatus	x			Rijpfjorden	Cult	1
		C. diadema	x			Rijpfjorden	Cult	1
		Cylindrotheca closterium	x			Rijpfjorden	Cult	1
Sea ice	Diatoms	Pennate diatoms, indet.	x			Rijpfjorden	LM	1
		Diatom spores	x				LM	
	Dinoflagellates	Naked dinoflagellates		x	X?		LM	

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 = heteretrophic and mixo = mixotrophic species. *Potentially osmotrophs, but not secured information.

4.5.2. Macroalgae: Season anticipators

Contrary to microalgae that struggle to secure survival during the Polar Night darkness, some macroalgae algal 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 glaziers, 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 stabile 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 "heteretrophic" 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; 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 unmature 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 µmol m^{-2} s^{-1} (indicating high light acclimated tissue) whereas the 3-year old tissue of the same specimen obtained an E_k of 20 µmol m^{-2} 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 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 µmol m^{-2} s^{-1} while the average E_k value of vegetative lamina in adult specimens was 38 µmol m^{-2} 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 mol m^{-2} yr–1, the lowest ever documented for kelp populations globally. In comparison, the temperate *L. hyperborea* , received 71 mol m^{-2} yr^{-1} (Lüning and Dring 1979).

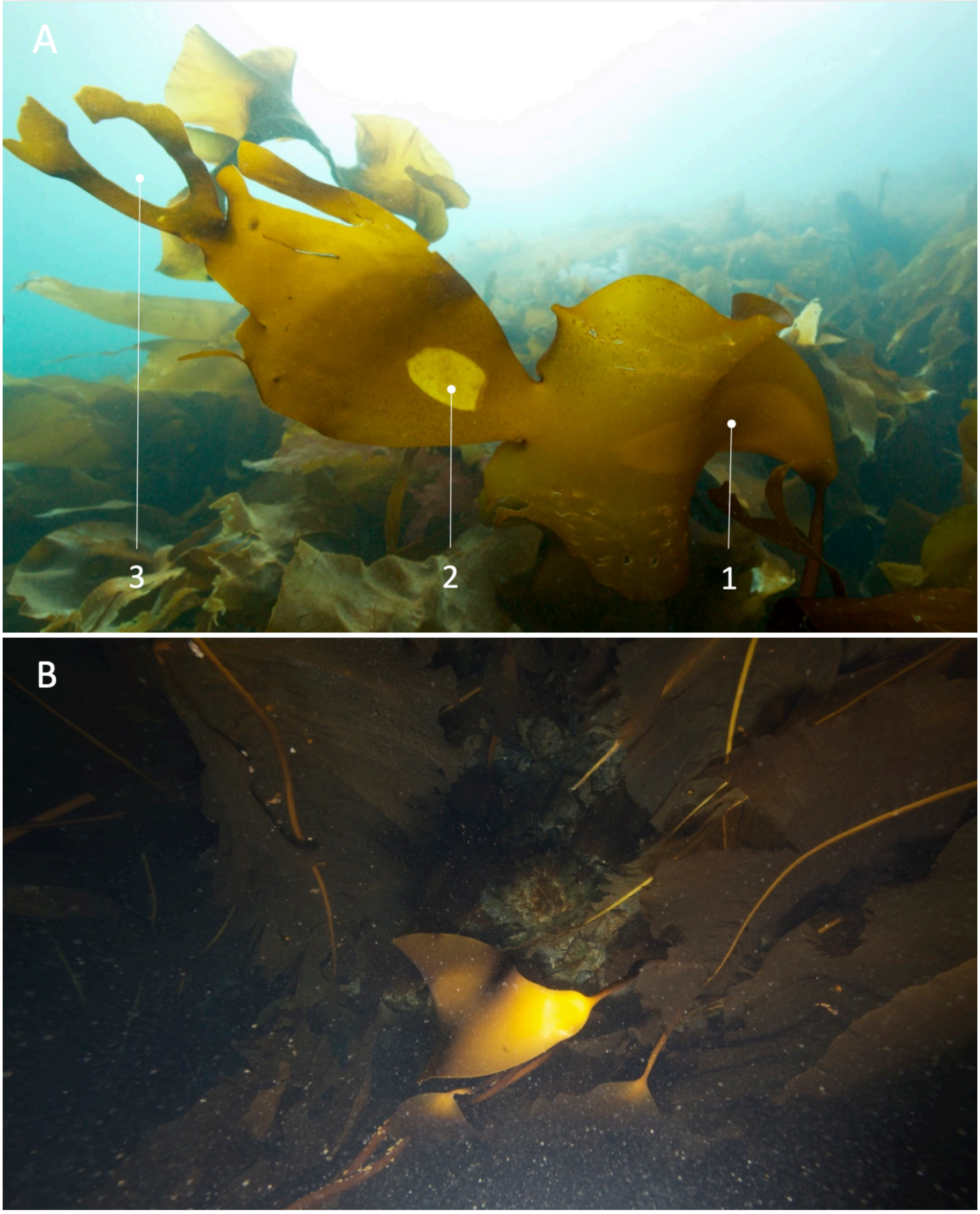


Fig. 4.5 (**a**) The endemic arctic kelp species *Laminaria solidungula* (Hinlopenstredet, Sep 2009). Tissue 1-3 denotes age (year) of lamina with different developmental stage of sorus (fertile tissue). 1 year old sorus (1) is clearly seen as a bright area from the basis of meristem (new growth), 2 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 latissimi* (Fig. 4.2): 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 µmol photons m^{-2} 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 $E_{PAR} > 350$ µmol photons m^{-2} 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 ($\Phi_{PSIImax}$) at any time point during the recovery studies. After 25 minutes in dark after RLC experiments, the $\Phi_{PSIImax}$ 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 µmol m^{-2} 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 $_{c1+2}$ (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. solidungul*a 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

Albeit still being heavily understudied, we have now started to shed some light on the survival and ecophysiology of algae during the Polar night. Increasing our understanding of this is critical as the processes during the darkest period of the year pave the ground for all the biological activity in the Arctic spring providing time for growth and development. Microalgae have unique adaptions including life cycles and ecophysiology that allow them to rapidly resume growth once light returns in spring, while some macroalgae can utilize the Polar Night for growth.

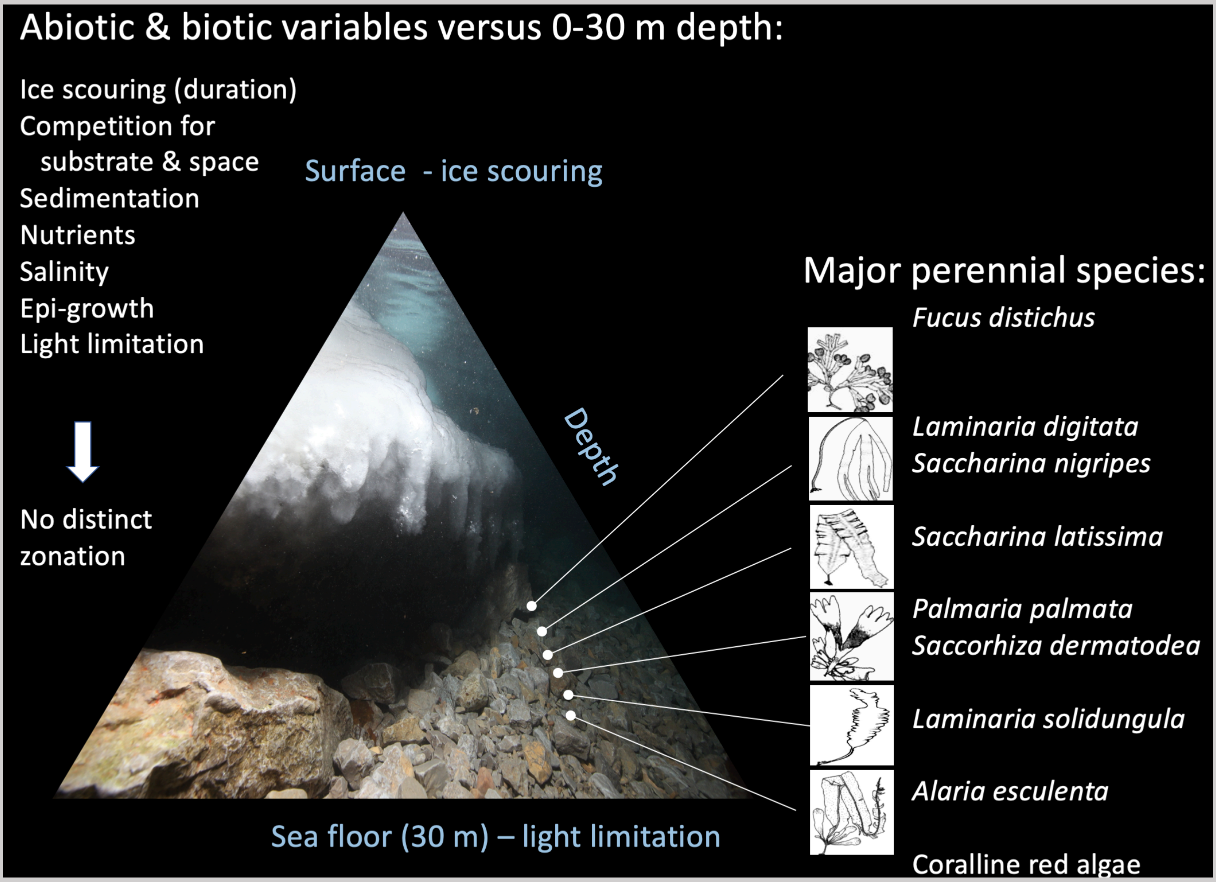
For microalgae, resting stages and mixotrophy appear to be adaptive traits to survive the winter season. One could argue that at high latitudes, an alternative food web based on mixotrophy may dominate the pelagic lower food web during much of the year, causing a unique functioning of the microbial network. Alternatively, many micro- 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 many microalgae do include specialized cell types built to last long periods without being attacked by bacteria or animals. These cysts or spores 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.

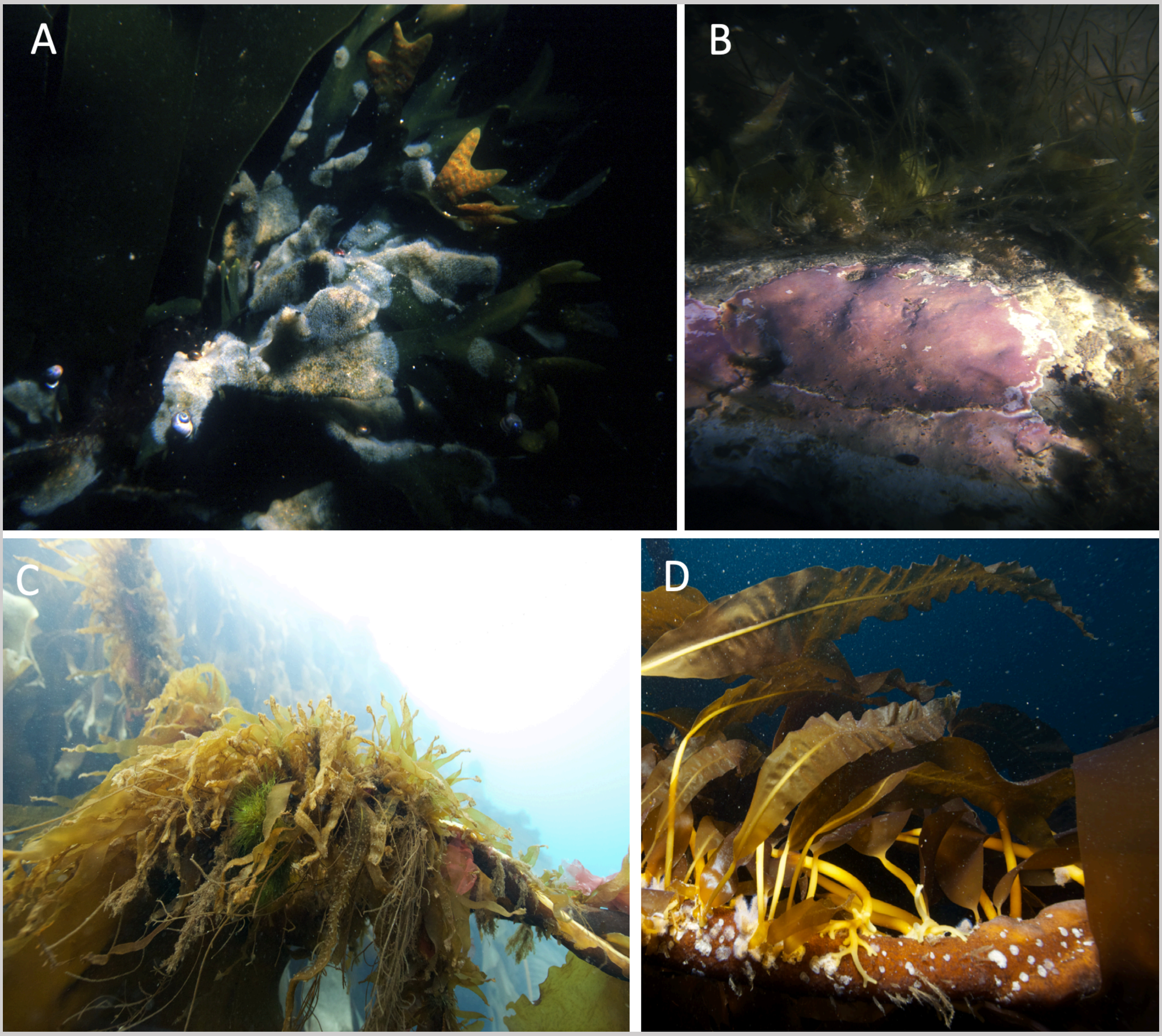
Some macroalgal species may act as "season anticipators" and utilize the winter darkness or initial spring period as major growth seasons. We have used two kelp species as examples of two different growth strategies, i.e. an endemic Arctic kelp species actively growing during the Polar Night with laminar 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.

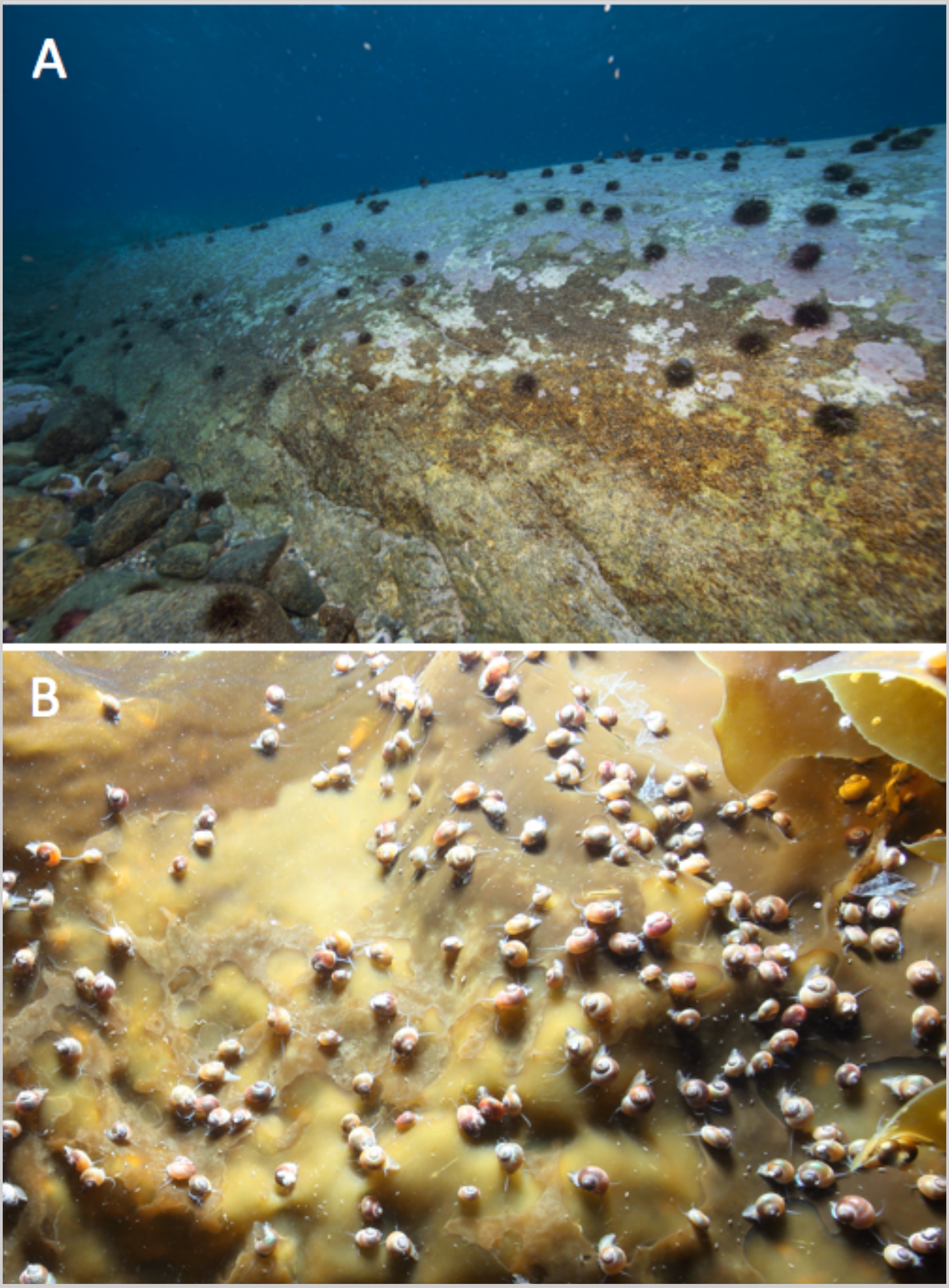
To provide a knowledge-based management of polar marine systems including marine micro- and macroalgae in general and e.g. kelp forests we need to identify, map and monitor these habitats using new enabling technology using autonomous instrument carrying platforms and sensors, elucidated in Chapter 9 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.



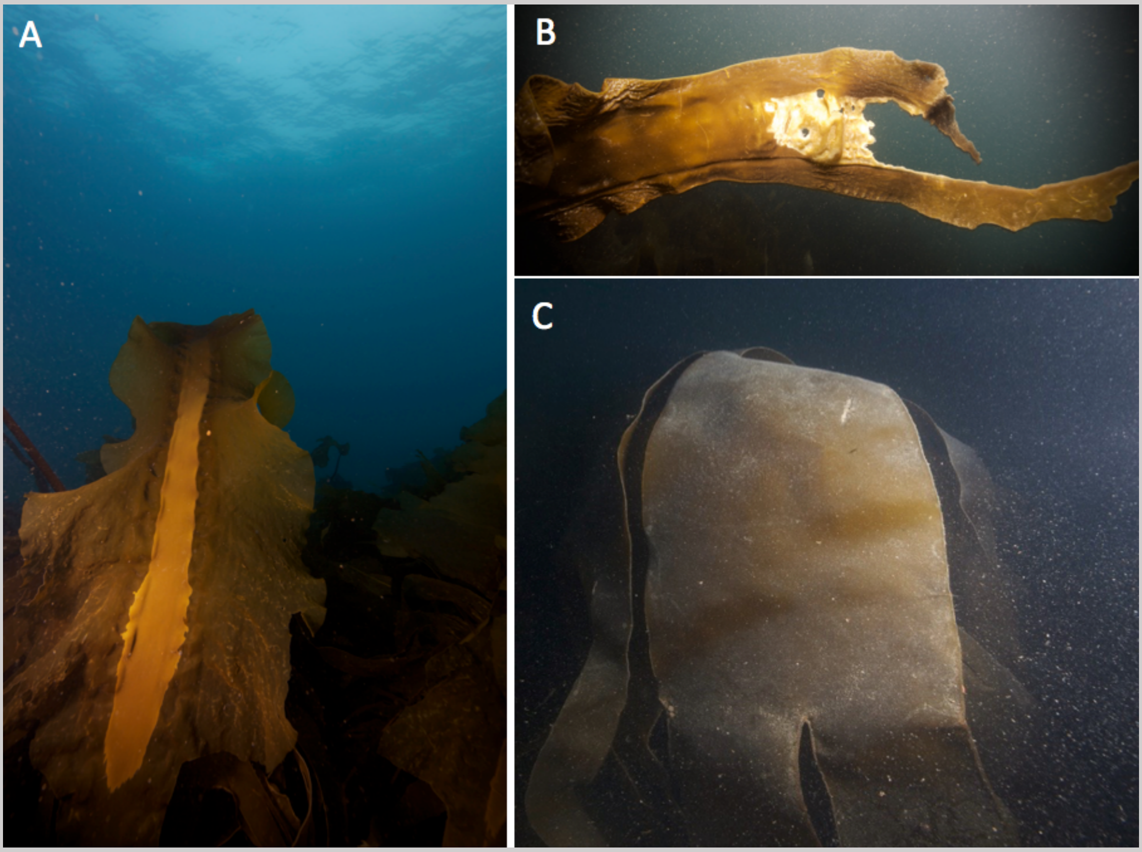
Box 4.1 Absence of distinct macroalgal zonation due to abiotic and biotic variables. The major variables affecting macroalgal biodiversity in the eulittoral zone (0-3m) is ice-scouring: Heavy ice-scouring may leave the upper 4m barren and only with annual species growing as "bio-film" in summer months. Perennial species are found in cracks and in between rocks. There is a zone devoid of ice-scouring and providing enough light for photosynthesis (4-30m) 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. 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). Photo: Geir Johnsen



Box 4.2 Epigrowth on macroalgae. (**a**). The wrack *Fucus distichus* with epigrowth of bryozooans and *Margarites* sp. Kongsfjorden, 1 m depth, September. (**b)** Coralline red algae produces substances for biological "warfare" 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.

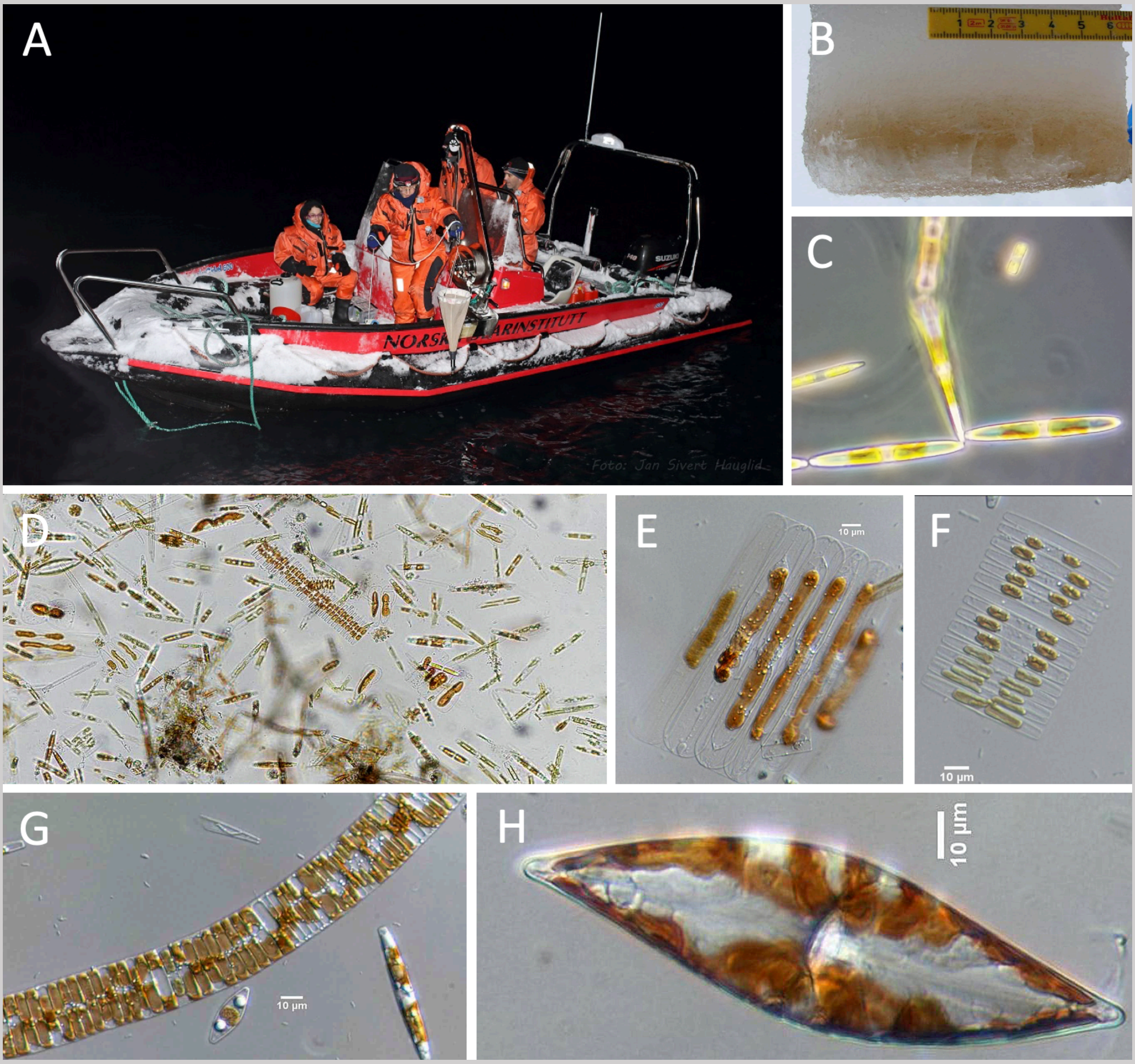


Box 4.3 Grazing of macroalgae. A. The urchin *Strongylocentrotus droebachiensis* grazes both on kelp and coralline algae. Rijpfjorden, Nordaustlandet, Svalbard (Sep). B. During autumn and winter, protein rich sorus regions of kelp, such as *Saccharina latissima* pictured here, may be visited by a high 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. 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, including surviving the Polar Night, 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 the kelp *Saccorhiza 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 the crab *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.



Box 4.6 Phytoplankton sampling and ice algal sampling of diatoms. (**a**) Polar Night sampling during January 2014 using phytoplankton net. (**b**) Lower part of sea ice-core containing ice algae. (**c**) *Nitzschia frigida*, a common ice algae in annual sea ice. (**d**) Ice algae assemblage at peak of bloom in April. (**e**) *Entomoneis* sp. (**f**) *Nitzschia* cf. *promare*. (**g**) *Navicula septentrionalis*. (**h**) *Pleurosigma stuxbergii*. Images: A Jan S. Hauglid, B-F (light microscopy images) Jozef Wiktor.

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Chapter 5

Zooplankton in the Polar Night

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Abstract

Pelagic communities play a key role in Arctic ecosystems. Although zooplankton occupy several different trophic levels in the food chain, their primary niche is often considered that of a link between pelagic and ice-associated primary production on one side and higher trophic levels on the other. In fact, most of the biological energy (organic carbon) ending up in top predators such as seabirds, fish and marine mammals have been funneled through one or more zooplankton species. As such, zooplankton ecology is often viewed and understood in relation to primary production regimes. However, recent research has also showed that processes occurring in the zooplankton community during winter is crucial for our understanding of Polar Night ecology. As a group, they are active throughout the entire year, they conduct various forms of vertical migration in relation to both the moon and solar background illumination, and some species utilize the Polar Night for reproduction. Evidence of reproduction among short-lived omnivorous zooplankton species during the Polar Night suggests that production is sustained by feeding opportunistically throughout winter and Polar Night, and that life history strategies are tuned to support fast turn-over rates and not on building up large lipid reserves. This chapter provides an introduction to the main zooplankton taxa inhabiting Arctic waters during the Polar Night and describes the main processes typical for zooplankton taxa during te Polar Night.

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One makes a trip by day, but by night one sets out on a journey - Tove Jansson

5.1 Introduction

The long periods of low to nil solar illumination in the high-Arctic, with the Polar Night as an acme of the dark season, are undoubtedly challenging parts of the annual cycle for pelagic organisms. They have developed a variety of adaptive strategies to cope with the often sub-zero temperatures, and extremely low food and light availability that impact their feeding capacities, growth and development rates. Zooplankton play a key role in the polar marine ecosystem. Most of the biomass produced by pelagic primary producers is funnelled through a few key zooplankton species before being transferred to marine top predators. Due to the high seasonality in incoming solar radiation at high latitudes (Chapter 3), primary production is severely limited for extended parts of the year (Chapter 4). It is the seasonal limitation in food supply, not low temperatures, that is the main constraining factor on polar zooplankton (Clarke 1983), in particular for herbivorous species, but also for omnivores and carnivores that rely on these grazers of pelagic algae for food.

The polar summer is characterized by high activity within the zooplankton community to accomplish reproduction, growth, development and energy storage within a short time window of high sympagic and pelagic primary production (Chapter 4, Fig 4.1). The Polar Night, on the other hand, has traditionally been viewed as a period of low biological activity during which herbivorous species recede into diapause at greater depth while omnivorous and carnivorous species are just inactively waiting for biological activity to resume with the return of light and food in spring. Given the remoteness of polar regions, zooplankton studies from the Polar Night are rare and largely based on overwintering scientific campaigns. Early accounts of Arctic zooplankton from the polar basin are based on such expeditions, such as the 3-year Fram drift (1893-96) and later on Russian and US drift ice stations. However, these pioneer studies largely focused on describing the taxonomic composition while seasonal patterns in species composition, abundance and vertical distribution were overlooked. An account of the seasonal vertical migration of prolific copepods in the polar basin, including the Polar Night, was first published in 1983 based on data collected from Russian drift ice stations (Geinrikh et al. 1983). To this day, the winter vertical distribution of copepods in the Arctic Ocean remains poorly documented. Furthermore, only few year-round investigations of pelagic communities from high latitude include data from the Polar Night. The annual cycle in abundance, distribution and size of dominant copepod species was investigated during the SHEBA drift in the Western Arctic Ocean (Ashjian et al. 2003). Seasonal studies of the zooplankton community have been conducted in Greenland fjords (Ussing 1938; Digby 1954; Madsen et al. 2001). And overwintering campaigns such as Canadian Arctic Shelf Exchange study (CASES, 2003-2004) and the Circumpolar Flaw Lead System study (CFL, 2007-2008) have provided new insight into zooplankton ecology in the Canadian Beaufort Sea during the Polar Night (Seuthe et al. 2007; Darnis and Fortier 2012; Darnis et al. 2012; Darnis and Fortier 2014; Darnis et al. 2019). There, analysis of swimmers caught by sediment traps have also provided insights into the species composition and the contribution of zooplankton to the vertical flux during the Polar Night (Sampei et al. 2009a; Sampei et al. 2009b; Forest et al. 2011a; Forest et al. 2011b; Darnis et al. 2019; Dezutter et al. 2019).

In Svalbard, data on the zooplankton community collected during the Polar Night are rare prior to 2012 (Bailey 2010; Seuthe et al. 2011), and mainly based on material sampled using moored instruments such as sediment traps and hydroacoustics (Willis et al. 2008; Berge et al. 2009; Wallace et al. 2010). Over the last decade, the research focus in Svalbard has shifted towards seasonal studies, providing new insights into numerous aspects of zooplankton ecology also during the Polar Night (Table 5.1).

Table 5.1 New insights into the ecology of arctic zooplankton during the Polar Night based on Polar Night campaigns, seasonal studies and ocean observatories in Svalbard over the last decade

Subject	**New insight**	**Reference**
Seasonal vertical migration	Herbivorous and omnivorous mesozooplankton species are distributed throughout the water column in January. *Calanus* spp. become active and ascend as early as early January	Berge et al. (2015); Błachowiak-Samołyk et al. (2015); Grenvald et al. (2016); Bandara et al. (2016); (Daase et al. 2018)
	C. finmarchicus is found in surface waters north of Svalbard	Basedow et al. (2018)
Feeding	*Themisto* spp. is feeding on *Calanus* spp. during the Polar Night	Kraft et al. (2013)
	Low feeding rates in *Parasagitta elegans*	Grigor et al. (2014; 2015)
	Evidence of *C. glacialis* carnivory on metazoan (copepod eggs) in January	Cleary et al.(2017)
Non-consumptive mortality	High non-consumptive mortality in January in *Calanus* spp.	Daase et al. (2014)
Reproduction	Copepod nauplii are abundant in January, indicating reproduction of planktonic cyclopoids (e.g. *Oithona similis*) and some calanoids (e.g. *Microcalanus* spp., *Metridia longa*).	Berge et al. (2015); Błachowiak-Samołyk et al. (2015); Grenvald et al. (2016)
	Males of *Calanus glacialis* are abundant and active during the Polar Night, together with females bearing spermatophores confirming the importance of the Polar Night as the major mating period.	Daase et al. (2018)
	No reproduction in *Parasagitta elegans*	Grigor et al. (2014; 2015)
	Juvenile stages of ctenophores (*Mertensia ovum*) and pteropods (*Clione limacina, Limacina* spp.), as well as meroplanktonic larvae (Nudibranchia, Bivalvia, Polychaeta, Bryozoa) are observed in January	Berge et al. (2015)
	Gastropoda and bryozoa larvae present from November to February	Stübner (2016); Kuklinski et al. (2013)
Physiology	Weight-specific respiration rate of two size classes of mesozooplankton was higher in January than in May in Kongsfjorden	Berge et al. (2015)
	Euphausiid respiration rates were similar in January and May	Darnis et al. (2017).
	Respiration rates of *C. glacialis* was three times lower in November than in July. Addition of light increased respiration rates in November to levels comparable with that of active copepods in summer, but respiration only remained high if food was present	Morata and Søreide (2013)
	Seasonal changes in lithium concentrations and pH in *C. glacialis* suggests that ion and pH play a role in regulating diapause processes	Freese et al.(2015)
	Activity patterns of proteinase and	Freese et al. (2016)

	Lipase/esterase were reduced by at least 75 % during winter compared to spring indicating that low feeding activity in winter	
Diel vertical migration	DVM signal detectable throughout Polar Night.	Berge et al. (2009); Grenvald et al. (2016); Hobbs et al. (2018)
	DVM mainly asynchronous close to solstice, becoming more synchronized as soon as some light returns	Wallace et al. (2010); Darnis et al. (2017)
	Zooplankton conduct short-scale DVM of 8 m even in complete darkness	Ludvigsen et al. (2018)
Lunar vertical migration	Zooplankton adjust diel rhythm to lunar cycle in darkest month	Last et al. (2016); Webster et al. (2013)
	Zooplankton avoid top 30-50 m of water column during full moon	Last et al. (2016)
Light pollution	Zooplankton show light avoidance behaviour to artificial light sources during Polar Night	Ludvigsen et al. (2018)

Here, we review overwintering strategies of common Arctic zooplankton species and summarize findings on zooplankton ecology, composition, vertical distribution and physiology made during recent Polar Night campaigns. We focus on Svalbard waters and to some degree on the Canadian Arctic, since the majority of Polar Night observations have become available from these regions over the last decade.

5.2 Arctic zooplankton species composition in the Polar Night

The Arctic metazoan holoplankton community consists of ~300 species from eight large metazoan phyla. Crustaceans dominate in terms of species numbers, with copepods being the most diverse group (>50% of all Arctic zooplankton species) and dominating in both abundance and biomass (e.g. Kosobokova and Hopcroft 2010; Kosobokova et al. 2011). In addition to the holoplankton species, a number of benthic invertebrate taxa (commonly referred to as meroplankton) have pelagic larval stages that supplement Arctic zooplankton communities. The Arctic zooplankton community contains a mix of Arctic endemic and boreal species of either Atlantic, Pacific or cosmopolitan origin that are advected into the Arctic Ocean. Diversity increases with depth, making the polar basin more diverse than the shelf waters (Kosobokova et al. 2011). While species of Pacific origin seldom occur in the Atlantic side, and vice versa, the taxonomic variation across the Arctic is otherwise low, as most species regularly occur throughout the Arctic. In fact, differences in the zooplankton community structure across the Arctic are mainly manifested through variations in the species relative densities rather than through variations in taxonomic composition. This pattern seems to hold for seasonal variability in species composition as well.

In Svalbard waters, zooplankton diversity does not seem to differ markedly between the Polar Night and the light season, i.e. most species encountered during summer are also present during winter. As observed on a pan-Arctic scale there are, however, differences in the species community composition between seasons. Data from Svalbard fjords and the open ocean north of Svalbard show that the mesozooplankton community during the Polar Night is dominated by copepod species (Fig. 5.1). Copepods of the genus *Calanus* spp. can be abundant, but small copepods including *Oithona similis* and *Microcalanus* spp. make up the largest share of the community. Other non-crustacean species such as chaetognaths, pteropods and appendicularians, are present but in low numbers. In spring (May), small copepod species are still relatively common but meroplankton taxa and copepod nauplii usually dominate the mesozooplankton community. By the end of summer, *Calanus* species have built up large populations, and non-crustacean taxa play a larger role in the mesozooplankton community, especially pteropods (*Limacina* spp.) that can dominate the community in summer.

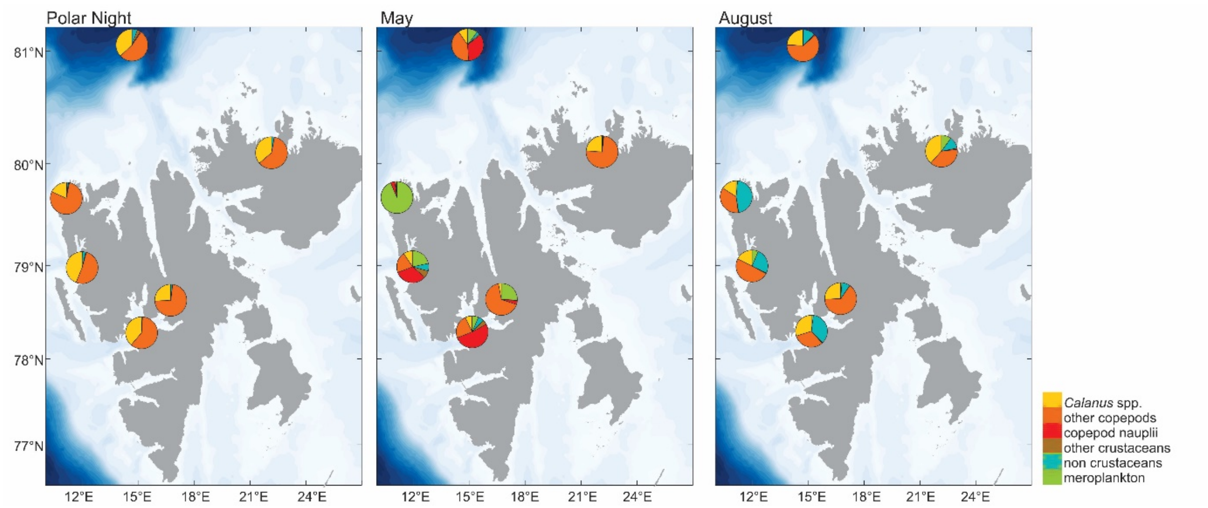


Fig. 5.1 Seasonal variability in the mesozooplankton community composition in different locations in Svalbard based on Multinet samples (opening area 0.25 m^2, mesh size 180 µm)

The relatively low numbers of non-copepod taxa observed in Multinet samples from the Polar Night are due to the low abundance of meroplankton and pteropods. Other crustaceans and non-crustaceans, such as *Themisto* spp., euphausids and chaetognaths, may be caught more efficiently in their juvenile stage with the relatively small-aperture (0.25 m^2) Multinet during summer, while they are highly likely to be undersampled in their faster-swimming adult stage and are thus absent from these samples during the Polar Night. Grenvald et al. (2016) found that euphausids can be abundant in January in Kongsfjorden. Data collected in January using a macrozooplankton net (MIK net, 3.14 m^2, 1.5 mm mesh size) show a numerical dominance of copepods, but also a high contribution of euphausids to the biomass (Fig. 5.2). Similar to multinet data, the community sampled in August with the larger net is characterized by a higher contribution of pteropods and chaetognaths (Fig. 5.2). Larger individuals of chaetognaths and euphausiids dominated during the Polar Night (Fig. 5.3), indicating that the low abundance of these taxa in the multinet samples during the Polar Night may indeed be due to net avoidance of adult stages.

Seasonal changes in the dominance of different taxa are related to differences in their life history traits, with some organisms being better adapted to deal with extreme conditions encountered during the Polar Night.

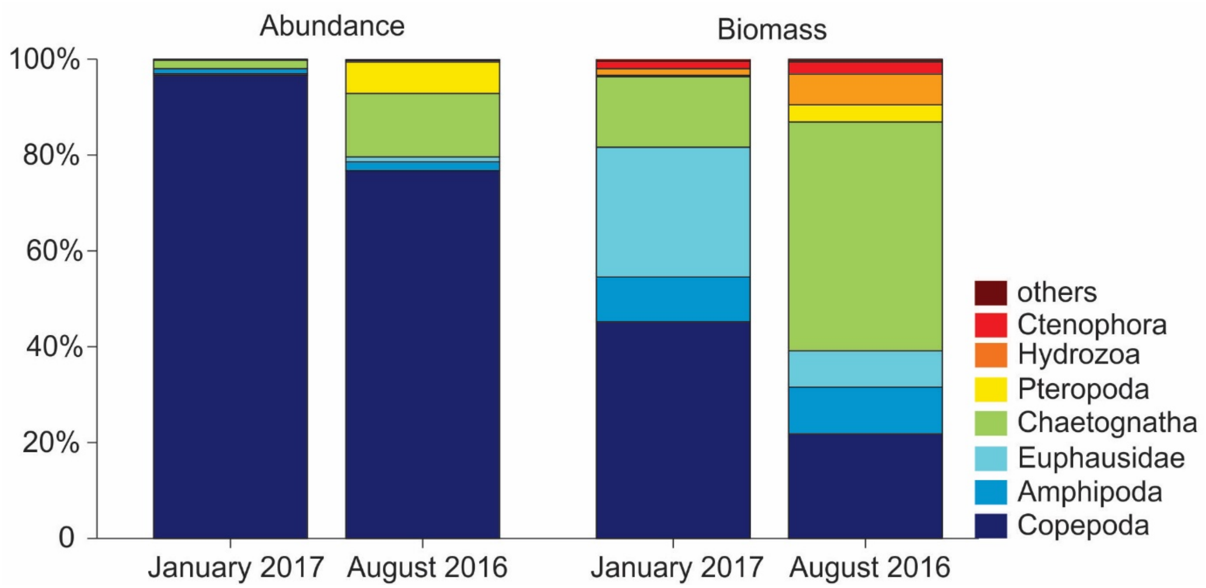


Fig. 5.2 Community composition of zooplankton sampled with a macrozooplankton net (MIK net, opening 3.14 m^2, mesh size 1.5 mm) north of Svalbard in January 2017 and August 2016, based on abundance (% total number of individuals) and biomass (estimated wet weight)

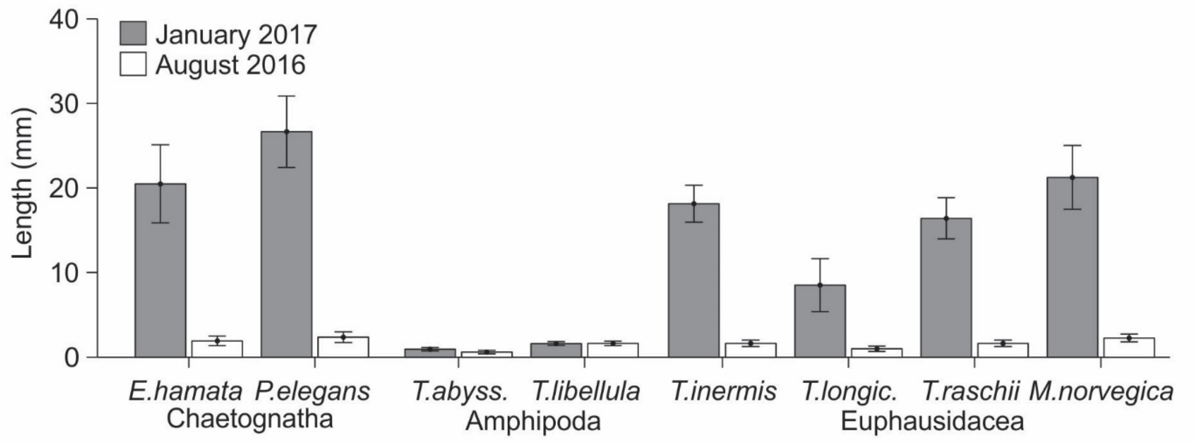


Fig. 5.3 Mean length (mm) of common macrozooplankton species collected with MIK net north of Svalbard in January 2017 and August 2016. Error bars show standard deviation

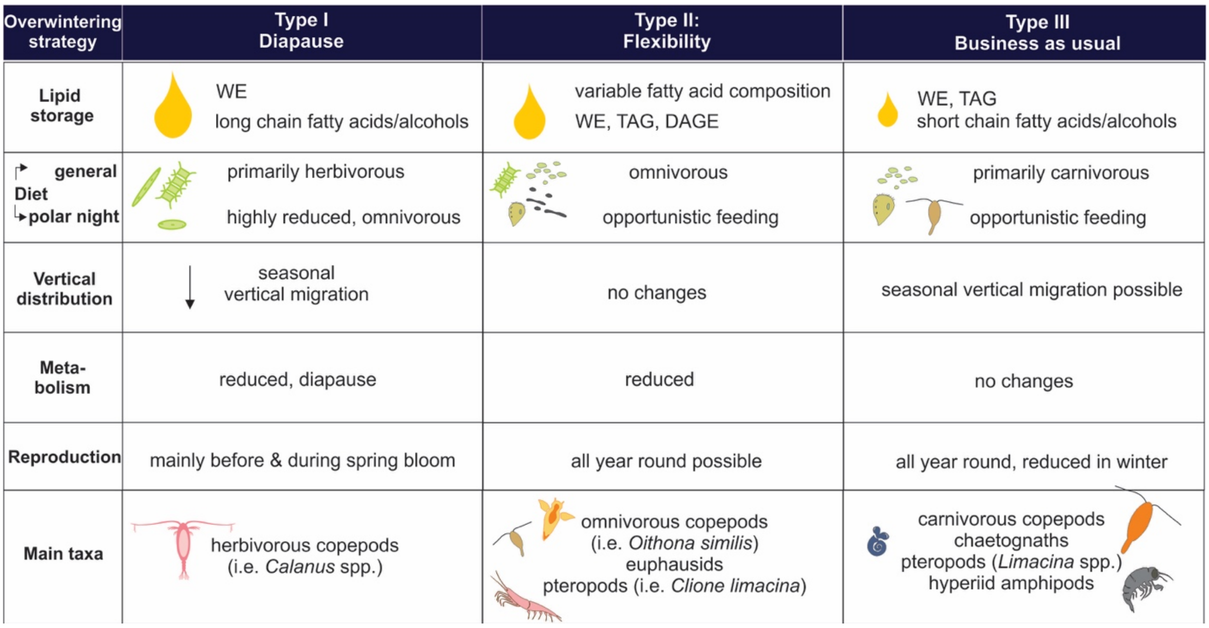
5.3 Overwintering strategies of Arctic zooplankton

Arctic zooplankton have evolved a number of adaptations to deal with the seasonal resource limitation. Adaptations include: a shift in dietary preferences to a more omnivorous, carnivorous or detrivorous diet during winter; the ability of body shrinkage and sexual regression to reduce energetic costs; reduced feeding rates; and a general reduction of metabolic activity through diapause. Diapause is characterized by arrested development and reduced metabolism, and requires a preparatory phase, including lipid accumulation and the descent to depth (Baumgartner and Tarrant 2017). Diapause can be highly variable in timing and duration within and between species, relating directly to seasonal changes in the environment.

Diapause often follows an ontogenetic/seasonal vertical migration at the end of the productive season. The overwintering advanced life stages descend to deeper waters to spend winter in a non-feeding state with reduced metabolism, a process leading to prolonged life cycles of up to several years. The most conspicuous adaptation is the accumulation of large energy reserves in form of lipids. Lipid reserves are common in most arctic zooplankton species and constitute highly efficient energy storages, storing twice as much energy per unit mass as proteins and carbohydrates (Kattner and Hagen 2009). Lipids are to some extent utilized during overwintering to maintain activity and cover metabolic costs related to the migration to and from overwintering depth, but are mostly utilized to fuel energy-demanding reproductive processes as well as growth and development at the end of the winter and in spring and summer (Jonasdottir 1999; Visser and Jónasdottir 1999; Hagen and Auel 2001). In addition, lipids provide buoyancy as the density of lipids is lower than the surrounding seawater (Kögeler et al. 1987; Visser and Jónasdottir 1999; Campbell and Dower 2003). Two types of neutral lipid classes are commonly used for energy storage: Triacylglycerols (TAGs) and wax esters (WE). TAGs are important as readily accessible short-term energy storage, while wax esters function as long-term stores (Kattner and Hagen 2009). The type and relative amount of stored lipids is related to life history strategies. Primarily herbivorous species store high amounts of lipids in form of WE, which are also common among omnivorous copepods. TAGs are commonly found in more carnivorous arctic zooplankton species that do not undergo diapause, remaining active throughout the winter (Lee et al. 2006; Pond 2012). Since lipid storage is an adaptation to seasonal fluctuations in food supply, the amount of lipids stored tends to follow a seasonal pattern. However, year-round observations of lipid content are not available for most Arctic zooplankton species. Lipids play a central role in Arctic pelagic food webs. Lipids biosynthesized by *Calanus* copepods can be traced throughout the pelagic food web, from carnivorous zooplankton to fish, sea birds and marine mammals (e.g. (Falk-Petersen et al. 1990; Dahl et al. 2003; Haug et al. 2007)). The evolution of these lipid reserves makes polar zooplankton an attractive food source not only for resident predators but also for migrating predators, such as baleen whales and seabirds, the charismatic posterchildren of polar regions.

Three types of strategies for overwintering in polar zooplankton have been suggested (Torres et al. 1994; Hagen 1999) (Fig. 5.4):

Type 1: Accumulation of large lipid reserves (usually WE), and entering a dormant state. The Polar Night is spent in a non-feeding state, with reduced metabolism, arrested development and preferably at greater depth.
Type 2: Metabolic activity is modulated downward but the organism stays active. Opportunistic feeding and/or a shift in dietary preferences and a depletion of body mass enables the species to survive the winter.
Type 3: “Business as usual”: metabolic activity is not particularly modified, opportunistic feeding and some combustion of tissues carries the organisms through the winter.



Overwintering strategy	Type I Diapause	Type II: Flexibility	Type III Business as usual
Lipid storage	WE long chain fatty acids/alcohols	variable fatty acid composition WE, TAG, DAGE	WE, TAG short chain fatty acids/alcohols
↱ general Diet ↳polar night	primarily herbivorous highly reduced, omnivorous	omnivorous opportunistic feeding	primarily carnivorous opportunistic feeding
Vertical distribution	↓ seasonal vertical migration	no changes	seasonal vertical migration possible
Meta-bolism	reduced, diapause	reduced	no changes
Reproduction	mainly before & during spring bloom	all year round possible	all year round, reduced in winter
Main taxa	herbivorous copepods (i.e. *Calanus* spp.)	omnivorous copepods (i.e. *Oithona similis*) euphausids pteropods (i.e. *Clione limacina*)	carnivorous copepods chaetognaths pteropods (*Limacina* spp.) hyperiid amphipods

Fig. 5.4 Conceptual understanding of overwintering strategies of polar zooplankton (modified after Hagen (1999)). WE= wax esters, TAG= Triacylglycerols, DAGE= diacylglycerol ethers

The different strategies are closely related to functional traits of different zooplankton species. Strategy 1 is mainly employed by primarily herbivorous species such as *Calanus* spp. although there may be ontogenetic variation in activity during the Polar Night. Strategy 2 is more common in omnivorous species such as euphausiids and small copepod species. Strategy 3 applies to carnivorous and omnivorous zooplankton, such as predatory copepods, chaetognaths and amphipods, which can afford to maintain their normal activity although food may be less abundant and harder to come by. A lack of data on seasonal change in lipid content, feeding activity and metabolic rates for most Arctic zooplankton species complicates a clear classification into one of the three types (especially 2 and 3), though the most common zooplankton species are most likely classified as follows:

5.3.1 Overwintering strategy I: Herbivorous copepods

Calanoid copepods of the genus *Calanus* (the Arctic *C. glacialis and C. hyperboreus,* the Atlantic *C. finmarchicus* and the Pacific *C. marshallae*) are key species in Arctic and subarctic seas, dominating the mesozooplankton community in terms of biomass. All *Calanus* species are seasonal vertical migrators, overwintering at depth in a state of diapause and spend several weeks to months in spring and summer in the surface layer to reproduce, grow and develop. During periods of high food availability, *Calanus* accumulate large lipid reserves (Conover 1988) that sustain the animals during periods of low food supply and fuel reproduction in winter and early spring before any substantial algal production occurs (Sargent and Falk-Petersen 1988a). Lipids can account for >60% of *Calanus* dry weight at the start of the overwintering period when lipid content is highest (Falk-Petersen et al. 2009). Lipids are stored as 90% WE in a lipid sac (Mayzaud et al. 2016). To build up WE, *Calanus* spp. biosynthesize *de novo* long-chained fatty acids (FA) and fatty alcohols from carbohydrates, protein and FA precursors synthesized by phytoplankton (Lee 1975; Kattner and Hagen 1995). Relatively few lipids are actually depleted during overwintering (Jonasdottir 1999). Monthly measurements of lipid content of *Calanus* population in Svalbard (Fig. 5.5) show that lipid content remains relatively stable throughout the Polar Night and only decreases markedly after the winter solstice. The decline in lipid coincides with the time of ascent from overwintering depth (see below), indicating that lipid storage are primarily utilized when the organisms becomes active to fuel mating, moulting, gonad maturation and egg production at the end of the winter.

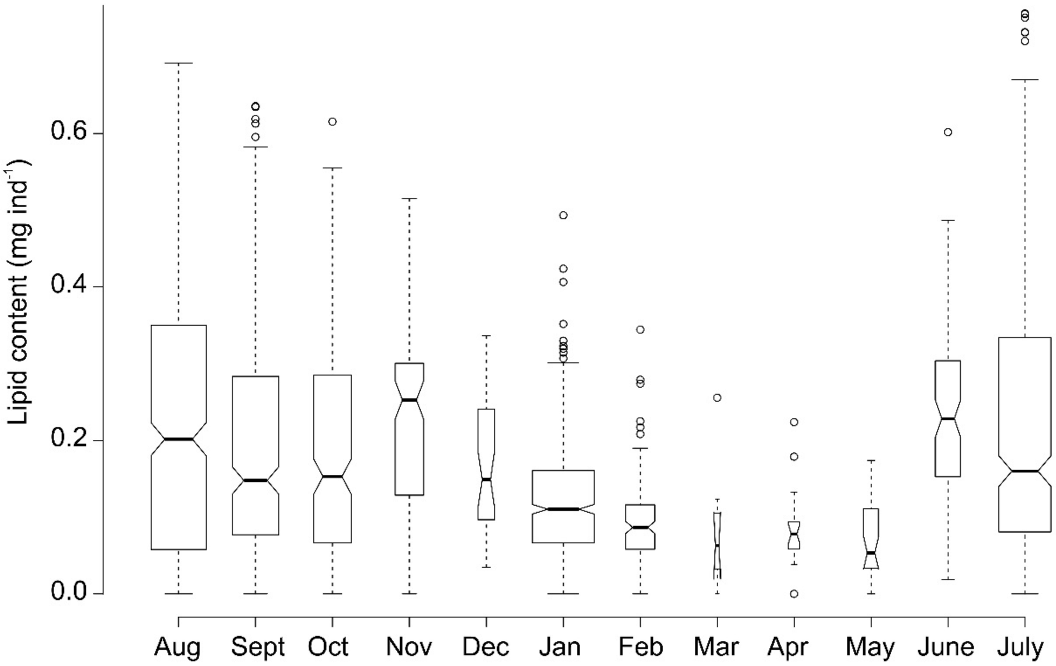


Fig. 5.5 Variability in lipid content of *C. glacialis* CV from August to May. Based on measurements of lipid sac area of copepods collected in Svalbard waters between 2012-2016 (n=2457) (Daase unpubl. data.). Horizontal line shows the median. The bottom and top of the box show the 25 and 75 percentiles, respectively. Whiskers extend 1.5 times the interquartile range of the sample. The boxes are drawn with widths proportional to the square-roots of the number of observations in the groups. Notches display the variability of the median between samples. The width of a notch is computed so that box plots whose notches do not overlap have different medians (Chambers et al. 1983)

There are discrepancies in life strategies among the *Calanus* species about energy requirements for reproduction and growth and the timing of reproductive events. These disparities reflect adaptations to differences in the timing and predictability of the spring bloom, ice cover and other factors in their main area of distribution (Falk-Petersen et al. 2009). Generally, energy demands for reproduction and length of life cycle increase with latitude and/or duration of sea ice cover. Species-specific differences are apparent in the importance of lipids for reproduction. The high-Arctic oceanic species *C. hyperboreus,* the largest of the Arctic complex of *Calanus* species, is a special case that produces lipid-rich floating eggs at depth during the Polar Night, completely independently of external food supply (cf. (Darnis et al. 2019). This winter breeding, solely fuelled by lipid reserves, allows the offspring to take full advantage of the short but intensive season of biological production to grow and develop to overwintering stages. On the other hand, the boreal *C. finmarchicus* is dependent on the spring bloom to fuel reproduction (Falk-Petersen et al. 2009). The Arctic shelf species *C. glacialis* shows high plasticity, being able to initiate maturation and egg production using lipid reserves, but taking advantage of external food supply such as ice algae and phytoplankton as soon as they become available (Daase et al. 2013).

5.3.2 Overwintering strategy II: Omnivorous euphausids and copepods

The euphausid genus *Thysanoessa* spp. can be particularly abundant in the Arctic where it is one of the preferred prey of top predators that spend the Polar Night at high latitudes (Berge et al. 2015). This includes both fish and sea birds, utilizing the abundant and bioluminescent krill as they search for prey in the dark. A year-round study of growth, population dynamics and lipid biochemistry of three common Arctic and sub-Arctic krill species (the herbivorous *Thysanoessa inermis,* omnivorous *Thysanoessa raschii* and carnivorous *T. longicaudata* and *Meganyctiphanes norvegica*) in Arctic fjords at 70°N (Falk-Petersen 1981; Falk-Petersen and Hopkins 1981; Henderson et al. 1981; Sargent and Falk-Petersen 1981) found that these euphausids tune their life history to cope with the seasonally limited food supply, using strategies similar to the *Calanus* species. *Thysanoessa inermis*, the most common krill in Arctic waters, has a prolonged life cycle, maturing and spawning for the first time at age 2, and has a life span of 3–4 years (Dalpadado and Skjoldal 1996). Spawning occurs after the onset of the spring bloom and the phytoplankton diet is rapidly converted into lipids. Similar to *Calanus*, lipid reserves can amount to >60% of the dry weight in *T. inermis* by the end of the summer (Falk-Petersen 1981; Falk-Petersen et al. 2000; Huenerlage et al. 2016). *Thysanoessa inermis* stores lipids mainly as WE that are largely used from mid-winter to spring to fuel reproduction (Falk-Petersen et al. 2000). The other krill species commonly found in Arctic and sub-arctic seas, *T. raschii* and *T. longicaudata,* and *M. norvegica,* store lipids mainly as TAGs (Huenerlage et al. 2016). Lipid reserves are likely not enough to sustain these species throughout the entire winter without additional food intake and/or cutting metabolic costs (Huenerlage et al. 2015). A temporary shift to a more benthic detritivores and carnivorous feeding during winter has been suggested for *T. raschii* based on FA composition and stomach content analyses (Berkes 1976; Sargent and Falk-Petersen 1981; Schmidt 2010), and also *T. inermis* has been observed close to the sea floor in winter in Kongsfjorden/Svalbard (Huenerlage et al. 2016).

Overwintering strategies of euphausids have been studied in more detail in Antarctic krill (*Euphausia superba*). Adaptations observed in Antarctic krill include changes in feeding preferences, lipid utilisation, reduced metabolic rates and sexual regression (e.g. (Quetin and Ross 1991; Huntley et al. 1994; Hagen et al. 2001; Nicol et al. 2004; Meyer et al. 2010). Experimental studies have also demonstrated that this species is able to shrink when food is absent (Ikeda and Dixon 1982) but this has so far not been clearly demonstrated in natural populations. However, Falk-Petersen (1985) showed that the mean carapax length decreased during winter for *T.inermis, T. raschii* and *M. norvegica* in an Arctic fjord at 70°N. Sexual regression is regarded as an adaptation to conserve energy during winter, with a subsequent redevelopment of sexual organs in the following summer. In the Arctic, sexual regression has been observed in *T. inermis* in late summer in the Barents Sea (Dalpadado and Ikeda 1989b) and in Svalbard/Kongsfjorden (Huenerlage et al. 2016), likely triggered by low food availability (Dalpadado and Ikeda 1989a). However, there is a lack of data on metabolic rates, feeding activity, size structure and sexual regression to conclude on how far strategies observed in Antarctic krill populations are employed by Arctic krill species during the Polar Night.

Small copepods *Oithona similis*, *Triconia borealis*, *Microcalanus* spp. and *Pseudocalanus* spp. together with the larger copepod *Metridia longa* dominate the Arctic zooplankton community numerically year-round (e.g. (Kosobokova et al. 1998; Thibault et al. 1999; Auel and Hagen 2002; Hopcroft et al. 2005; Hop et al. 2006; Darnis et al. 2012). All of these species accumulate lipid reserves mainly in form of WE (Båmstedt and Ervik 1984; Sargent and Falk-Petersen 1988b; Kattner et al. 2003; Lischka and Hagen 2007; Narcy et al. 2009). However, the FA composition differs from those of *Calanus* lipids, reflecting the more opportunistic feeding behaviour of these species (Kattner and Hagen 2009). Lipid stores of these copepods are insufficient to allow for overwintering without feeding (Kattner et al. 2003; Lischka et al. 2007; Lischka and Hagen 2007). By being omnivorous, these species are less constrained by the seasonal restriction in primary production and remain active year-round, feeding opportunistically throughout the winter. However, other food sources may also be limited during the low productive season, as microbial processes slow down and prey species may migrate to deeper waters and/or decrease in abundance. Prolonged generation cycles are therefore commonly observed in these species compared to more southern populations. None of these copepods go into diapause, but a weak seasonal migration from surface waters in summer to mid-depth during winter has been observed in *O. similis* and *Pseudocalanus* spp. (Lischka and Hagen 2005; Darnis and Fortier 2014). *Triconia borealis*, *Microcalanus* spp. and *M. longa* have a generally deeper distribution and remain at intermediate depths throughout the year (Hirche and Mumm 1992; Ashjian et al. 2003; Kosobokova et al. 2011; Darnis and Fortier 2014). Activity and metabolic rates may be reduced during the Polar Night. There is however a general lack of data on lipid content, metabolic rates and feeding activities from the Polar Night period for most of these species to describe their overwintering strategies accurately.

Oithona similis is an ambush feeder with an omnivorous/carnivorous/detritivorous diet (Lischka and Hagen 2007). It stores lipids in a small droplet, with wax ester as the dominant lipid class (Narcy et al. 2009). Lipid content increases in spring and lipids are mainly used to fuel reproduction in summer (Lischka and Hagen 2007; Narcy et al. 2009). Data on lipid content or feeding activity during the Polar Night are not available but active feeding on protozooplankton has been observed in late February in Disko Bay/Greenland (Zamora-Terol et al. 2013), although ingestion rates were rather low and may be insufficient to cover metabolic costs. There is also evidence that *O. similis* is reproducing in winter albeit at low rates (Lischka and Hagen 2005; Zamora-Terol et al. 2013), see below), thus lipid reserves may be utilized during the Polar Night to fuel reproduction.

Similar to *Calanus*, the complex of *Pseudocalanus* species is primarily herbivorous during the spring bloom and stores lipids in a lipid sac. In contrast to *Calanus* spp. *Pseudocalanus* spp. switch to a more opportunistic feeding mode for the rest of the year (Lischka and Hagen 2007) and do not go into diapause but remain active in the surface layers during the Polar Night. Lipid reserves need to be complemented by food supplied by the spring bloom to fuel gonad maturation and reproduction (Lischka and Hagen 2007).

The bioluminescent copepod *Metridia longa* also feeds opportunistically and remains active during the Polar Night (Hopkins et al. 1984) (Båmstedt and Tande 1988, Chapter 3). It also stores lipids mainly as WE (Falk-Petersen et al. 1987; Albers et al. 1996). Falk-Petersen et al. (1987) observed a decrease in the proportion of WE and a change in the FA composition in *M. longa* during winter in the sub-Arctic indicating either a selective retention of specific FA or active feeding. In Svalbard, lipid content in *M. longa* females was found to be lower than that of *Calanus* in January (Fig. 5.6), supporting the notion that *M. longa* needs to actively feed during the Polar Night.

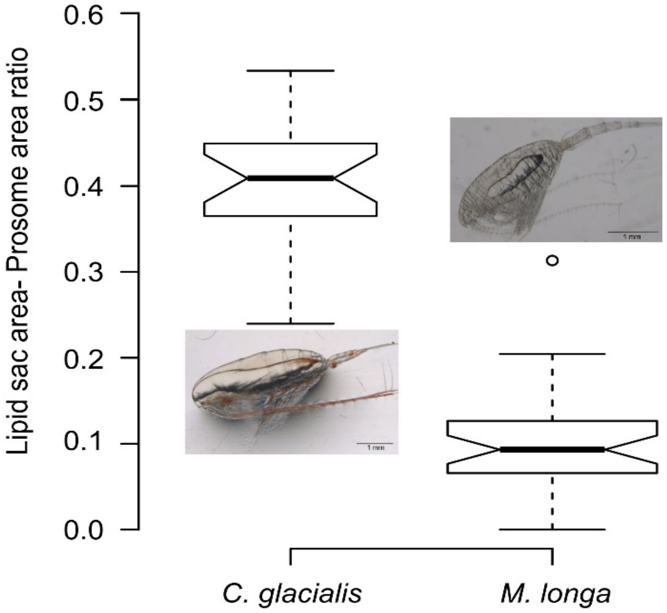


Fig. 5.6 Boxplot of lipid sac area-prosome area ratio of adult females of *C. glacialis* and *M. longa* from Kongsfjorden in January 2017. (Daase, unpubl. data)

5.3.3 Overwintering Type III: omnivores and carnivores

Pteropods: Among non-copepods, a number of taxa play important roles in Arctic zooplankton communities. The thecosomatous pteropod *Limacina helicina* can be found throughout the Arctic and in sub-Arctic waters, where its distribution overlaps with the temperate species *Limacina retroversa*. Little is known of the Polar Night ecology of pteropods. Lipids account for <20% of the dry weight of thecosomatous pteropod *Limacina helicina* (Percy and Fife 1981; Gannefors et al. 2005), consisting mainly of phospholipids. Gannefors et al. (2005) found high variability in the contribution of storage lipids (TAGs) between season and age. Lowest TAG proportion (<2%) were found in females in autumn after spawning, indicating that lipid stores play no role sustaining the species during the Polar Night, and that *L. helicina* employs a "business as usual" overwintering strategy. *Limacina helicina* is an important grazer of the microbial community, producing a mucous web to prey on a varied diet ranging from phytoplankton to degraded organic material (Gilmer and Harbison 1991; Falk-Petersen et al. 2001; Gannefors et al. 2005). They are therefore likely to find food even during the Polar Night. In Svalbard waters, *Limacina* spp. has been observed in low abundance during the Polar Night (Fig. 5.7) and veligers and juveniles seem to dominate the winter population (Gannefors et al. 2005). However, their generally highly patchy distribution and occurrence lead to notoriously unreliable abundance estimates that, in turn, can result in biased seasonal comparison.

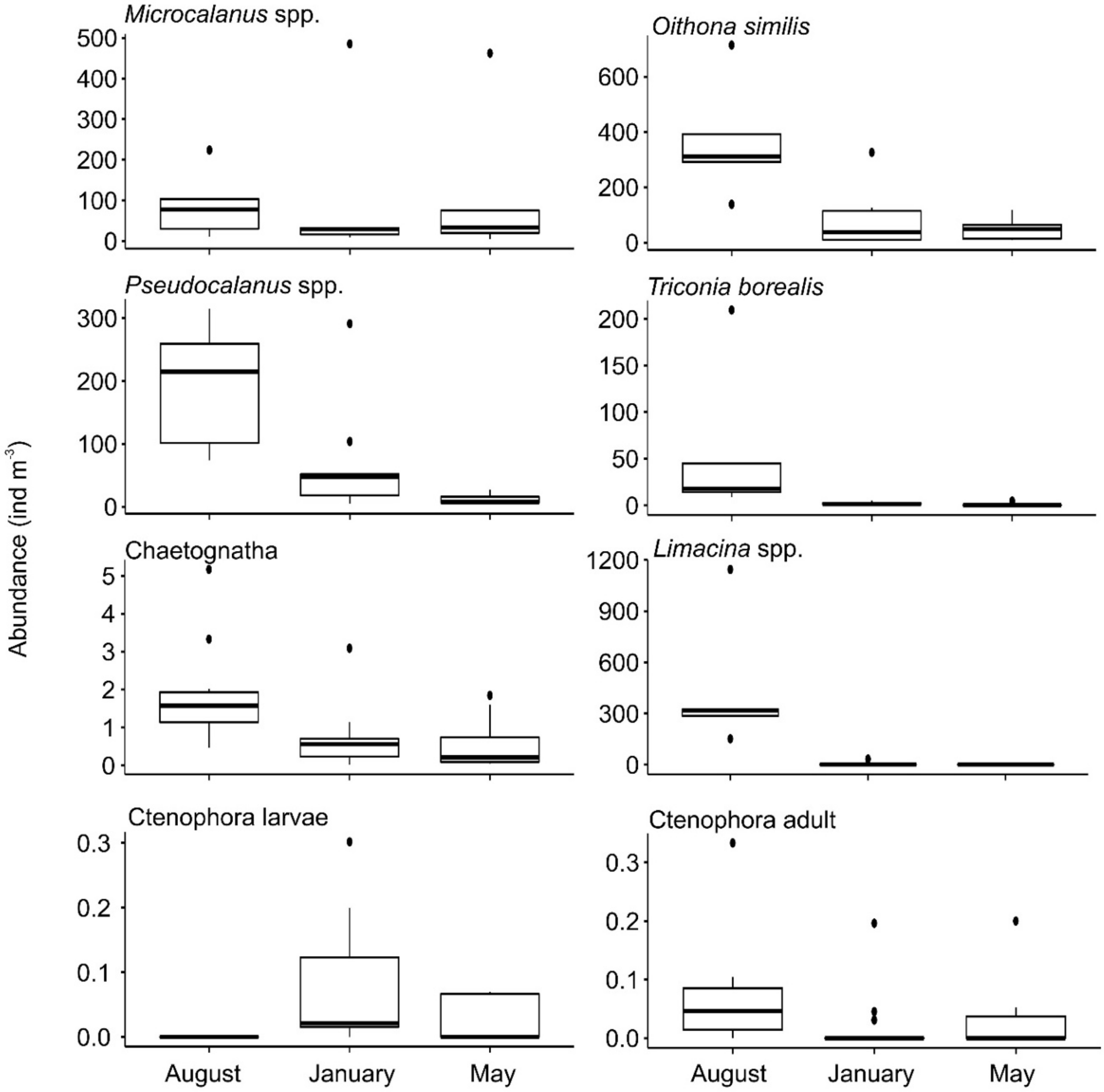


Fig. 5.7 Boxplot of abundance (ind m^3) of selected common zooplankton species from Svalbard based on samples collected with a Hydrobios Multinet (180-200 µm mesh size, opening 0.25 m^2) in August 2016, January 2016 & 2017 and May 2016 in Billefjorden, Isfjorden, Kongsfjorden, Smeereneburgfjorden and Rijpfjorden. Chaetognaths: sum of *Eukrohnia hamata* and *Parasagitta elegans*; Ctenophora adults: *Mertensia ovum* and *Beröe cucumis.* Horizontal line shows the median. The bottom and top of the box show the 25 and 75 percentiles, respectively. Values outside this range are marked by dots

The gymnosomatous pteropod *Clione limacina* is argued to be monophagous, only preying on *Limacina* spp. (Conover and Lalli 1972; Falk-Petersen et al. 2001; Boer et al. 2005), and employs a different overwintering strategy than *Limacina helicina*. *Clione limacina* is able to biosynthesize storage lipids *de novo* and accumulates high amounts of lipids over the summer accounting for 50% of their dry mass (Boer et al. 2007). Lipid composition is dominated by TAGs (53%) and 1-O-alkyldiacylglycerol ethers (DAGE, 22%), another long-term energy storage (Kattner et al. 1998; Boer et al. 2007)). While lipids are depleted over summer to fuel reproduction, they are replenished by autumn (Boer et al. 2007), indicating that lipids play a more important role in surviving periods of food scarcity for *C. limacina* than for *L. helicina*. Given its supposed monophagous feeding mode, *C. limacina* may be confronted with long periods of starvation, since their prey (*Limacina* spp.) often occurs in pulses (either forming dense patches or being almost absent) and is therefore a rather unreliable food source necessitating energy stores, not only during the Polar Night.

Hyperiid amphipods: The Arctic hyperiid amphipod *Themisto libellula* and the subarctic-boreal *T. abyssorum* are abundant in all Arctic shelf seas and have been recorded in the central Arctic Ocean (Dalpadado et al. 1994; Koszteyn et al. 1995; Dalpadado et al. 2001; Auel and Werner 2003). Both species are epipelagic, although the latter has a deeper distribution than the former (Dalpadado et al. 2001), and both are visual and opportunistic predators. Over the summer, *T. libellula* accumulates lipids derived from its preferred diet of *Calanus* spp. (Scott et al. 1999; Dale et al. 2006). Lipids can account for up to 23% of its dry mass during the Polar Night (Kraft et al. 2015) consisting of 60-76% WE, compared to 50% WE during summer when lipid content only accounts for 8% of the dry mass. The boreal congener species *T. abyssorum* has a lower lipid content (8-13% of dry mass) with TAGs as the dominant lipid class (60% in winter, 40% in summer). Differences in diet and life history between species may account for the differences in lipid composition. *Themisto abyssorum* has a more diverse diet including omnivorous prey such as appendicularians (Dalpadado et al. 2008) and reproduces during or after the spring bloom (May to July), while reproduction of *T. libellula* occurs between February and May (Koszteyn et al. 1995; Dalpadado 2002) (Weslawski et al. 2006; Kraft et al. 2012). No differences in lipid content between winter and summer have been observed in the deep water species *Cyclocaris guilemi* (25%- 27% in summer and winter) but the WE content decreases in winter, indictaing year round feeding but a change in diet during winter (Kraft et al. 2015). Despite being visual predators, both *Themisto* species have been found to actively feed on Arctic *Calanus* species during the Polar Night (Kraft et al. 2013; Kraft et al. 2015). How these visual predators are able to feed in darkness is not yet fully understood (see also Chapter 3).

Chaetognaths: Chaetognaths comprise about 7-18% of zooplankton biomass (dry weight) in the Arctic (Kosobokova et al. 1998; Kosobokova and Hirche 2000; Hopcroft et al. 2005). Three species occur in Arctic waters: *Parasagitta elegans,* commonly found in Arctic Shelf seas (Dunbar 1962; Welch et al. 1996), and *Eukrohnia hamata* and *Pseudosagitta maxima* (Hopcroft et al. 2005), inhabiting meso- and bathypelagic depths in the oceanic realms of the Arctic (Kosobokova et al. 2011). They are pelagic predators feeding year-round, often on calanoid and cyclopoid copepods (Falkenhaug 1991; Terazaki 2004; Fulmer and Bollens 2005; Grigor et al. 2015).

Storage lipids (WE, TAGs) have been observed in high-latitude chaetognaths (e.g. (Lee 1975; Falk-Petersen et al. 1987; Kruse et al. 2010)). Chaetognaths are assumed to employ a "business as usual" strategy (Hagen 1999) feeding opportunistic on a varied diet (Terazaki 2004). They are non-visual predators and, thus, should be able to find food during the Polar Night and hunt successfully in darkness, particularly in deep layers where diapausing copepods may be found in high densities (Darnis and Fortier 2012). Indications for seasonal vertical migration suggest that they follow their *Calanus* prey to overwintering depth (Grigor et al. 2014). Grigor et al. (2014; 2015) observed lower growth and feeding rates in *Parasagitta elegans* in winter compared to summer in Svalbard waters, suggesting that some metabolic adaptation enable this species to cope with the Arctic winter. The population is dominated by larger individuals (adults) during the Polar Night (Fig. 5.3) and only few offspring have been observed (Grigor et al. 2014).

Ctenophores: The ctenophore *Mertensia ovum* are occasionally found in high numbers in Arctic waters, accounting for up to 60-95% of the total gelatinous calories (Percy and Fife 1985) or up to 70% of the abundance (Hop et al. 2002). *Mertensia ovum* is an opportunistic feeder preying mainly on the large *Calanus* copepods (Falk-Petersen et al. 2002; Majaneva et al. 2013). Lipids (~50% WE) can account for 10% of the dry weight (Larson and Harbison 1989; Falk-Petersen et al. 2002; Graeve et al. 2008). Highest lipid content has been observed in autumn (Lundberg et al. 2006; Graeve et al. 2008), but no data on lipid content and feeding rates are available for the winter. Lundberg et al. (2006) and Graeve et al. (2008) suggested that lipids are mainly used to fuel growth and reproduction in spring and summer rather than providing energy storage during winter. The population of *M. ovum* is mainly controlled by another Arctic ctenophore species, *Beröe cucumis* (Swanberg 1974) but no data on Polar Night strategies of this species are available. It is unknown if ctenophores are feeding during winter, although they should be able to find food despite low light since they are tactile predators. While they can often occur in high abundance during summer and autumn, clogging zooplankton nets, they appear to be less abundant in net samples during the Polar Night (Daase, pers. observations). Quantitative abundance data based on mesozooplankton net hauls, although biased, show lower abundance of adult individuals in January. Nevertheless, the presence of juvenile stages indicates that reproduction occurs also during the Polar Night (Fig. 5.7). Large individuals of *B. cucumis* have been regularly observed in shallow areas such as in kelp forest by means of SCUBA diving in January from 2010-18 (see picture in Chapter 11). Both *B. cucumis* and *M. ovum* are bioluminescent and are common ctenophores in the upper 20 m during Polar Night (Johnsen et al. 2014; Cronin et al. 2016).

5.4 Seasonal vertical migration

By definition, zooplankton are not capable of actively migrating horizontally and, thus, cannot leave unproductive regions or seasons for greener pastures elsewhere. Vertical migration is their only way to escape unfavourable conditions in some water layers at certain times of the day or year. In order to occupy the most preferential depth in each season, zooplankton change their vertical positioning through seasonal vertical migration (SVM). In the Arctic, it is primarily herbivorous zooplankton that display this behaviour, in particular *Calanus* spp. The most common SVM patterns include a downward migration to greater depth at the end of the productive season during late summer/ early autumn and an ascent from overwintering depth to the productive surface layers at the end of winter in time to utilize the spring bloom for reproduction, growth and development. By spending the winter at depth organisms reduce predation risk and minimising the risk of being advected out of an area as currents speed are often lower at depth. However, different seasonal vertical migration patterns have also been observed. For example *Microcalanus* spp. and *M. longa* have been observed higher up in the water column during winter compared to summer in Greenland waters (Ussing 1938; Digby 1954), although now SVM has been observed in these species in the Candian Arctic(Darnis and Fortier 2014). SVM is often also an ontogenetical vertical migration, i.e. the migration is conducted by different developmental stages. While young developmental stages grow and develop in surface waters, older stages migrate to overwintering depth.

Overwintering depth is largely dependent on the bathymetry but not only, and varies from several hundred meters on the shelf to over 2000 m in the oceanic basins (Hirche 1997). For the Polar Night, data on overwintering depth is limited to a few observations. In the Greenland Sea, *Calanus hyperboreus* concentrates below 1000 m and down to 3000 m (Hirche 1997). In the polar basin, year round observations on the vertical distribution of *Calanus* are only available from a few studies conducted on drift ice stations in the 1950s-1970s. Dawson (1978) concluded that *C. hyperboreus* was centred in the upper 900 m throughout the year, with older copepodite stages centred between 300-600 m and females in the upper 400 m during the Polar Night. In the deep central Arctic, Geinrikh et al. (1983) found *C. hyperboreus* females at similar depth during the period October-February, and overwintering stages CIII-CV between 500-1200 m. Ashjian et al. (2003) also observed that *Calanus* spp. overwintering stages were distributed at mid-depth of the water column in the Canada Basin. In Arctic Shelf seas overwintering depth is naturally confined by the bottom depth (< 500 m) and shelf populations of *C. hyperboreus* as well as the Arctic shelf species *C. glacialis* are found to concentrate in bottom-near water layers during the Polar Night (Geinrikh et al. 1983; Daase et al. 2013; Darnis and Fortier 2014).

Since lipids are less dense than seawater (Kögeler et al. 1987) and lipid content is highest in *Calanus* at the start of the overwintering period, *Calanus* are positively buoyant when they descend to depth. To remain motionless and thereby save energy and reduce predation risk, diapausing *Calanus* have to become neutrally buoyant at depth (Jonasdottir 1999). How neutral buoyancy is achieved and maintained throughout the winter is still not well understood, but lipids must play an important role (Jonasdottir 1999; Visser and Jónasdottir 1999; Pond and Tarling 2011; Clark et al. 2012; Pond 2012). For example, Pond and Tarling (2011) found that lipids with a high degree of unsaturation undergo a lipid phase transition below 500 m, thereby altering the lipid density, which may help to achieve neutral buoyancy at depth (Pond 2012). Since shelf populations of *Calanus* are overwintering at locations shallower than the 500 m depth beyond which lipid phase transition takes place, other mechanisms to regulate buoyancy have been suggested, such as ion replacement (Campbell and Dower 2003; Sartoris et al. 2010). By replacing heavier ions in the hemolymph with lighter ones, such as ammonium, an organsim can remain iso-osmotic with seawater while being able to selectively regulate its density up or down. Sartoris et al. (2010) and Schründer et al. (2013) found higher concentration of ammonium in diapausing copepods compared to non-diapausing species in Antarctica, suggesting that diapausing copepods achieve neutral buoyancy during overwintering by replacing high density ions with ammonium (NH_4^+). No seasonal trends in ammonium concentration could be observed in *C. glacialis* from Billefjorden, Svalbard (Freese et al. 2015). However, the lithium ion (Li+) concentration of *C. glacialis* increased towards the end of the overwintering period suggesting that the accumulation of lithium reduced the density of the organism and promoting the upward migration. Since the active uptake of lithium is energy-demanding, such changes in lithium concentrations are unlikely to be random, indicating instead a biological function. Freese et al. (2015) also observed a seasonal pattern in pH, with lowest values (i.e. highest acidity) in winter, and highest values in summer, arguing that low pH may be related to low metabolic activity during diapause.

The triggers of descent and ascent to and from overwintering depths are still not fully understood. External environmental cues such as changes in photoperiod, food availability and temperature as well as internal cues such lipid threshold value and changes in lipid composition have been proposed to trigger the descent and ascent (Hirche 1996; Pond and Tarling 2011; Baumgartner and Tarrant 2017; Häfker et al. 2018). The timing of decent and ascent is highly variable across the Arctic and often not well documented due to the lack of high temporal sampling resolution. In areas where surface waters warm up substantially in summer, the downward migration of *C. glacialis* can occur as early as June as a response to high surface temperatures (Kosobokova 1999; Niehoff and Hirche 2005). Data from late summer show that the *Calanus* populations in Svalbard migrate down as early as July with the bulk of the population being at depth by the end of August (Daase et al. 2013; Bandara et al. 2016) (Fig. 5.8). Similar observations have been made in Greenland (Madsen et al. 2001). In the Amundsen Gulf (Canadian Arctic), *C. glacialis* appears to descend later in autumn with part of the population still found in surface layers in October (Daase et al. 2013) (Fig. 5.9). This delayed descent in the Canadian Arctic can be explained by a prolonged growing season at somewhat lower latitude in a region where autumn blooms are common.

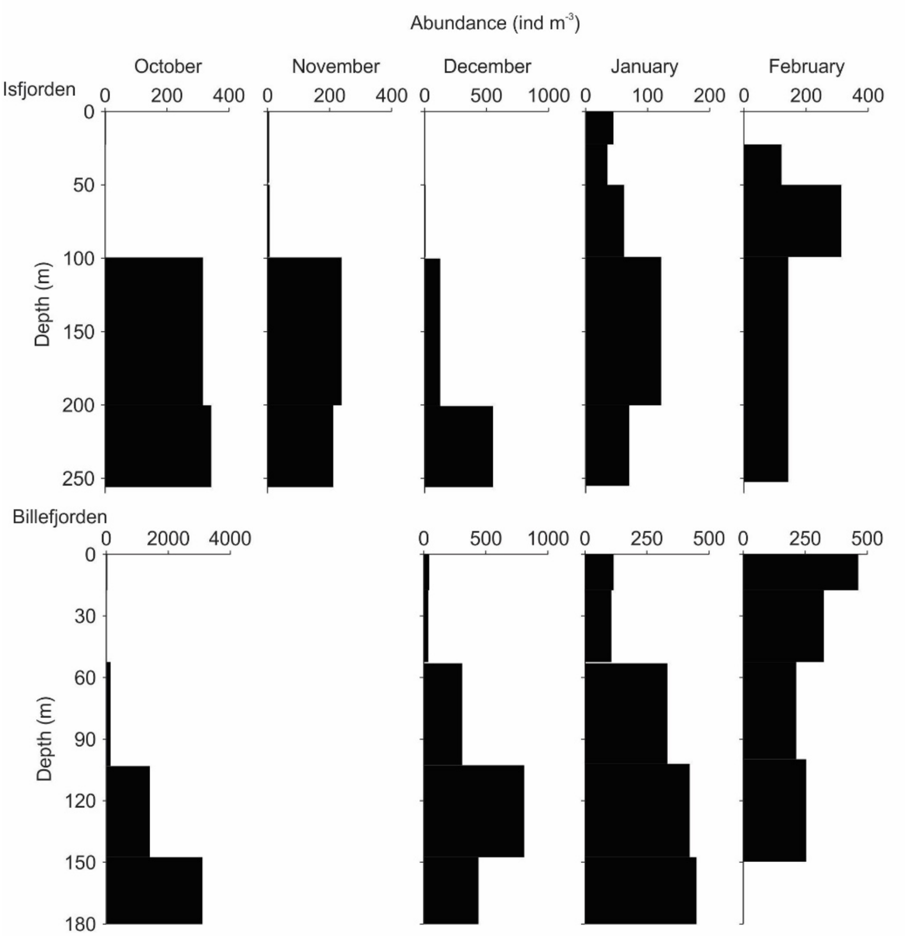


Fig. 5.8 Vertical distribution of *C. glacialis* during the Polar Night in Isfjorden (2015-2016) and Billefjorden (2012-2013), Svalbard (Søreide et al. unpubl.)

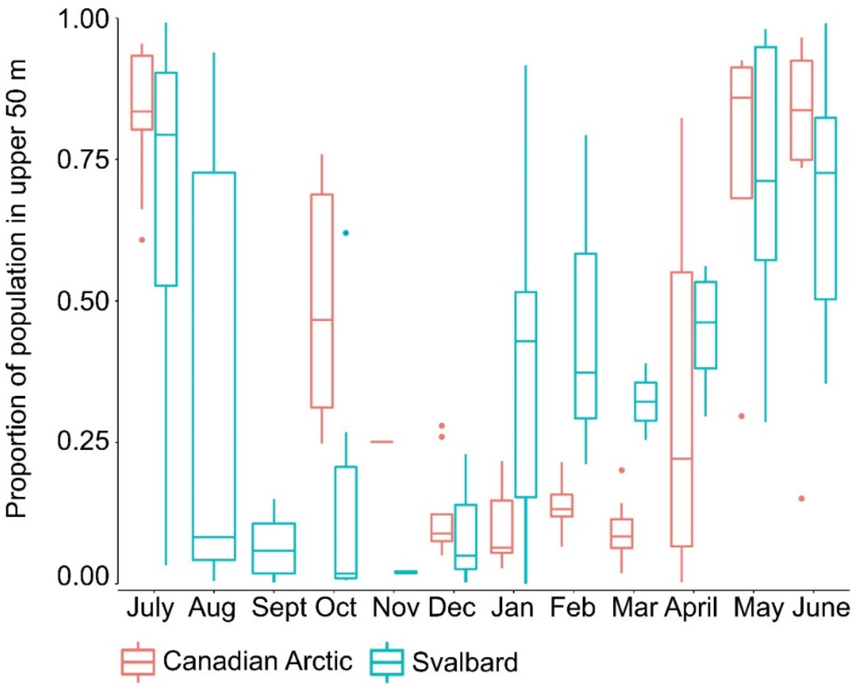


Fig. 5.9 Boxplot showing proportion of *C. glacialis* population found in upper 50 m of the water column in each month of the year in the Canadian Arctic (Franklin Bay 2003-2004, Amundsen Gulf 2007-2008) and in Svalbard waters (pooled data from Billefjorden, Kongsfjorden, Isfjorden, Rijpfjorden and North of Svalbard 2012-2017). No data available for August and September in Canada, few data points for November in both regions. Horizontal line shows the median. The bottom and top of the box show the 25 and 75 percentiles, respectively. Values outside this range are marked by dots (Søreide unublished).

Calanus are found in surface waters in spring feeding prior to the spring bloom (Madsen et al. 2001; Søreide et al. 2010). The traditional understanding is that the ascent from overwintering depth occurs at the end of winter just prior to the spring bloom (Digby 1954; Conover 1988). However, one reoccurring observation throughout the Polar Night campaigns in Svalbard waters in recent years has been that *Calanus* populations are already distributed throughout the water column in early January (Figs. 5.4 and 5.6), long before the light returns and the onset of the spring bloom. These observations have been made in different fjords as well as in the oceanic waters north of Svalbard (Daase et al. 2014; Berge et al. 2015; Błachowiak-Samołyk et al. 2015; Grenvald et al. 2016) for both *C. glacialis* (Fig. 5.8) and *C. finmarchicus* (Fig. 5.10). They are, however, not consistent with observations from other regions in the Arctic. In the Arctic Ocean, *C. hyperboreus* females were found in surface layers in December and January, while other stages were first observed in surface layers in summer (Dawson 1978; Geinrikh et al. 1983). Similar observations were made in the western Arctic Ocean for *C. glacialis* and *C. hyperboreus* (Ashjian et al. 2003). In Disko Bay (Greenland), *Calanus* spp. appeared in the surface layers first in April (Digby 1954; Madsen et al. 2001). In Franklin Bay and Amundsen Gulf (Canadian Arctic), *C. glacialis* were concentrated at depth in January and higher abundances in surface layers were first observed in April (Daase et al. 2013). Comparing seasonal changes in the proportion of the *C. glacialis* population found in the upper 50 m between the Canadian Arctic with observations from Svalbard shows that the period when the majority of the population is below 50 m is similar in both regions (~4 months) but it is offset by 2 months (Fig. 5.9). In Svalbard, the majority of the population has left the surface waters in September and emerges in January, while in the Amundsen Gulf region a high proportion is still in surface layers in October and November and emerges first in April. Thus, the observation in Svalbard waters of *Calanus* ascending and becoming active much earlier than previously assumed seems to be the exception rather than the rule on a pan-arctic scale.

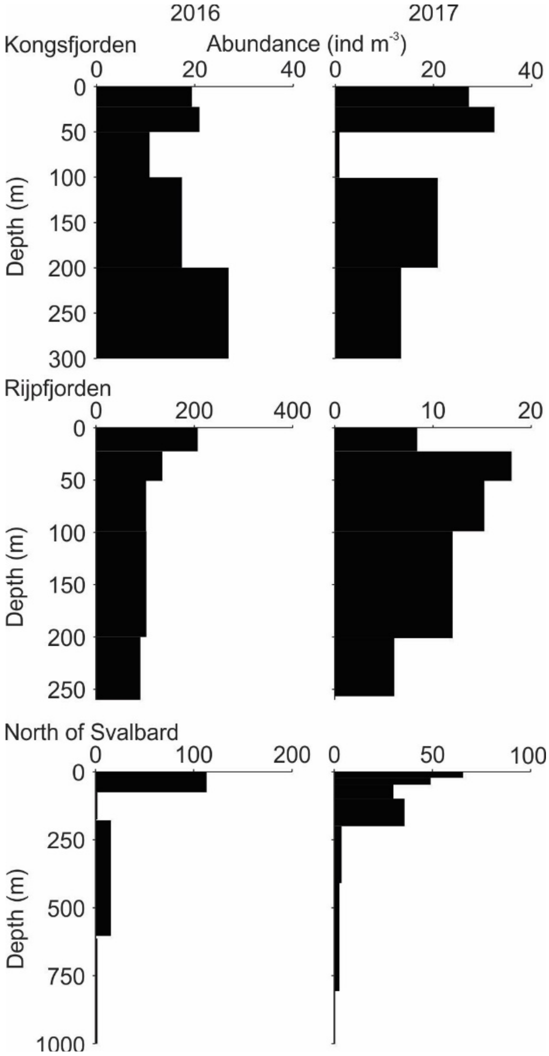


Fig. 5.10 Vertical distribution of *C. finmarchicus* in January in Kongsfjorden, Rijpfjorden and off-shelf north of Svalbard in January 2016 and 2017 (Daase, unpubl. data). Note difference in scale on the x-axis.

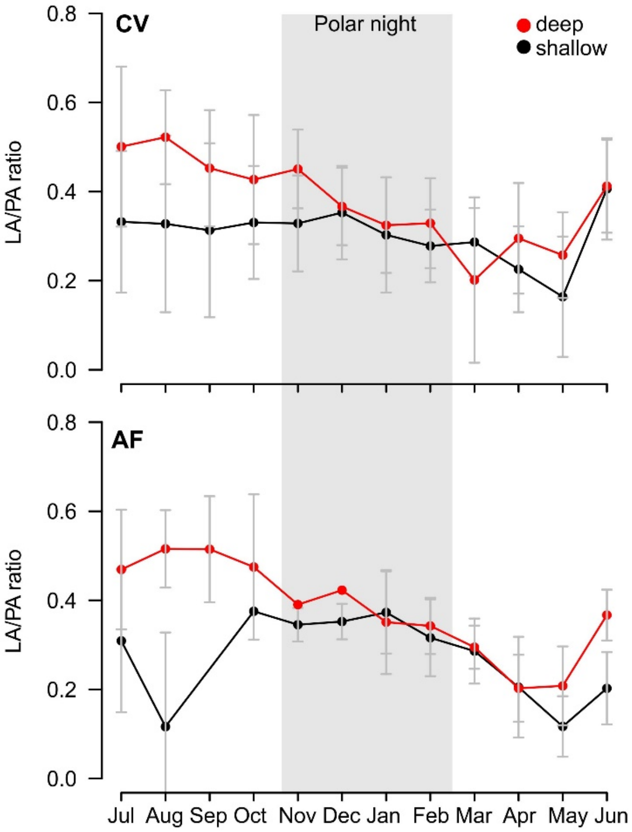


Fig. 5.11 Seasonal variability in lipid sac area to prosome area ratio (LA/PA ratio) of *C. glacialis* CV and adult females in surface waters (upper 50 m) and deeper water layers (>100 m). Based on measurements of lipid sac area and prosome area of *C. glacialis* collected in Svalbard waters between 2012-2016 (n= 1475 (AF); 2457 (CV)). Means calculated for each month; error bars show standard deviation

We can only speculate on possible reasons for the mid-winter ascent in Svalbard waters. No difference in lipid content between individuals in the surface and those at depth in January has been observed, indicating that the ascent is not triggered by critical lipid reserves limits (Fig. 5.11). Ascending early may be a fitness-increasing strategy in a highly variable environment where the onset of spring bloom is difficult to predict due to high interannual variability in the timing of ice breakup. By ascending early, reproductive events fuelled with internal energy stores can be initiated so that, by the time food becomes available, the bloom can be fully utilized. Furthermore, *Calanus* may be able to feed on heterotrophic food sources such as protists (ciliates, dinolagellates, flagellates) (Levinsen et al. 2000) but also copepod eggs and juveniles chateognaths that are available during the Polar Night (Cleary et al. 2017). A model study indicates that if low levels of food are consistently provided through the Polar Night, there is no difference in fitness of individuals ascending early or late in spring (Hobbs 2016), indicating that this behaviour is energetically sustainable as long as alternative food sources are utilized. On the other hand, *Calanus* suffers high winter mortality (see below) indicating that an early ascent may come with high energetic costs straining energy reserves to their limits.

Furthering our understanding of the timing of ascent and end of diapause should provide valuable knowledge of *Calanus* life cycles and energy demands during winter, but also on the role of overwintering populations for the export of carbon into the Arctic during winter, and the overall role of *Calanus* for the carbon sequestration at depth.

The largest inflow of boreal zooplankton into the Arctic occurs through the Fram Strait, and *C. finmarch*icus is a major contributor to the biomass advected from the Atlantic into the Arctic. Advection of *Calanus* during the Polar Night has been regarded as negligible since long-range SVM removes the population from the core area of the Atlantic inflow. However, recent observations of *C. finmarchicus* in surface layers west and north of Svalbard (Fig. 5.10), already in January, reduces the time the species resides at depth by two months. This increases estimations of the amount of *C. finmarchicus* that is advected into the Arctic annually by 25-33% (Basedow et al. 2018).

Seasonally migrating copepods actively transport stored lipids to overwintering depth where a significant fraction of these lipids is respired during winter, thus promoting carbon sequestration at depth (Darnis and Fortier 2012; Jónasdóttir et al. 2015; Visser et al. 2017). Estimates of the amount of carbon that is sequestered by *Calanus* during overwintering are sensitive to diapause duration and reducing the time that *Calanus* spend at depth will affect those estimates significantly (Jónasdóttir et al. 2019). Thus, a thorough understanding of *Calanus* overwintering strategies is essential to correctly estimate carbon transport and sequestration.

5.5 Reproduction during the Polar Night

Despite low food availability, several Arctic zooplankton species have been found to reproduce during the Polar Night. Copepod nauplii were abundant in samples taken with a mesh size of 50 and 60 µm in Kongsfjorden in January (Grenvald et al. 2016). Nauplii were primarily those of cyclopoid copepods, most likely *Oithona similis* that dominated numerically the community at that time of the year. Calanoid nauplii could also be identified, likely belonging to *Microcalanus* spp. (Fig. 5.12). During one of the overwintering expeditions in the Canadian Beaufort Sea, eggs sacs detached from females copepods and nauplii of *Oithona* and *Oncaeidae* were also observed in significant number in January, indicating that these small detritivorous copepods reproduce during the Polar Night (Darnis et al. 2012). Lischka and Hagen (2005) previously suggested year-round reproduction in *O. similis* in Kongsfjorden. (Ashjian et al. 2003) observed year-round presence of nauplii of *O. similis*, *Microcalanus* and *M. longa* during the SHEBA drift in the western Arctic. Digby (1954) and Ussing (1938) observed nauplii of *O. similis* and *Microcalanus* year round in Scoresby Sound, Greenland, with peak abundance in January. All these observations strongly suggest that these species are reproducing during the Polar Night. While Digby (1954) also observed nauplii of *Pseudocalanus* spp. year round in Scoresby Sound, only low numbers were recorded from December to March and Digby (1954) was doubtful that *Pseudocalanus* nauplii observed during the Polar Night would develop and survive.

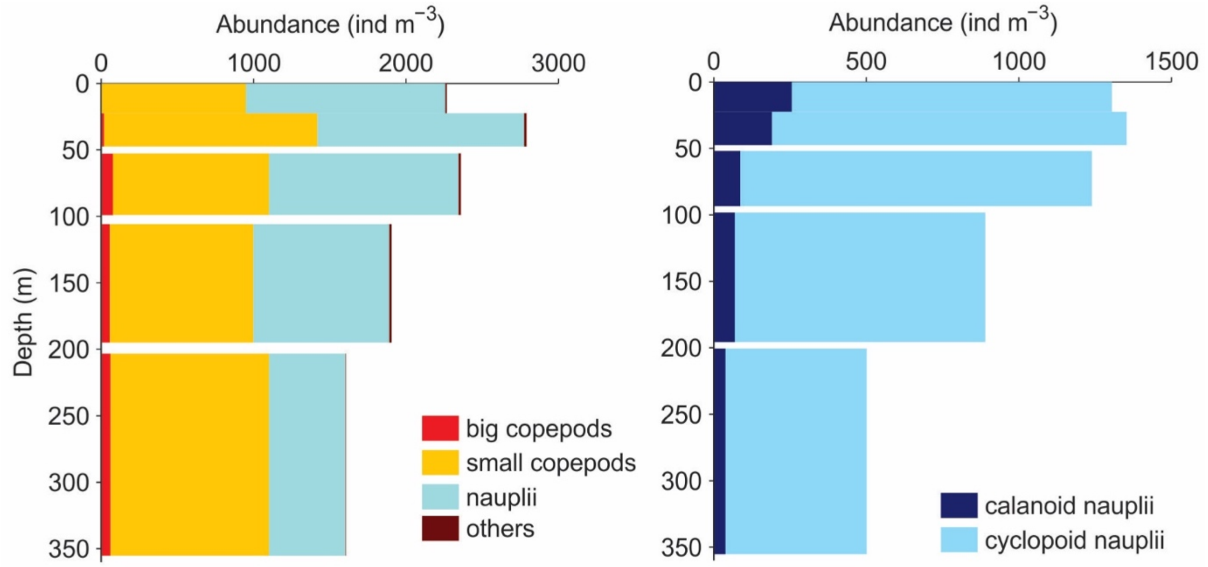


Fig. 5.12 Mesozooplankton community composition in Kongsfjorden in January 2015. Zooplankton collected using a WP2 net with 50-µm mesh size (0.25 m^2 opening area)

Calanus hyperboreus produces eggs during the Polar Night (November-March) (Hirche and Niehoff 1996; Darnis et al. 2012; Darnis et al. 2019) and its reproduction is completely decoupled from the spring bloom and entirely fuelled by internal energy stores. This stands in sharp contrast with the reproductive strategies of *C. finmarchicus*, largely reliant on the spring bloom to fuel reproduction, and *C. glacialis*, which can produce eggs using stored lipids but usually times reproduction to occur closely to the onset of the spring bloom. The Polar Night is however not completely deprived of reproductive events for *C. glacialis*. Males of *C. glacialis* are abundant during the Polar Night in Svalbard fjords, together with females bearing spermatophores, indicating that adults of *C. glacialis* stay active and demonstrate active mating behaviour in mid-winter (Daase et al. 2018).

Reproduction during the Polar Night has also been observed among non-copepods. In Svalbard, juvenile stages of ctenophores (*Mertensia ovum*) and pteropods (*Clione limacina*, *Limacina* spp.), as well as meroplanktonic larvae (Nudibranchia, Bivalvia, Polychaeta, Bryozoa) have been observed in January (Berge et al. 2015). Throughout the year, meroplankton can dominate Arctic zooplankton communities in terms of numbers during periods of mass occurrence. The majority of benthic larvae are either released in time with the spring bloom, or later in the summer if food provided by the spring bloom is needed to first fuel maturation and reproduction in the benthos. The highest abundances of meroplankton are therefore commonly observed in spring and summer, while they are largely absent from the water column for the rest of the year. Seasonal studies on meroplankton occurrence in Svalbard fjords have shown that only pelagic larvae of bryozoans and gastropods are present during the Polar Night (November- February) (Stübner et al. 2016), indicating that these groups are able to reproduce in the absence of pelagic primary production (see Chapter 4).

Given the low food supply during the Polar Night and the fact that the spring bloom may be months away, what are the advantages of reproducing during the Polar Night? While food may be abundant in summer, the predation pressure on eggs and nauplii by other zooplankton species is also significantly higher at that time (Darnis et al. 2019). Digby (1954) and Ussing (1938) suggested high grazing pressure on eggs and nauplii of *O. similis* by *Calanus* during summer, a predation severely reduced during the Polar Night when *Calanus* reside at overwintering depth and there is a general decrease in abundance of other predators. Being able to reproduce year-round may increase the overall reproductive success of a population provided that the new generation can survive on limited food abundance.

Reproduction during the Polar Night may also work as niche separation. While some species migrate to overwintering depth, the normally deep-dwelling copepod *Microcalanus* has been observed to ascend to surface waters, thus taking advantage of decreased competition and predation pressure during the dark months.

Evidence of reproduction (presence of eggs and nauplii) during the Polar Night has been mainly found for omnivorous species with relatively short life cycles (1 year) and small lipid reserves, suggesting that production is sustained by feeding opportunistically throughout winter and that life history strategies are tuned to support fast turn-over rates and not on building up large lipid reserves. The exception to this is *C. hyperboreus*. This large copepod exhibits a multi-year life cycle in response to living in permanently ice-covered waters where the spring bloom may be late and short. The adaptive strategy is to devote more time to growth that allows the accumulation of large lipid reserves on which food-independent reproduction relies, with the production of lipid-rich eggs and nauplii able to survive the first weeks and months without food (Halvorsen 2015). By the time food becomes available, the offspring will have progressed through the first developmental non-feeding stages and, thus, there will be no delay between the onset of the bloom and the ability of the offspring to utilize it. Large copepod specimens indicate that they need several years to fulfil a life cycle, such as *C. hyperboreus.*

5.6 Seasonal changes in abundance & winter mortality

In Arctic waters, zooplankton abundance and biomass generally peak in late summer and autumn, while lowest values are observed in spring (Fig. 5.7), giving the impression that abundance and biomass decrease sharply during the Polar Night. However, data with high temporal resolution, including samples taken during the Polar Night, show that abundance does not decline evenly through the winter. Digby (1954) observed little change in biomass during late autumn and winter after an initial sharp decrease in biomass in early autumn in Scoresby Sound, and the biomass declined steeply again in early spring. Seasonal data on the abundance in *C. glacialis* from Svalbard also show a decrease in abundance during the Polar Night with a major decline often observed at the end of the Polar Night and abundance minima at the start of the spring bloom (Fig. 5.13). Drastic decreases in population size of Arctic and boreal *Calanus* species from autumn to spring have repeatably been reported across the Arctic (Conover and Siferd 1993; Madsen et al. 2001; Arnkværn et al. 2005; Leu et al. 2011; Daase et al. 2013). Thus, despite the above described adaptations to deal with the seasonal resource limitations, winter mortality may be high, particularly during the latter part of the Polar Night. This view is supported by the high proportion of copepod carcasses (whole organisms) found throughout the water column during the Polar Night (Daase et al. 2014). A seasonal comparison showed that the proportion and abundance of *Calanus* carcasses is indeed higher during the Polar Night compared to spring and summer (Fig. 5.14), indicating that winter mortality is not due to predation alone.

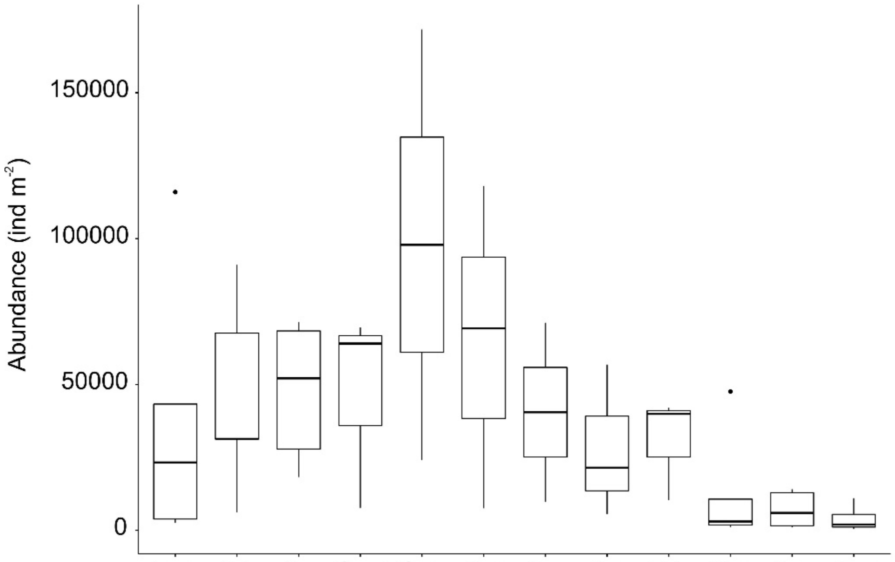


Fig. 5.13 Boxplot of *C. glacialis* abundance (ind m^{-2}) in different months. Based on data (Daase, unpublished) sampled with a Hydrobios Multinet (180-200 µm mesh size, opening 0.25 m^2) in Billefjorden (monthly, 2008-2009, 2012-2013; 180-0m), Rijpfjorden (Mar-Oct 2007; 260-0 m) and Isfjorden (monthly, 2015-2016; 260-0 m). Horizontal line shows the median. The bottom and top of the box show the 25 and 75 percentiles, respectively. Values outside this range are marked by dots

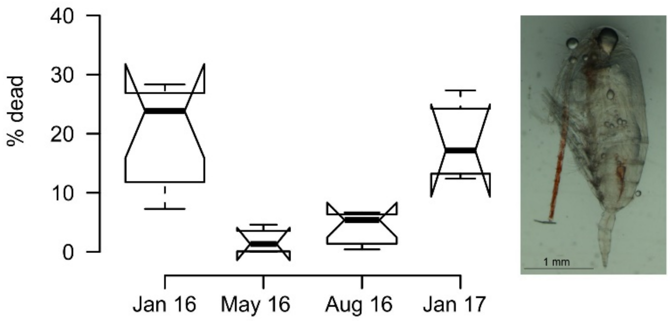


Fig. 5.14 Contribution of *Calanus* carcasses (% dead) to total *Calanus* population in Svalbard waters in January, May and August 2016, and January 2017. Pictures shows a *Calanus* carcass. (Daase unpubl. data). Horizontal line shows the median. The bottom and top of the box show the 25 and 75 percentiles, respectively. Whiskers extend 1.5 times the interquartile range of the sample. The boxes are drawn with widths proportional to the square-roots of the number of observations in the groups. Notches display the variability of the median between samples. The width of a notch is computed so that box plots whose notches do not overlap have different medians (Chambers et al. 1983)

What causes this non-consumptive mortality during the Polar Night? The early emergence from overwintering depth and resuming activity during the Polar Night (see above) may lead to a fast depletion of energy reserves. Mean lipid content of *C. glacialis* decreases by ~45% between August and January and by another 45% between January and May, with only ~30% of the August lipid content remaining in May (Fig. 5.5). At the same time, energetic costs increase in late winter due to reproductive events such as moulting, mating, gonad maturation and egg production that commence after the organisms emerge from diapause, putting constraints on the remaining lipid reserves at the end of the Polar Night.

Life-history strategies such as lipid stores and diapause are not an exclusive adaptation to the Arctic but rather an adaptation to a seasonal environment (Hagen and Auel 2001) and thus also common in temperate regions. The Arctic in its present state is a relatively young ecosystem which has been invaded/settled by boreal species. While adaptations that had evolved in response to a seasonal environment at temperate latitudes probably helped the expansion into the Arctic, high winter mortality may be an indication that these adaptations are not sufficient to ensure survival over extended periods of limited production, such as the Arctic Polar Night. However, despite high decreases in abundance over winter, *Calanus* spp. population can recover quickly and build up high biomass over the course of the short Arctic summer. This ability to successfully build up the population from a low standing stock over the short productive season likely makes up for their reduced fitness in terms of winter survival and may be the crucial trait that has enabled *Calanus* to establish themselves at high latitudes. On evolutionary time scales we may expect that winter survival should increase if natural selection favours phenotypes that survive the winter.

Copepod carcasses can make up a high proportion of the mesozooplankton biomass during the Polar Night (Daase et al. 2014). They provide an additional carbon source in the water column at times when other food sources are limited and may therefore play a so far underestimated role sustaining marine ecosystems during the Polar Night. In addition, they provide carbon in larger portions, making it available to consumers that cannot utilize particulate or dissolved carbon. Sampei et al. (2009a) suggested that, particularly during winter when sources of carbon in general are limited to recycled and degraded matter, copepod carcasses present a high quality food source for pelagic predators such as omnivorous and carnivorous copepods (Forest et al. 2007).

5.7 Zooplankton metabolic rates during the Polar Night

The highly seasonal pulsed regime of biological primary production in the high Arctic influences greatly the metabolism of zooplankton, and in particular the large *Calanus* herbivore copepods making up the bulk of zooplankton biomass. In turn, physiological dynamics of pelagic organisms modulate trophic interactions within the marine food web, as well as biogeochemical cycles. Due to the great logistical challenges posed by conducting field experiments in the high latitude remote areas, and possibly to the long-held belief that little biological activity occurred outside of the spring-summer productive season, only a handful of studies aimed at investigating the variability of zooplankton physiological rates such as respiration and excretion rates exist throughout an Arctic annual cycle. Conover and Gustavson (1999) found that the weight-specific rate of oxygen consumption (hereafter referred to as respiration rate) of the main zooplankton herbivores (*Calanus glacialis*, *C. hyperboreus* and *Pseudocalanus acuspes*) in Resolute Bay, central Canadian Arctic, was more than 2 times lower during the Polar Night than during the Midnight Sun season, as expected, and the specific excretion rates of ammonium and urea of these copepods were more than 5 times lower in the Polar Night. Interestingly, Darnis and Fortier (2012) also found that the daily specific respiratory carbon loss for the mesozooplankton large size fraction (>1 mm), comprising mainly late developmental stages of *Calanus* spp., was 2 times lower during the civil twilight period (sun $<6^o$ below horizon) than in midnight sun in Amundsen Gulf west of Resolute Bay (Darnis and Fortier 2012). One common feature of these two regions along the Northwest Passage is the presence of a seasonal sea-ice cover, and overlying snow layer, that lasts for several months including the period with sun below the horizon. By contrast, the respiration rates of two size classes of mesozooplankton was higher in January than in May in the sea-ice free high-Arctic Kongsfjorden (Berge et al. 2015), and euphausiid respiration rates were found to be similar in January and May (Darnis et al. 2017). In the ice-covered Resolute Bay, the weight-specific respiration rate of bulk zooplankton did not show any seasonal pattern over another overwintering study (Welch et al. 1997).

These contradictory observations, their paucity and different taxonomic resolution make it difficult to link discrepancies in seasonal patterns of zooplankton metabolism across the Arctic with the presence/absence of sea-ice affecting microbial primary and secondary production at the base of the food web, or with any other environmental drivers. Furthermore, crucial aspects of zooplankton biology during the Polar Night are still missing to explain the physiological differences, or lack thereof, between the dark season and the rest of the annual cycle. For instance, Polar Night data on digestive enzyme activity, feeding and fecal pellet production rates, and more detailed information on the winter prey field, could inform us on the processes fuelled by the metabolic activity, and also on trophic interactions within the pelagic food web. At this point, it is not clear what mechanisms were responsible for the relatively high mesozooplankton activity in January in Kongsfjorden. One sure thing is that the large copepods within this zooplankton size class were not in diapause, but swimming. Fecal pellet fluxes measured by sediment traps at 40 m and 100 m depth were extremely low in January, suggesting either very low feeding or strong fecal pellet recycling in the surface layer (Darnis unpublished data; Swoboda, unpublished data).

A more thorough understanding of zooplankton processes during the much understudied Polar Night, the overall importance they play in the high-Arctic marine ecosystem, as well as their response to environmental manifestations of climate change will depend on the use of new approaches and technologies (Chapter 9 and 10) allowing for easier measurements of swimming and feeding activity and metabolism (see Chapter 8).

5.8 Diel vertical migration (DVM)

5.8.1 Patterns of DVM and its role in the biological pump

Zooplankton DVM is a characteristic feature of the world's oceans and lakes, and is suggested to be the largest synchronized movement of biomass on the planet (Hays 2003). In general, zooplankton perform vertical migrations to balance the need to feed close to the surface, where food is generally in larger quantity, with the need to reduce the accompanying risk of being eaten at surface (e.g. (Hays 2003)) where illumination creates favourable conditions for visual predators (Gliwicz 1986). This light-mediated behaviour is ultimately explained as a predator-avoidance strategy. Since the phenomenon was first described almost two centuries ago, there have been numerous studies into both the adaptive significance of this behaviour and its ecosystem consequences (for two reviews, see (Hays 2003) and (Ringelberg 2010)). Research has focused both on the proximate and the ultimate explanations of DVM (e.g. (Lampert 1989; Ohman 1990; Hays et al. 2001), as well as on the implications for the ecosystem regarding trophic interactions and the biological carbon pump (e.g. (Buesseler et al. 2007; Darnis et al. 2017)).

Typically, herbivore zooplankton feed on ice algae and phytoplankton in the epipelagic layer at night and migrate to depth before dawn to avoid predation by visual predators during daytime. While migrants rest at depth during the day, they release carbon and nitrogen during egestion and as CO_2 and NH_4^+ during respiration and excretion (Steinberg et al. 2008). In the temperate and tropical ocean, the extensive diel vertical migration (DVM) of zooplankton and micronekton has been shown to play a significant role in the downward flux of particulate and dissolved organic matter (e.g. (Le Borgne and Rodier 1997; Rodier and Le Borgne 1997; Zhang and Dam 1997; Hernández-León et al. 2008; Kobari et al. 2008; Putzeys et al. 2011). Active transport can make up to 70% and 82% of the gravitational fluxes of particulate organic carbon (POC), and nitrogen (PON), respectively (Dam et al. 1995).

In the Arctic, DVM is rather poorly understood, yet it is likely to play an important role regarding the fate of carbon sequestration, food web interactions and the processes coupling the pelagic and benthic realms. Under the unique light regime of the high Arctic, this behaviour has been frequently observed during autumn and spring when the day-night cycle is pronounced (e.g. (Blachowiak-Samolyk et al. 2006; Cottier et al. 2006; Falk-Petersen et al. 2008; Wallace et al. 2010), whereas a number of studies have failed to find any coordinated vertical migration during periods of continuous light (e.g. (Kosobokova 1978; Fischer and Visbeck 1993; Blachowiak-Samolyk et al. 2006). Berge et al. (2009) were the first to demonstrate that zooplankton conduct DVM during the Polar Night. Recent studies have documented that krill carry out DVM during the Polar Night and, in particular, during periods of civil twilight (solar altitude not exceeding 0° to −6°)(Grenvald et al. 2016). Although preliminary studies also reported DVM during the nautical Polar Night (solar altitude not exceeding −6° to −12°) and in response to lunar light (Last et al. 2016), a study by Ludvigsen et al. (2018) was the first that unequivocally described DVM in response to the diel solar irradiance cycle during nautical Polar Night (Fig. 5.15). This study documented a DVM restricted to surface layers and temporally centered on the very short period of elevated light intensity at solar noon due to small variations in ambient light that can only be detected by organisms near the surface.

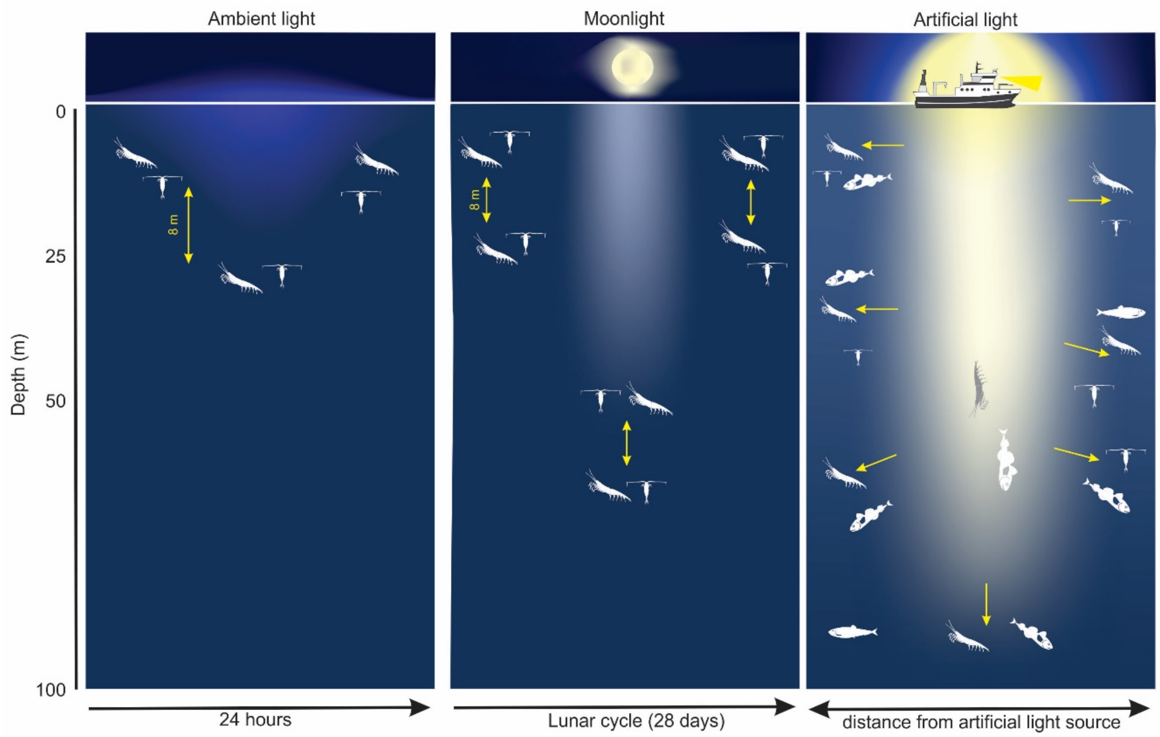


Fig. 5.15 Effects of different light sources on the vertical distribution of zooplankton during the Polar Night. Under ambient light, zooplankton perform DVM over short distances. During full moon, zooplankton are distributed deeper in the water column. Artificial light affects zooplankton distribution down to 100 m with organisms escaping the illumination of the water column in vertical and horizontal directions (modified after Ludvigsen et al. 2018)

Wallace et al. (2010) identified six separate phases of DVM throughout the year, each of which had a distinct pattern, suggesting that different species were dominating the observed patterns during different seasons: Autumn and spring DVM during which the majority of the zooplankton community is migrating. This can be thought of as the “classical DVM” during a time of year when the difference in E_{PAR} is at its greatest between night and day (Chapter 3). Also two phases of DVM named "early autumn " and "early spring" were identified, which are periods of "classical DVM" albeit with a weaker acoustic signal indicating that a relatively smaller part of the community performs DVM. Then, during the winter and summer periods, characterised by either a 24-hour continuous Polar Night or polar day, respectively, no synchronised DVM could be detected (Wallace et al. 2010). However~~,~~ it must be noted that the methods used by Wallace et al. (2010) were not optimised to detect either small-scale DVM nor DVM performed by a minority of the community. Also, our current state of knowledge does not yet permit any reliable identification of the ensemble of species involved in this behaviour, nor the mechanisms regulating the vertical positioning of the organisms. These factors are critical for a holistic understanding of the patterns and processes responsible for the functioning of Arctic marine systems, and are major obstacles for any predictive understanding of how ecosystem processes are likely to be affected by the current warming of the Arctic Ocean and surrounding shelf seas.

In Arctic ecosystems, the high seasonality in light climate, shifting between winter "Polar Night" and summer "midnight sun" conditions when the sun stays below the horizon or, inversely, does not set for days to months, makes zooplankton DVM patterns more complex than at lower latitudes (Ringelberg 2010). The rapid changes in the day-night cycle and other environmental factors affect timing, synchronism and vertical range of migration (Fischer and Visbeck 1993; Berge et al. 2014), which in turn influence the transport capacity of migration over the year. In such a variable light environment, snapshot fieldwork during scientific cruises presents limitations for assessing the function of zooplankton DVM. However, studies using multi-month time series of acoustic data from moored Acoustic Doppler Current Profilers (ADCP) shed light on the seasonal patterns of DVM at high latitudes. These instruments record seasons of classical DVM when the relative rate of change in irradiance is sufficient to trigger synchronous movements of zooplankton in winter and autumn (Fig. 5.16), contrasting with asynchronous (individual) vertical movements under the continuous illumination of the Arctic summer when algal food is usually plentiful in the surface layer (Cottier et al. 2006; Berge et al. 2009; Wallace et al. 2010). Plankton net data, sometimes combined with acoustic data, showed that euphausiids, hyperiid amphipods, large *Calanus* and *Metridia* copepods, chaetognaths and ctenophores are the main diel migrants in Arctic waters, their relative importance fluctuating with seasons and locations (Fischer and Visbeck 1993; Fortier et al. 2001; Daase et al. 2008; Berge et al. 2014). In a recent study from Kongsfjorden in Svalbard, using a combination of acoustics and plankton net data, (Darnis et al. 2017) showed that *Thysanoessa* spp. euphausiids made up >90% of the diel migrant biomass during the last part of the Polar Night (civil Polar Night). In total, this DVM accounted for >25% of the total sinking flux of particulate organic carbon. The study also concluded that climate warming is expected to result in tighter coupling between DVM and bloom periods, stronger stratification of the Barents Sea, and northward advection of boreal euphausiids. This may increase the role of DVM in the functioning of the biological pump on the Atlantic side of the Arctic Ocean, particularly where euphausiids are or will be prevalent in the zooplankton community.

The Polar Night presents a challenge to the behaviour of DVM, since it is driven by the diel solar cycle. What happens to daily migrations when there is no discernable diel variation in the solar cycle?

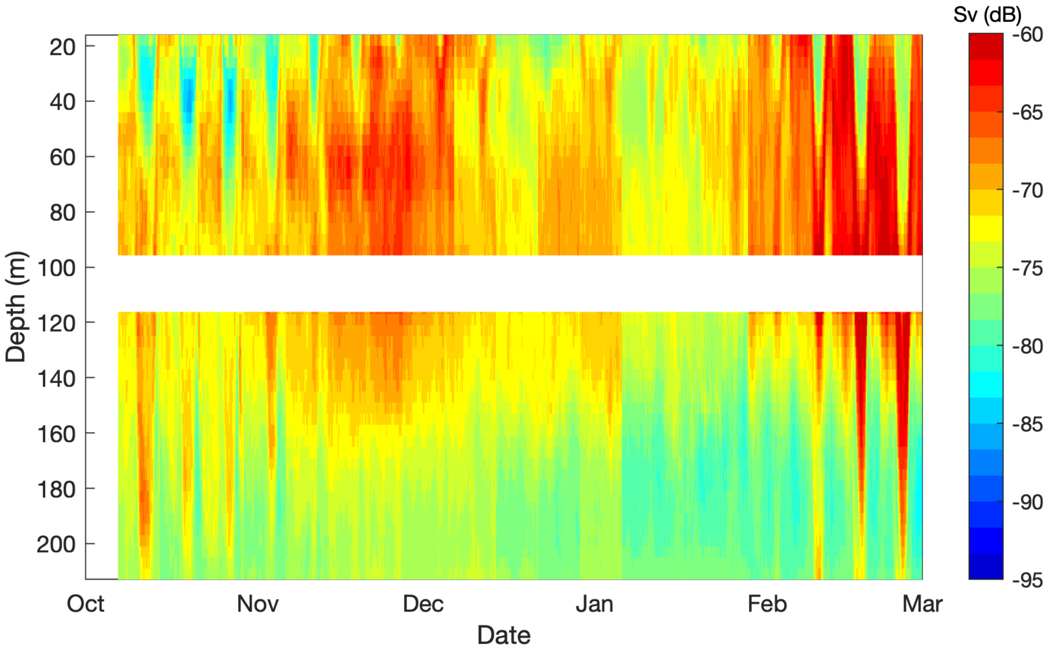


Fig. 5.16 Acoustic Doppler Current Profiler (ADCP) data sampled from October 2013 to March 2014 in Kongsfjorden, Svalbard. The ADCP samples at 300 kHz, with 20 minute and 4 m time and depth resolution respectively. Data are averaged weekly, so each 7 days of data is presented as a 24 hour period (i.e. 4 full DVM cycles exist each month).

5.8.2 Polar Night DVM

A continuous cue seems to be driving vertical migrations across the Arctic during the Polar Night period, unlike the midnight sun. Although there is a change in the Sun's altitude above the horizon during a diel cycle in the midnight sun period, the relative change in E_{PAR} is small. During the midnight sun, E_{PAR} is high, but the relative diel change in E_{PAR} is low. For the Polar Night, it is quite the opposite (Chapter 3); while E_{PAR} levels are generally low during the entire Polar Night, it may increase by several orders of magnitude at solar noon. Importantly, for many marine organisms performing DVM, it is the relartive, not the absolute difference in E_{PAR} that trigger their migration. Hence, it is perhaps not all that surprising that marine zooplankton ad fish do perform DVM during the Polar Night? Whilst large-scale (with respect to depth) synchronised DVM stops in the middle of the Polar Night period at high latitudes (> 74°N) (Hobbs et al. 2018), there is clear evidence that more shallow and restricted solar-driven synchronised migrations occur throughout the Polar Night at latitudes at least up to 79°N (Ludvigsen et al. 2018). It remains, however, an unresolved issue if this more depth-restricted DVM is a characteristic feature of the entire Arctic Ocean. What we do know, is that during periods of the Polar Night when the moon is a stronger illuminator the the background illumination of the Sun, deeper zooplankton migrations are instead driven by moonlight (Last et al. 2016). Migrations take place at the rise of each full moon right across the Arctic. Many species (or populations – some species may exhibit contrasting strategies) seem to spend the Polar Night and winter near the surface; with reduced risk of visual predation, it may provide a fitness benefit to remain in the surface where there is a higher chance of scavenging debris or other scarce food sources. As the full moon rises, however, populations descend typically ~50 m compared to their initial "working depth", often continuing their depth-restricted DVM 50 meters further down. Importantly, this depth-restricted DVM is typically shifted from a solar to a lunar diel cycle (Last et al. 2016), but only when the Polar Night is dark enough for the lunar light to be the dominating cue. In Kongsfjorden, this applies only to the two full moon periods in December and January (Fig. 5.17).

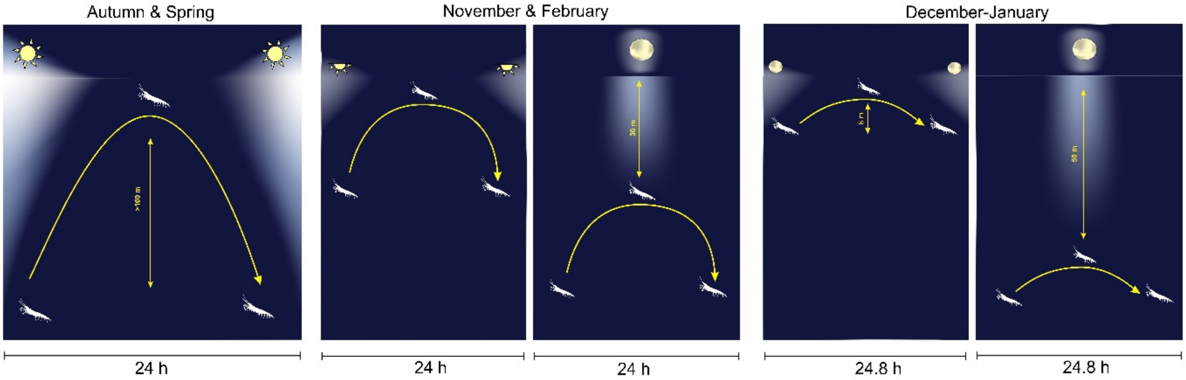


Fig. 5.17 Patterns of Diel Vertical Migration (DVM) in Kongsforden (79°N): Zooplankton conduct DVM over >100 m depth during autumn and spring driven by diel cycles in solar illumination/altitude. During the Polar Night, DVM over small distances (~8-10 m) take place in surface waters. During periods when lunar illumination is stronger than solar illumination, typically during full moon periods, DVM is both occurring at a greater depth and shifts from a 24 to a 24.8hr cycle

At the North Pole, the marine light climate is unparalleled anywhere on the planet. First of all, the entire year consist of one long night and one slightly longer day (see Chapter 1). Second, year-round sea-ice strongly regulate the light penetrating down into the water column. With a strongly reduced perceptible solar cycle at any time of the year, it is unsurprising that synchronised DVM hitherto has not been observed at any point at the geographical north pole (Hobbs et al. 2018). Depth-restricted DVM, as documented some 10 latitudinal degrees further south (Fig. 5.17), have, however, not been very poorly explored across the Arctic Ocean, and may for this reason very well be a common, yet undescribed, phenomenon even at the North Pole. What have been described is monthly lunar displacements and/or migrations during the Polar Night, across the entire Arctic when the moon becomes the strongest illuminator (Last et al. 2016). Despite no DVM (or at least not detectable by the instrumental design used), acoustic data used to observe zooplankton behaviour show that a seasonal cycle exists in migrations at the North Pole. Acoustic backscatter suggests that a portion of the zooplankton community remains in the surface waters through the Polar Night. As the sun rises above the horizon, the top 60 m of the water column becomes totally empty of any sound scattering biomass. During this time, zooplankton migrate to depth to avoid the threat of visual predation that comes with 24-hour daylight. As the sea-ice reaches its thinnest in late summer, and under-ice blooms are initiated, zooplankton populations return to the surface to feed on this short influx of food (Chapter 4; Fig 4.1). At this time they are likely performing unsynchronised migrations: taking refuge at depth when digesting and quickly moving to the surface to forage when required (these unsynchronised migrations during the midnight sun have been observed elsewhere in the Arctic (Cottier et al. 2006; Wallace et al. 2010). In the post-bloom phase, abundances in the surface waters decrease when much of the *Calanus* population migrates to depth and enters diapause and the cycle begins again.

The timings of these behaviours and movements in and out of the surface waters vary inter-annually (Hobbs, 2016), and are suggested to be driven by changes in the timing of sea-ice presence and prey availability. Primary production begins around August in the North Pole area (Falk-Petersen et al. 2009). Assuming these conditions, zooplankton are currently doing most of their foraging after the peak solar altitude (June 21st), and therefore avoid the surface waters during the time of highest predation risk. However, as sea-ice declines and its break up potentially becomes earlier, the bloom period might also occur earlier in the year. The consequences of this is likely to be that zooplankton are now having to forage during higher solar altitudes, resulting in a greater risk of predation. This mis-match of life history strategies is something that is being considered in several areas of the Arctic ecosystem, and might also apply to the seasonal strategies of high latitude under ice zooplankton.

5.9. Summary and knowledge gaps

Figure 5.18 sums up our recent observations of the zooplankton community during the Polar Night in Svalbard waters. Lipid reserves are common in most species, but the chemical composition may vary depending on dietary preferences and overwintering strategies. Wax-ester rich *Calanus* conduct seasonal vertical migration and go into diapause. *Calanus* stage CVs moult to adults during winter and in *C. glacialis* mating occurs mid winter. Part of the population starts to ascend as early as January. Lipids are depleted during winter, and omnivorous feeding on protists or copepod eggs and nauplii has been observed. Omnivorous and carnivorous species stay active and remain in upper water layers. Carnivorous predators such as chaetognaths, feeding on *Calanus*, may follow *Calanus* to overwintering depth. Omnivorous copepods feed on heterotrophic protists and bacteria, and serve as prey for carnivorous zooplankton species. Mid-winter reproduction has been observed in a number of species. Euphausids may shrink and/or regress sexual organs. Primarily herbivorous species switch to heterotrophic food sources.

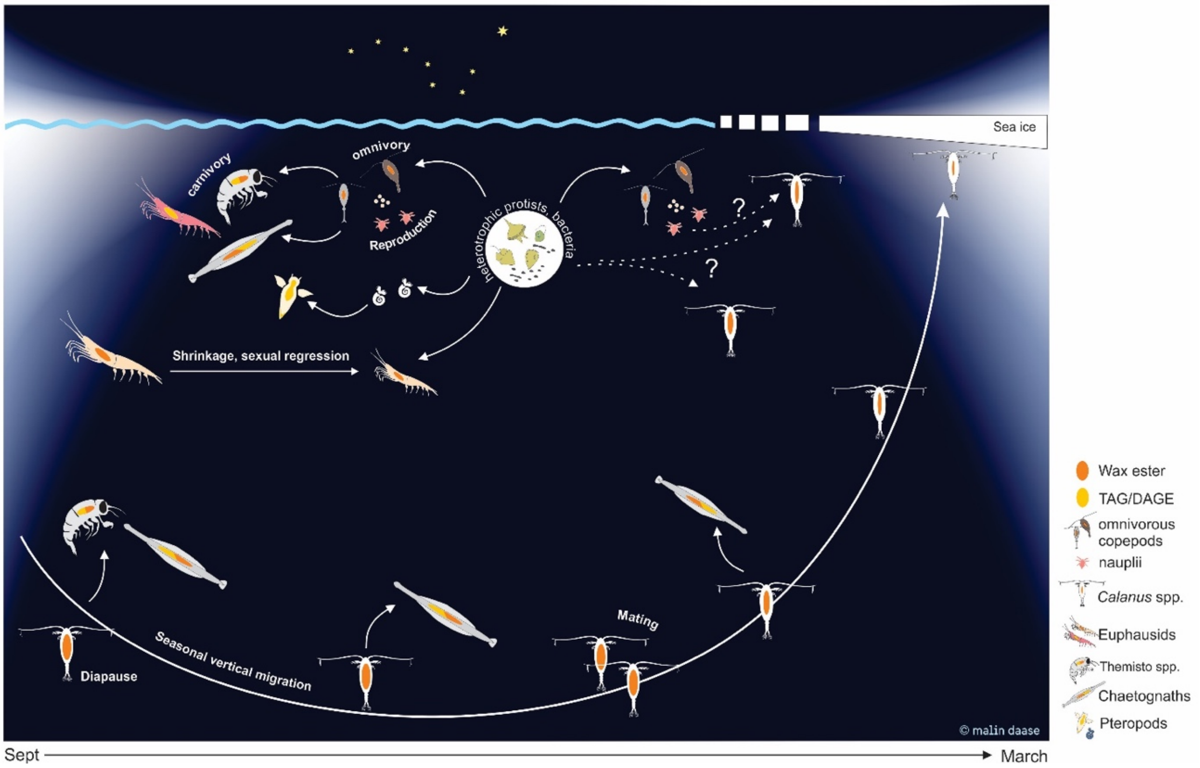


Fig. 5.18 Summary of polar night ecology of Arctic zooplankton around Svalbard. Note that this is valid for a Svalbard or nearby situation, not neccassarily transposable to the American side of the Arctic where sea ice forms earlier and is already significant in the dark period

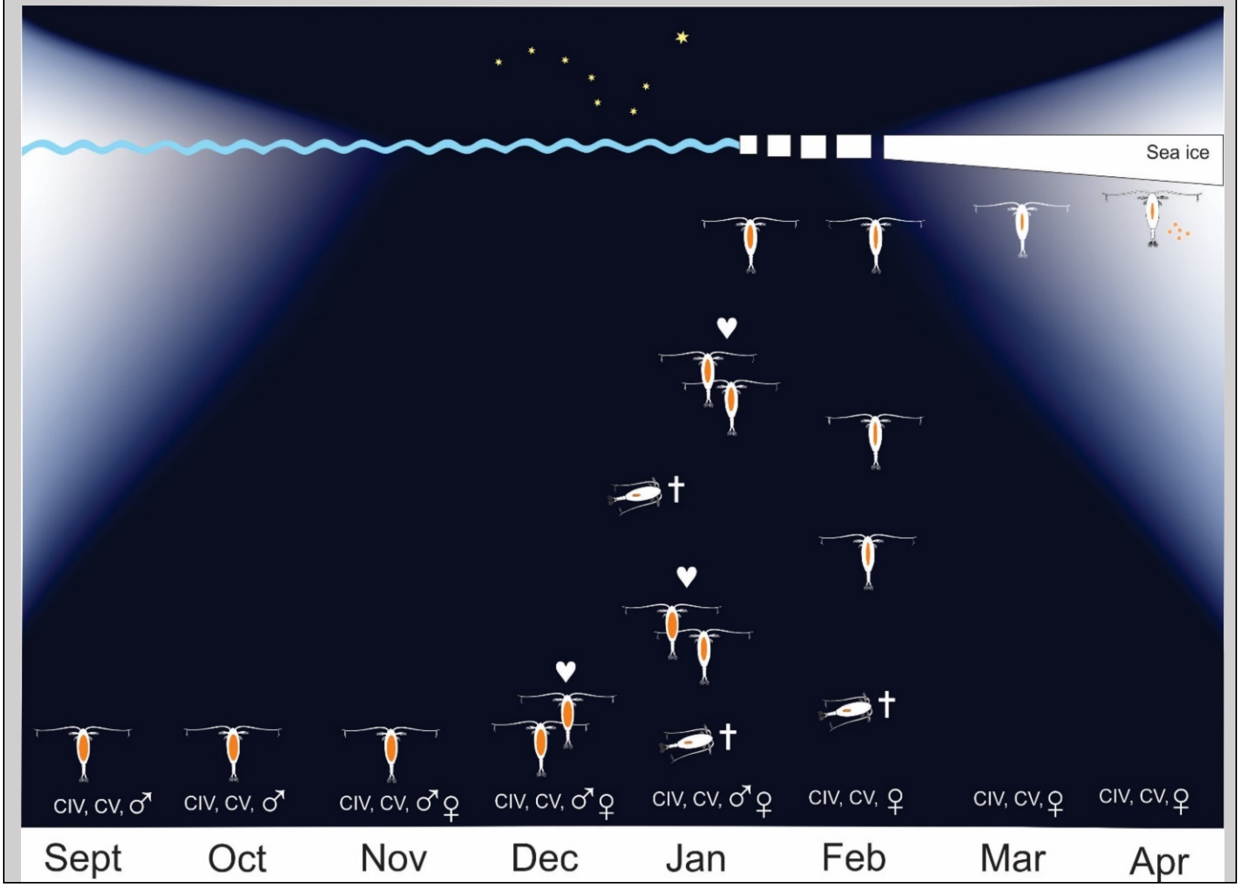
While we have advanced considerably our understanding of life history strategies of Arctic zooplankton species and processes in the pelagic ecosystem during the Polar Night over the past decade (Table 5.1), there are many aspects that remain unknown. Zooplankton studies during the Polar Night have largely focused on a few species, mainly *Calanus* and to some extent euphausiids, and on behavioural patterns such as DVM. For most species there are still considerable gaps in our knowledge of for example seasonal changes in lipid content, activity, metabolic rates, feeding rates, prey preferences, population and size structure that would provide a better indication on how these species spend the Polar Night and what their ecological role is during the unproductive season. The role of the microbial food web as an alternative food source and for sustaining activity during the Polar Night is poorly understood. When the large herbivorous copepod species become inactive and reside at greater depth, omnivorous small copepods, that remain abundant and active during Polar Night, become the main microbial grazers likely sustaining a continuous food chain towards higher trophic levels (Conover and Huntley 1991; Møller et al. 2006; Svensen et al. 2011; Zamora-Terol et al. 2013) but we lack understanding of their ecological role in the pelagic ecosystem during the Polar Night. Similarly, the ecology and the role of other common predators of the Arctic pelagic community such as chaetognaths, amphipods and jellyfish during the Polar Night have rarely been addressed.

Even for the relatively well-studied *Calanus* species complex we are confined by few measurements of enzyme activities, respiration and feeding rates that provide only limited insight into their overwintering strategies. Does *Calanus* indeed feed during winter and what are potential prey items and feeding rates? What are the energetic demands of overwintering and diapause? How and when are lipid reserves activated? What triggers ascent and descent?

While DVM patterns during the Polar Night are well described using hydroacoustics, the migrators are still not fully identified. Are we observing seasonal differences in migration patterns due to changes in the species composition, the age or size structure of the migrating community? What is the adaptive advantage of conducting DVM during the Polar Night? What is the effect of light pollution on observations conducted from well-lit research platforms? Also, while some aspects of the above described Polar Night scenario for the Svalbard region (Fig. 5.18) are applicable across the Arctic (e.g. mid winter mating, switch to opportuntistic feeding), others may not be transposable to other Arctic regions. There are for example clear difference between Svalbard and the Canadian Arctic, where sea ice forms earlier and is already significantly thick in the dark period, and we see differences in the timing of descent and ascent of seasonal vertical migrators. Polar Night studies covering a larger geographical regions are necessary to the Polar Night ecology of Arctoc zooplankton more precisely across the Arctic.

BOX 5.1 The seasonal characteristics of Calanus spp. population on the Svalbard shelf during the Polar Night can be summarized as follows:

Lipid content and abundance of *Calanus* are relatively stable throughout autumn and the first part of the Polar Night while the population resides at overwintering depth. Males of *C. glacialis* display active mating behaviour from midwinter (December) on. They are abundant in the populations and females bearing spermatophores are commonly observed. Shortly after the winter solstice the population becomes more active and a part of the population ascends from overwintering depth. This awakening is accompanied by a decrease in lipid content and increased mortality. High proportions of *Calanus* carcasses in the water column indicate that at least part of this mortality is non-consumptive. Lipid content decreases more steeply from January on indicating that energy reserves are activated. High mortality may be caused by insufficient energy reserves to sustain this activity until the onset fo the spring bloom.



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Chapter 6

Benthic Communities in the Polar Night

Paul E. Renaud, William G. Ambrose Jr. and Jan Marcin Węsławski

Abstract

Scientists generally believe that the products of photosynthesis raining down from above support the community of organisms living on the ocean bottom deeper than light can reach. Consequently, we have assumed that during the Polar Night, when there is insufficient light for photosynthesis, that these communities enter a stage of torpor and little occurs that is significant for the ecosystem. We review our limited knowledge of bottom-dwelling organisms and communities during the Polar Night and, while much remains unexplored, unexpected activity at many levels of the benthic system put previous beliefs of a general dormancy into question. Studies have revealed that some animals grow and reproduce during the Polar Night, presumably relying on stored resources or on detrital and advected sources of nutrition, and some species of marine macroalgae even grow during this dark period by using stored energy. We conclude that some processes occurring during the Polar Night may be important for understanding Arctic marine ecosystems and the organisms that comprise them. Furthermore, we suggest that changing food supply and increased winter metabolic requirements caused by warming temperatures make it difficult to predict the impact of climate change on these communities. Scientists need to learn more about the basic biology of Arctic organisms (life-history strategies, food sources) to more fully understand their ecosystem roles throughout the year. Furthermore, they must take advantage of opportunities to use new technologies and observing platforms to conduct year-round studies of Arctic benthos. Only then will we understand the importance of this long dark period in driving the structure and functioning of marine benthic communities.

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6.1 Introduction

Arctic benthic communities are rarely studied during the Polar Night for many of the same reasons other Arctic communities have received little research attention at this time of year: during a period of low food availability and low light, the Arctic system has been perceived as largely dormant (Berge et al. 2015a). Arctic benthic communities are considered energy limited (Piepenburg 2005), and food supply is viewed as the driving force controlling ecosystem structure and function (Grebmeier and Barry 1991). Much of the effort to understand benthic systems has focused, therefore, on pelagic-benthic coupling and how factors affecting this coupling vary in space and time (Piepenburg 2005). The absence of primary productivity during the Polar Night (Chapter 4) leads most investigators to dismiss this period of the year as unimportant to understanding Arctic benthic organisms, communities, and the ecosystem. In his review of the Arctic benthos, Piepenburg (2005) highlighted the lack of adequate data on benthic communities during the Polar Night as a knowledge gap. The few studies during this time have revealed that some benthic organisms are active during the Polar Night (Węsławski et al. 1990; Berge et al. 2015a, 2015b), and it now seems plausible that processes occurring during the Polar Night will be important for understanding Arctic marine ecosystems and the organisms that comprise them.

Fig. 6.1 Several skeleton shrimp (caprellid amphipods, most likely *Caprella septemtrionalis*), and a gammarid amphipod at the lower left, on the red alga *Desmarestia aculeata* in Kongsfjorden, Svalbard in January 2014. Skeleton shrimp brood their eggs during winter and are nearly absent from collections at other times of the year, indicating the 'hidden biodiversity' discovered by Polar Night sampling. They are often consumed by sculpins (Cottidae). Photo: Geir Johnsen

Not all Arctic organisms enter a state of torpor during the Polar Night, and for some this period appears to be a key period of activity and reproduction (Fig. 6.1). Larvae of benthic organisms are found during all months, though the overall abundance and diversity is lower in the winter than at other times of the year (Michelsen et al. 2017). The larvae of some taxa, however, are most abundant during the winter (Stübner et al. 2016), suggesting some advantage to reproducing during this time of year. Not all organisms stop growing during the polar winter (Berge et al. 2015b), and most surprisingly some species of kelp grow primarily during the winter ((Chapman and Lindley1980; Chapter 4). It is likely that, with further investigation, we will discover more organisms that grow and reproduce during the winter, leading us to ask: What is driving the winter activity of these organisms and what does it mean for the functioning of the ecosystem?

Important ecosystem components and processes operate during the Polar Night. The hyperbenthos (a group of invertebrates, largely crustaceans, which live just above the seafloor) is active during the winter in Kongsfjorden (Svalbard) (McGovern et al. 2018), and krill from the Gulf of Maine (Cleary et al. 2012), Svalbard (Deja personal communication), and the Antarctic (Cleary et al. 2016) feed on sediment in winter. These organisms could play an important, but yet unknown, role in elemental cycling and energy transfer from the benthos to higher up the food chain during the winter (McGovern et al. 2018) (Fig. 6.2).

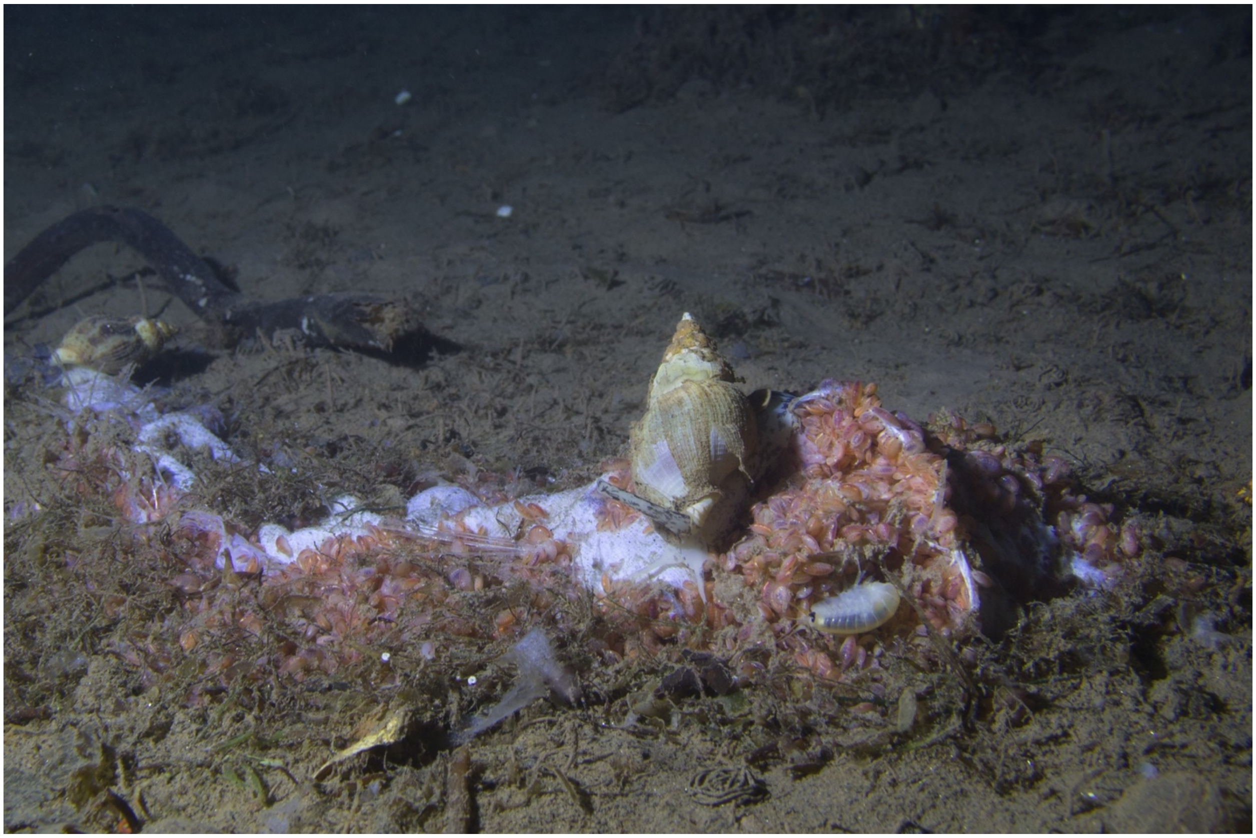

Fig. 6.2 Carrion-feeding scavengers on a dead cod in Kongsfjorden, Svalbard in January 2014. Here we see at least two amphipod species (the single large *Anonyx nugax* and many pink *Onisimus* spp.) and several whelks (*Buccinum* sp.). The amphipods are members of the hyperbenthos. These scavengers can reduce the fish to a skeleton in a period of several hours in the middle of the Polar Night. Photo: Piotr Bałazy

Climate change will not alter the astronomical day length at high latitudes, but it may change the patterns of input of food to benthic communities and how these systems function. The benthos below the photic zone receives food from a variety of sources, and climate change may differently affect the amount and temporal pattern of delivery of these sources of energy. We have begun to recognize the impact of climate change on pelagic-benthic and benthic-pelagic coupling (Griffiths et al. 2017), and on changes in the quality, quantity, and timing of food input to the benthos (ACIA 2005). Processes occurring during the Polar Night, however, have been largely ignored, but may be important in preconditioning the system for the spring. Furthermore, different processes may organize benthic communities at different times of the year: bottom-up during the spring and summer with food input from primary production the dominate factor, and top-down with predation and scavenging the dominant forces during the winter (Berge et al. 2015b).

6.2 Tradeoffs associated with winter activity of the benthos

Taking a step back, one should consider the basis for assuming little activity by the benthos during winter. Seasonality in the availability of fresh phytodetritus (sinking organic material produced by phytoplankton) is behind many of the arguments for reduced metabolism, reproduction, and growth of Arctic benthos during winter. Community structure of macro- and mega- fauna, however, is usually presumed to respond to food supply on longer periods due to the multi-year life cycles of many of these taxa (Renaud et al. 2008). Indeed, many (but not all) studies suggest metabolic rates, such as sediment oxygen demand and nutrient remineralization rates, respond rapidly to pulses of fresh food on Arctic shelves (Renaud et al. 2008), and even in the deep-sea (Boetius et al. 2013). The assumption that planktonic phytodetritus is the main food source for most benthos and their pelagic larvae, however, is difficult to assess given the sparse knowledge of the autecology of Arctic benthos.

Emerging data on significant winter populations of meroplanktonic larvae (e.g. Stübner et al. 2015) and settlement of benthic fouling organisms (Shunatova et al. 2018; Fig. 6.3) suggest that food supply is only one potential challenge, but that there must be other processes that make winter a better time for reproductive activity of some organisms than other times of the year. Reduced competition and predation, and potentially increased space for settlement in the winter compared to other periods, are possible, but again, difficult to evaluate given the current state of knowledge of winter ecology in the Arctic. Such trade-offs must, however, be integral for evolutionary mechanisms driving annual routines and life-history strategies. Some of these trade-offs and knowledge gaps are discussed in the following sections.

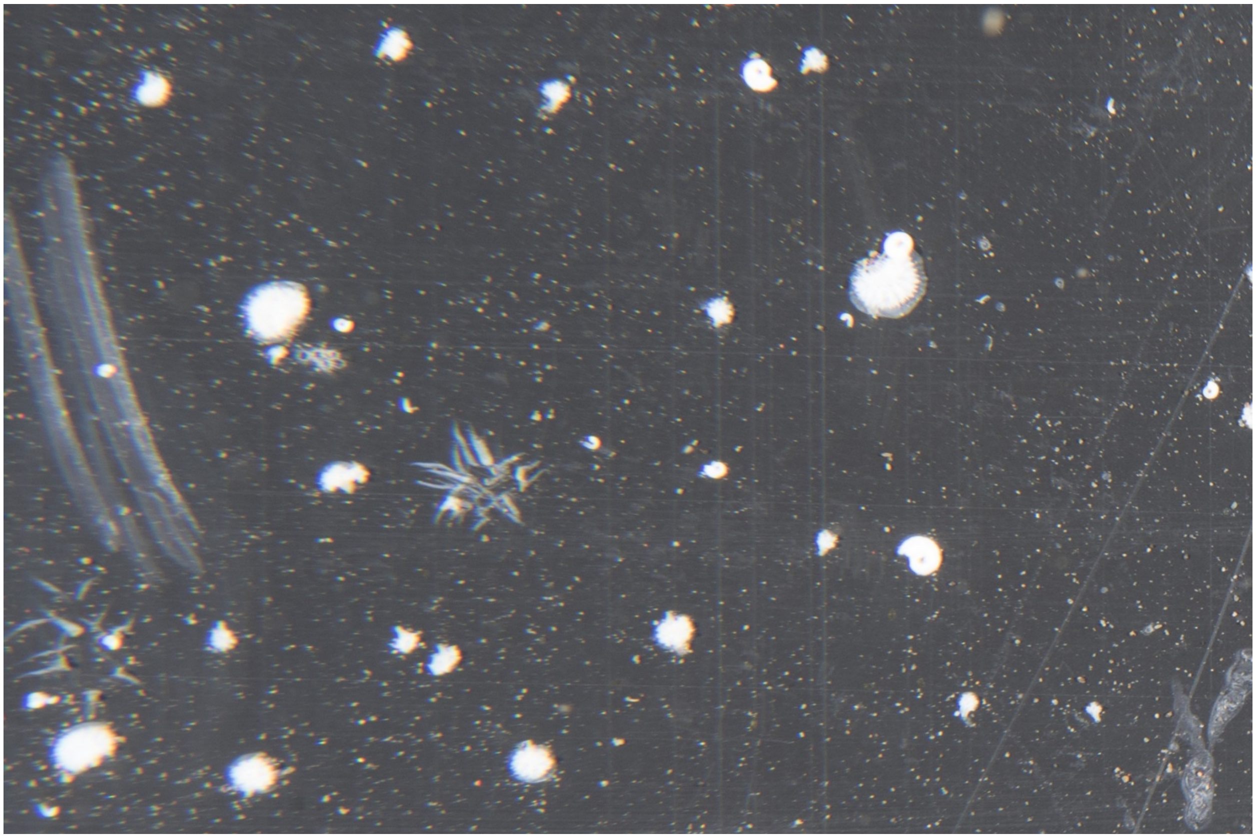

Fig. 6.3 High Impact Polystyrene plastic plate placed in Isfjorden, Svalbard, in August 2015 and photographed in January 2016. The major taxa on this plate are spirorbid polychaetes (white spiral shaped objects, approximately 2 mm across) and bryozoans. The star shaped object in the center of the photo is probably made by urchins grazing the surface, indicating activity during this time. Photo: Piotr Kukliński

6.3 Community Structure

Spatial and temporal patterns in the delivery of food to the benthos, and disturbance from ice scour and sedimentation from glacial runoff, are the dominant factors controlling Arctic benthic community structure (Grebmeier and Barry 1991; Conlan et al. 1998; Piepenberg 2005). Other factors, such as temperature and salinity, can also be important (Jernas et al. 2018). The seasonal signal of food and some disturbances might result in large seasonal changes in the structure of Arctic benthic communities with low abundance, biomass, and diversity in the winter. Many benthic organisms, however, are long lived, particularly in deeper waters and in systems that are not disturbed, leading to the prediction that these communities will exhibit little change over winter.

Most studies of Arctic benthic communities are conducted during the summer and rarely examine seasonality. Long-term studies of benthic community structure are becoming more common as data sets are extended (Grebmeier et al. 2018), revealing the impacts of environmental change on these communities, but sampling is still usually in the summer or fall. The limited seasonal sampling leaves a large gap in our knowledge of Arctic communities in general and benthic communities in particular.

The few analyses of soft-sediment community structure during the Polar Night do not reveal a benthic community that is depauperate compared to other times of year. Kędra et al. (2011) was the first Arctic study we know of that examined soft-sediment community structure at shallow (5-35 m) depths in winter. Their comparison of summer (August) and winter (March) communities in Kongsfjorden revealed similar infaunal abundance and biomass between the two seasons, with slightly higher species number during the winter compared to the summer. Interestingly, carnivorous and opportunistic species were more abundant during the winter. Kędra et al. (2011) limited their conclusions to the shallow water benthos of Kongsfjorden, but Włodarska-Kowalczuk et al. (2016), sampling in deeper water (80-305 m) in the same fjord, also detected no seasonal pattern in macrofaunal abundance, biomass, or diversity among samples collected in May, August, October, and January. Pawłowska et al. (2011) also found no clear seasonal trend in macrofaunal abundance at a shallow (40 m) site in another Spitsbergen fjord. They did record an increase in abundance, biomass, and species richness in response to the spring bloom and a decline in these parameters in the summer in response to glacial-fluvial deposition of sediment. Communities sampled during the Polar Night (October- February), however, did not exhibit low abundances, biomass, and diversity in response to low light, temperatures, and phytodetritus. Species richness was greatest in April, but Shannon-Wiener diversity was lowest in July and highest in February. A recent study in Kongsfjorden (Mazurkiewitz et al. in press) recorded no seasonal change in the size structure of small (meio- to macro-) infauna, despite observed seasonality in food supply.

We might expect that taxa with shorter longevity than many macrobenthic species would display seasonal patterns of abundance with low levels in winter. Pawłowska et al. (2011) also sampled the meiobenthos, and as was the case with the macrobenthos, they detected no clear seasonal trend. They recorded highest meiobenthic density in the spring (April and May) and in the winter (October-February) with lowest densities in February and the summer (July and August). In this system, the meiobenthic community appears to be driven by the same factors as the macrobenthic. Several species of foraminifera (greater than 63µm) in Kongsfjorden are limited to either the summer or winter, but most of the taxa were present year round (Olga Knyazev, personal communication). Individual foraminiferal taxa have specific growth seasons, with several species exhibiting significant growth in November in Kongsfjorden, but no samples were taken later in the Polar Night period (Skirbekk et al. 2016). These results echo early work that found a minimal response by the meiobenthos to the spring deposition of phytodetritus to the Arctic benthos (Ambrose and Renaud 1997).

Most of the studies examining seasonal including winter-changes in the macro- and meio-benthic infaunal communities have been conducted in the fjords on the west coast of Svalbard (Kongsfjorden, Adventfjorden, Hornsund). These fjords are heavily influenced by the warm, saline West Spitsbergen Current, and in recent years have been largely ice-free during winter. Limited winter sampling has been conducted in fjords more representative of the high Arctic. Rijpfjorden, located on the northeast part of the Svalbard archipelago, experiences high Arctic conditions with winter ice cover and colder temperature than Kongsfjorden (Ambrose et al. 2012). Though sampled in different years, the macrobenthic biomass in Rijpfjorden was lower in winter than in the summer (Morata unpublished data). A greater variety of systems must be sampled year round before we can generalize about seasonal abundance patters in Arctic benthic communities.

As already noted, there are limited data from the Polar Night upon which to draw conclusions. Some benthic species (e.g. *Mytilus*, Thyrring et al. 2015) are metabolically flexible, and the long life of many taxa likely contributes to minimal changes in soft-sediment communities through the Polar Night. But survival is only one aspect of life during the winter.

6.4 Growth/activity

While we have known for a long time that benthic Arctic organisms survive the Polar Night, they were not assumed to grow during this period. With light for photosynthesis below usable levels (Berge et al. 2015b; and see Chapter 3), primary production stops during the Polar Night (Chapter 4). Many benthic organisms slow or stop growth in the winter due to low temperatures and low food availability, even in more southern areas. This period of low or no growth is often recognizable as annual growth checks, e.g. in bivalve shells (Ambrose et al. 2012). Growth of these species often resumes in the spring coincident with the spring bloom even before the water warms (Ambrose et al. 2012). Some animals, and even some macroalgae, however, grow throughout the Polar Night.

The bivalve *Chlamys islandica* exhibits a constant growth rate throughout the year in Kongsfjorden (Berge et al. 2015b), and maintains a circadian rhythm of valve opening and closing throughout the Polar Night (Tran et al. 2016). The authors hypothesize that this behavior is relatively new, coinciding with the loss of winter ice in Kongsfjorden 10-15 years ago. Recently, oysters at a temperate latitude have been seen to synchronize their shell-opening cycles with lunar cycles (Payton and Tran 2019), so moonlight might be a stimulus during the Polar Night for some shallow-water benthic organisms as has been shown for Arctic zooplankton (Last et al. 2016). We need more year-round studies with a variety of bivalves in ice covered and ice-free areas before we will fully understand their behavior during the Polar Night.

The amphipod *Onisimus litoralis* grows year round with no annual change in its total energy content (Nygård et al. 2010). *Onisimus litoralis* is a major component of Arctic shelf soft-sediment communities and part of a guild of scavenging amphipods that are active year round (Nygård et al. 2012) (Fig. 6.2). In addition, several amphipod species in Hornsund, on Spitsbergen’s west coast, have similar caloric values in the summer and winter (Szaniawska and Wołowicz 1986). Winter energy demands for maintenance and growth are likely covered by stored protein and winter-feeding since lipid content does not decrease in winter.

It is probable that more animals than one scallop and some amphipod species are active during the polar winter and display modest growth. We need more studies of winter diet, energy management, and growth before we can make any generalizations about winter activity of animals during the polar winter. Furthermore, it is likely that there are regional differences in strategies among taxa and maybe even within the same taxa as suggested by Tran et al. (2016) and demonstrated by Bridier et al. (2019) in their study of two bivalve species in Young Sound, Greenland.

6.5 Reproduction and recruitment

Reproduction is a critical phase in any organism’s life cycle. The lack of significant energy reserves in feeding larvae or new recruits suggests food may be limiting factors for these life stages. In the Arctic, low temperatures and highly seasonal food supplies prompted the formation of Thorson's Rule, stating that the percentage of planktotrophic larvae should decrease with increasing latitude and water depth (Thorson 1936). Whereas a number of studies have criticized the generality of this paradigm (see Pearse 1994), it is still generally believed that reproduction in marine benthos, at least those with planktonic larvae, is timed to the spring bloom. Indeed, the often-observed dramatic peak in planktotrophic barnacle larvae is closely timed with the Arctic spring bloom, but recent studies have shown secondary peaks of barnacle larvae later in the season outside periods of high pelagic productivity (e.g. Stübner et al. 2016). In fact, meroplankton (planktonic larvae of benthic organisms) representing multiple phyla are found year-round, or at least well outside of periods of pelagic primary production, in Arctic shelf systems (Węsławski et al. 1990; Kuklinski et al. 2013; Stübner et al. 2016). Larvae of some groups even exhibit peaks in abundance during winter (bryozoans and some gastropods: Stübner et al. 2016; king crabs, gastropods: Michelsen et al. 2017). Thus, it clear that Thorson's Rule, at least as it has been extrapolated in the last decades, is not a reliable guide to which larval feeding strategies or reproductive seasonality can be expected *a priori* in Arctic systems.

Few studies have assessed recruitment of benthic organisms during winter, and these have been restricted to fouling organisms. Recruitment takes place throughout the year, although it is generally lower than during other times of the year in terms of both diversity and abundance (e.g. Kukliński et al. 2013). Still, some taxa, such as spirorbid polychaetes and bryozoans, exhibit higher settlement on experimental panels in autumn-winter than in spring-summer (Meyer et al. 2017) (Fig. 6.3). Shunatova et al. (2018) studied seasonal variability of sessile fauna on kelp and understory stones, and found juveniles of several species across three phyla to occur only in winter, and overall species richness to be highest in winter. Most larvae of recruits on these kelps are lecithotrophic (non-feeding). In a companion study of motile fauna on kelp thalli, high interannual variability was observed, but the highest abundances noted were when thousands of juvenile gastropods (*Margarites* sp.) per m^2 were found during winter (Natalia Shunatova personal communication; Box 4.3).

What may explain observed patterns of reduced seasonality, leading to significant larval abundance and/or recruits even during the Polar Night? First, reproductive strategies are complex, flexible, and numerous across benthic invertebrates. Generalizing to one rather rigid rule based on food limitation and developmental time is overly conservative. Second, food limitation is difficult to assess for many organisms, especially in Arctic systems where autecology is poorly understood (see Renaud et al. 2015b). Recruiting benthic organisms are generally quite small compared to their adult size, and thus may not rely on the same food sources (see Tyler et al. 1992). Thus, we do not understand the primary food sources for many Arctic taxa, and the dominance of deposit and carrion feeders in Arctic benthos suggests fresh phytodetritus may not be the primary food source for even a majority of taxa (Figure 2). Malocostracan crustaceans, for example, are generally predators and opportunistic detritovores/scavengers, and brood their young while continuing to grow during winter (Węsławski et al. 2002).

Even assuming food limitation is a good approximation of the state of benthos, it is unclear which phase of reproduction may be dependent on high productivity periods. Pulses in phytodetritus may fuel gametogenesis, vitellogenesis, and/or larval release, and lag times between these processes and appearance of meroplankton or recent recruits may vary from days to months to even years. Thus, winter peaks in reproductive events could still reflect some link with pelagic processes. Finally, a population's reproductive strategy/timing represents a tradeoff between multiple pressures: e.g. energy acquisition, growing and maturing under various environmental conditions, and avoiding competition and predation. Winter reproductive activity may represent the evolutionarily best compromise for many species.

6.6 Primary producers - kelp

Primary producers require light and inorganic nutrients, but in the Arctic there is often a temporal mismatch in the availability of these two variables (see Chapter 4 for details). Phytoplankton blooms during spring generally result from the coincidence of both resources, along with a stabilized water column (Fig. 4.1). Macroalgae of the genera *Laminaria, Saccharina* and *Alaria*, however, are able to store the chemically-bound light energy as carbohydrates and sugar alcohols derived from summer/autumn photosynthetic periods, but delay growth (lamina elongation) until winter or next spring (Chapman and Lindley 1980, see details in Chapter 4). In fact, up to 90% of annual linear growth in the kelp *Laminaria solidungula*, which occurs under ice cover during winter months (Dunton et al. 1982) when inorganic nutrients are in high concentration (Gerard 1982). Kelps can, thus, accumulate inorganic nitrogen in winter when it is abundant for use in photosynthesis the following spring when light is available (Nielsen et al. 2014). Thus, carbon and nitrogen cycles within the kelp are decoupled due to the current mismatch in periods of organic carbon production and nutrient availability.

Winter and early spring kelp growth provides an enhanced food resources and new settlement substrate for benthic grazers and epifauna (Fig. 6.4). This fresh, potentially nutrient rich, resource available in winter is paradoxical considering the general belief that fresh organic material is only available associated with the spring bloom (see below under 'Detrital pools and advective supplies'). The expected decline in ice cover in most areas of the Arctic is predicted to increase the depth distribution, latitudinal extent, and photosynthetic season for Arctic kelp (Krause-Jensen et al. 2012). In some nearshore areas, however, increased turbidity due to greater glacial or riverine outflow may limit light and lower salinity resulting in negative impacts on kelp (Krause-Jensen et al. 2012; Krause-Jensen and Duarte 2014; Filbee-Dexter et al. 2019; see Chapter 3). It is unknown whether the availability of inorganic nitrogen will be sufficient to support this expected increase in winter growth, or if the current physiological mechanisms that allow Arctic kelps to deal with the mismatch in light and nutrient availability will still function effectively under future conditions. Research at lower latitudes found that *Laminaria* populations in warmer locations stored less carbon and released less particulate carbon than populations in colder locations, suggesting that climate change may affect the amount of carbon fixed and released in some ecosystems (Pessarrodona et al. 2018). See Chapter 4 for more details on macroalgae in the Polar Night.

Fig. 6.4 Kelp (*Saccharina latissima*) with a snailfish (*Liparis* sp.). Photograph is from Ny-Ålesund, Svalbard, in January 2015. Photo: Piotr Balzay

6.7 Benthic processes

Sediment community oxygen demand (SOD) in many areas of the Arctic is at its annual minimum during winter (Bourgeois et al. 2017), presumably due to reduced availability of labile food (e.g. phytodetritus). Rapid response to the arrival of food has been found to increase community respiration rates by a factor of >10 within days (Renaud et al. 2007), most likely caused by deposition of ice algae and an increase in bioturbation (Morata et al. 2011). Experimental studies confirm the overarching effect of food supply on SOD: addition of fresh organic matter to intact sediment cores collected in the middle of winter leads to an almost immediate enhancement in oxygen consumption by sediment communities (Morata et al. 2015). Biogeochemical studies of mineralization rates in Arctic sediments, especially during winter, suggest that these processes are limited more by labile carbon than by low temperatures (e.g. Rysgaard et al. 1998). Thus, the low level of activity displayed by many Arctic sedimentary communities is not caused by some type of dormancy or temperature limitation, but instead by the availability of labile organic matter at the seafloor.

These results reinforce the paradigm of tight pelagic-benthic coupling in the Arctic, but recent studies have indicated that not all benthic processes vary seasonally as in the studies referenced above. Metabolic rates of two common Arctic amphipods are only twice as high in summer as in winter, and are still significant during winter (Węsławski and Opaliński 1997). Bourgeois et al. (2017) reviewed the literature on Arctic carbon cycling/SOD and found little seasonal change in the central Arctic Ocean and the northern Greenland Sea (in contrast to other areas). They suggested these findings could be caused by generally low phytodetrital inputs across the year due to the greater depths, but also noted that few studies have been conducted in these areas. Surprisingly, little seasonal variability is evident in either SOD or bioturbation rates in Kongsfjorden (Nathalie Morata, personal communication). Some west Svalbard fjords have high inventories of marine-derived organic carbon (Zaborska et al. 2016), which may be responsible for higher SOD than in fjords dominated by terrestrially derived organic material. Further, benthic carbon sources such as macroalgae, microphytobenthos, or terrestrial plants can buffer the seasonal signal from pelagic microalgae, thus stabilizing benthic processes through the year (Renaud et al. 2015b). These new results can also provide further understanding of the spatial variability in the response of benthic processes to the Polar Night.

6.8 Detrital pools and advective supply

There is increasing recognition that the food fueling benthic communities varies not only in quantity, which we have long appreciated, but also in quality (Camanyà-Llovet et al. 2017). The relative difference in food quality of phytoplankton and ice algae reaching the Arctic benthos is of considerable interest because the amounts of these two food sources are anticipated to change with changing ice conditions (Mäkelä et al. 2018). This change may profoundly affect benthic community structure and function. While ice algae growth and under-ice phytoplankton blooms may develop earlier in the spring with thinning ice, thereby relieving the benthos from winter food limitation, many communities may be surviving and even thriving on a detrital-based system (Camanyà-Llovet et al. 2017). The source of detritus and sedimentary carbon in general is spatially variable across the Arctic and may be changing with climate change.

Detritus represents the most important energy source for many highly productive marine ecosystems (Camanyà-Llovet et al. 2017). It has even been argued that polar benthic communities prefer lower quality but more permanent food source, which enters the food web via bacterial degradation to a higher but more temporally variable food source (Camanyà-Llovet et al. 2017). While low-quality food may act as a trophic buffer (*sensu* Levinton 1972), there is no evidence from experiments that manipulate food quality and quantity that benthic organisms prefer low to high quality food (see above under 'Benthic Processes'). Kelp contributes to temperate food webs and enhances the growth of some suspension feeders (e.g. blue mussels, *Mytilus edulis*, and barnacles *Balanus glandula*; Duggins et al. 1989), though there is no evidence that the bivalves *Mya truncata* and *Astarte moerchi* consume macroalgae during winter in Young Sound (Bridier et al. 2019). In one Arctic fjord, kelp-derived detritus makes a significant contribution to the benthic food web (Renaud et al. 2015a) and there is little seasonal difference in the benthic food web in this fjord (Kędra et al. 2012). The winter growth of kelp (see above) clearly provides a source of food during the Polar Night and may be increasing in areas with thinning ice, but this contribution of macroalgae to benthic nutrition will vary spatially and among taxa.

Macroalgae are not the only source of carbon to Arctic benthic communities, Arctic food webs also derive energy from terrestrial sources via runoff from rivers and glaciers (Harris et al.

2018; Ambrose unpublished data) (Fig. 6.5). The major Arctic rivers transport approximately 6000 and 700 gigatons of particulate carbon and particulate nitrogen, respectively, to the Arctic Ocean annually (McClelland et al. 2016). This terrestrially derived carbon, at least in one system, includes a large proportion of young organic matter (Arimitsu et al. 2017). Changes in runoff from Arctic rivers (Peterson et al. 2006) and glaciers (Nolan et al. 2001), and increased coastal erosion (Barnhart et al. 2014), will change the input of terrestrial material. Even in areas where we have studied the input of terrestrial carbon to coastal food webs, it is unclear what these changes will mean to the coastal food web (Harris et al. 2018). It is likely that there will be large differences across the Arctic with commensurate effects on benthic communities. Greater runoff lasting longer into the autumn could provide more food for benthic communities during the Polar Night increasing the activity of these communities and their inhabitants during this period and reducing coupling with pelagic productivity cycles.

Fig. 6.5 Melting permafrost and eroding shoreline. Kotzebue Alaska, summer 2006. Photo: William Ambrose

6.9 Climate change perspectives: benthos in the new Polar Night

It is clear from recent studies (Berge et al. 2015b, and those reviewed by Berge 2015a and in this volume), that biological processes do not cease during the Polar Night. In benthic systems, this is particularly dramatic, but strong seasonality does exist in many parameters measured in many

Arctic locations. For example, we have shown here that seasonality of quality and quantity of food inputs to the benthos contributes strongly to determining community structure and function. Exceptions to this, where strong spatial variation and/or low seasonality exists, however, may suggest new underlying mechanisms and drivers. Many of these insights revolve around alternative sources of food, particularly on continental shelves. We expect ongoing climate change to alter many physical, biological, and chemical drivers of these potential food sources, perhaps altering how we view the benthos during the Polar Night.

Climate warming is affecting the Arctic more significantly than most other areas in the world's oceans (ACIA 2005). Declining coverage and thickness of sea-ice, accelerating retreat of glaciers, increased coastal erosion, and increasing air and sea temperatures are likely to affect strongly Arctic coastal benthos and arguably deep-sea benthic communities as well. As mentioned above, kelp communities are expected to expand northward and into deeper waters due to increasing light, and circumstantial evidence already supports this prediction (Krause-Jensen et al. 2012), although effects of grazers, sedimentation, and warmer temperatures may affect growth and survival of early life stages of kelps (Zacher et al. 2016) and the carbon they donate to the ecosystem. Time-series data have also indicated dramatic increases in cover of other macroalgae in some areas (Kortsch et al. 2012). These developments hint at more macroalgal-based food for benthic systems, enhancing resources for both grazers on the macroalgae, and organisms assimilating detrital carbon. This could improve winter-feeding and settlement conditions for benthic organisms, lessening the seasonal extremes we see in many areas today.

Whereas much of the focus of climate change has been, understandably, on sea ice, change in or decoupling of river/sea-ice phenologies is also likely to have strong impacts on benthic communities and carbon cycling in the coastal Arctic (Macdonald et al. 2015, 2018). Later freeze-up and early ice melt will extend the period of river flow into the Arctic coastal region. Whereas winter (November-April) inputs by the six largest Arctic rivers constitutes only 5% of the annual total (McClelland et al. 2016), broadening of seasonality of river flow may substantially increase organic carbon and nitrogen inputs from land. Coupled with permafrost melting and mobilization of modern and ancient carbon and increased coastal erosion, this means greater delivery of terrestrial organic carbon to coastal communities. Due to very little top soil (decomposing terrestrial plants) in Svalbard, however, the expected importance of terrestrial organic carbon is and most likely will remain low for the marine ecosystem. Once thought to be largely inert, recent evidence indicates substantial lability of this material (Bröder et al. 2016) and rapid incorporation into coastal benthic food webs (e.g. Harris et al. 2018). Increased labile organic matter in Arctic sediments will likely significantly affect benthic organisms, both enhancing total annual food supply and sediment organic carbon inventories available for processing during the Polar Night. These processes will exhibit considerable spatial variability, but even small rivers and lagoon systems across the Arctic could show similar trends.

Warmer water temperature will increase the metabolism of benthic organisms increasing their food demand. Even slightly warmer winter water temperature will increase metabolic demands during a time of year when food resources are at a minimum, potentially enhancing food limitation. Reduced summer growth with increasing water temperature has been attributed to metabolic demand exceeding food resources for some Arctic bivalves (Mette et al. 2016). The balance between changing food supply and increased winter metabolic requirements caused by warming temperatures is an important unknown for predicting impacts of climate change.

6.10 Challenges and future research needs

Our review of benthic communities during the Polar Night demonstrates how little we know about the benthos during this period. We know the dietary requirements, reproductive strategies, and growth during the Polar Night for very few species. We need to expand our understanding of the autecology of benthic species, not just during the Polar Night but also for periods immediately before and after, if we are going to appreciate the role of the Polar Night in benthic processes. The initial focus of this work should be on species that are key to the structure and function of Arctic benthic communities (e.g. kelp, hyperbenthos, abundant amphipod and bivalve species).

There have been significant advances in biomarker work in the last decade that make it possible to differentiate the contributions of terrestrial carbon, microphytobenthos, ice algae, phytoplankton, and macroalgae to the nutrition of benthic organisms (e.g. Brown et al. 2013; McMahon and McCarthy 2015; Harris 2018). These methods need to be more widely applied to encompass a greater diversity of organisms and areas across the Arctic if we are to evaluate the importance of different carbon sources in driving benthic process during the Polar Night. We can still not answer the questions: What are the food sources that support benthic activity during the Polar Night? and, how does nutrition during the Polar Night vary across the Arctic or even interannually at one location? These are pressing questions because we predict that carbon sources to the benthic communities will change with climate change. One way to address questions concerning benthic food supply during the Polar Night is to perform complementary natural and manipulative experiments. Benthic processes (growth, reproduction, energetics) in areas with contrasting food supply (quantitative and qualitative) can be compared and important factors isolated with on-board or laboratory experiments.

Prior work during the Polar Night required freezing in ships (e.g. Nansen's expedition, Sheba, CASES, and N-ICE projects) or working from ice islands (see Berge et al. 2015b for review). The lower ice concentrations we are experiencing today means that many research vessels can operate during the winter in ice-covered waters. In the past 10 years, more research stations have begun operating year round across the Arctic (e.g. the new Canadian High Arctic Research Station), and marine observatories are becoming more widespread. Scientists are also relying more on autonomous technology (e.g. moorings, buoys, drones and underwater robots, see Chapter 9) to collect data year round. We need to pose compelling questions about the Polar Night in order to garner research support for winter work, however. Opportunities to use new and existing infrastructures coupled with new methods and technologies can help us address questions about what happens during the Polar Night and the importance of processes during this time to ecosystem structure and function. We should not ignore this period based on prior conceptions.

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Chapter 7

Fish ecology during the Polar Night

Maxime Geoffroy and Pierre Priou

Abstract

This chapter summarizes the winter ecology of the ten most abundant species captured in bottom and midwater trawls during Polar Night surveys conducted in January 2016, 2017 and 2018 in the Svalbard region. It reviews the distribution and feeding habits of these species during the Polar Night as well as their spawning ecology. Most species feed to a certain extent in the dark of night, but their stomach fullness is generally lower and the proportion of empty stomachs consistently higher during winter than the rest of the year. A combination of low irradiance and seasonal factors, such as reduced energy intake during spawning and change in prey availability during winter, likely explains the higher proportion of empty stomachs during the Polar Night. In contrast to Arctic (i.e. polar cod and arctic cod) and arcto-boreal (i.e. Greenland halibut and daubed shanny) fishes that reproduce during winter to benefit from the Arctic spring bloom just after yolk resorption, most boreal species reproduce from spring to autumn which, in the Arctic, results in a mismatch between the apparition of first-feeding planktonic larvae and the production of zooplankton prey. This review thus supports the hypothesis that the ability to reproduce during the Polar Night, rather than the ability to feed, might be the key adaptive trait of Arctic fishes and the main factor limiting boreal fishes to colonise the high Arctic.

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No wise fish goes anywhere without a porpoise.

- Lewis Carroll

7.1 Introduction

Most fishes are visual predators and rely on light to forage. Curiously, several polar and subpolar species thrive during the Polar Night and continue to feed and even reproduce in the dead of night. In the Arctic, seabirds continue to prey on teleost fishes during the winter months. Despite the accumulation of evidence that fishes and their predators continue their biological activities throughout winter (Darnis et al. 2012; Berge et al. 2015a), knowledge on fish ecology during the Polar Night remains an important data gap in polar regions.

Fisheries activities at high latitudes are marginal during winter. Because humans depend on light for their daily activities, the Polar Night was historically a resting period for the few inhabitants of the Arctic and fishing was restricted to survival activities during the darkest months. Inuit generally resumed their subsistence fishing efforts in springtime, after the Polar Night, and mainly focussed on arctic charr (*Salvelinus alpinus*) (Stewart 2005). Ice fishing remains a popular activity in northern communities up to this day. Yet, it is generally not done in the middle of the winter, but rather after the sun comes back, with some exceptions such as the winter-spring (January-May) ice fishery for Greenland halibut (*Reinhardtius hippoglossoides*) in the eastern Canadian Arctic (Hussey et al. 2017). Commercial fishers in the high Arctic mainly target northern shrimp (*Pandalus borealis*) and Greenland halibut in Baffin Bay (Wheeland et al. 2018) and Atlantic cod (*Gadus morhua*), northern shrimp, capelin (*Mallotus villosus*) and redfish (*Sebastes* spp.) in the Barents Sea (Gjøsæter 2009). Although fishing in the southern Barents Sea continues throughout the winter (ICES 2018), most fishing activities in the high Arctic occur prior to the Polar Night in summer and autumn, when Arctic seas are ice-free. Hence, traditional knowledge on fish ecology during the Arctic winter is limited.

Most information on fish ecology during the Polar Night results from overwintering scientific studies and dedicated Polar Night surveys. Since the 1990s, overwintering missions like the North Water Polynya study in Baffin Bay (NOW, 1997-1998; Deming et al., 2002), as well as the Canadian Arctic Shelf Exchange study (CASES, 2003-2004; Fortier et al., 2008) and the Circumpolar Flaw Lead System study (CFL, 2007-2008; Barber et al., 2010) in the Beaufort Sea provided new insight on marine ecosystems in the Canadian Arctic during the Polar Night, including that of fishes. Over the same period, winter surveys from the Norwegian Institute of Marine Research (Jakobsen and Ozhigin 2011) and Polar Night scientific cruises from UiT the Arctic University of Norway and the University Centre in Svalbard (UNIS) (Berge et al. 2015a, c) provided crucial new knowledge on winter ecology of fish in the northern Barents Sea. However, the difficulty of trawling under the ice during scientific surveys results in rather opportunistic sampling lacking spatial resolution at higher latitudes.

This chapter focuses on the winter ecology of Arctic marine fishes. It emphasizes the ten most abundant fish taxa sampled in the northern Barents Sea in January 2016, 2017 and 2018 (> 0.5 % of the assemblage in terms of abundance; Fig. 7.1 and Table 7.1), as well as on *Arctogadus glacialis*, a true Arctic species with a circumpolar distribution. We also summarise the ecology of arctic charr, the most northerly fish found in freshwater and the main anadromous species to really experience the Polar Night. There are, of course, other important fishes present in the Arctic, but if knowledge on the winter ecology of abundant and ubiquitous species is scarce, that of rare species is elusive.

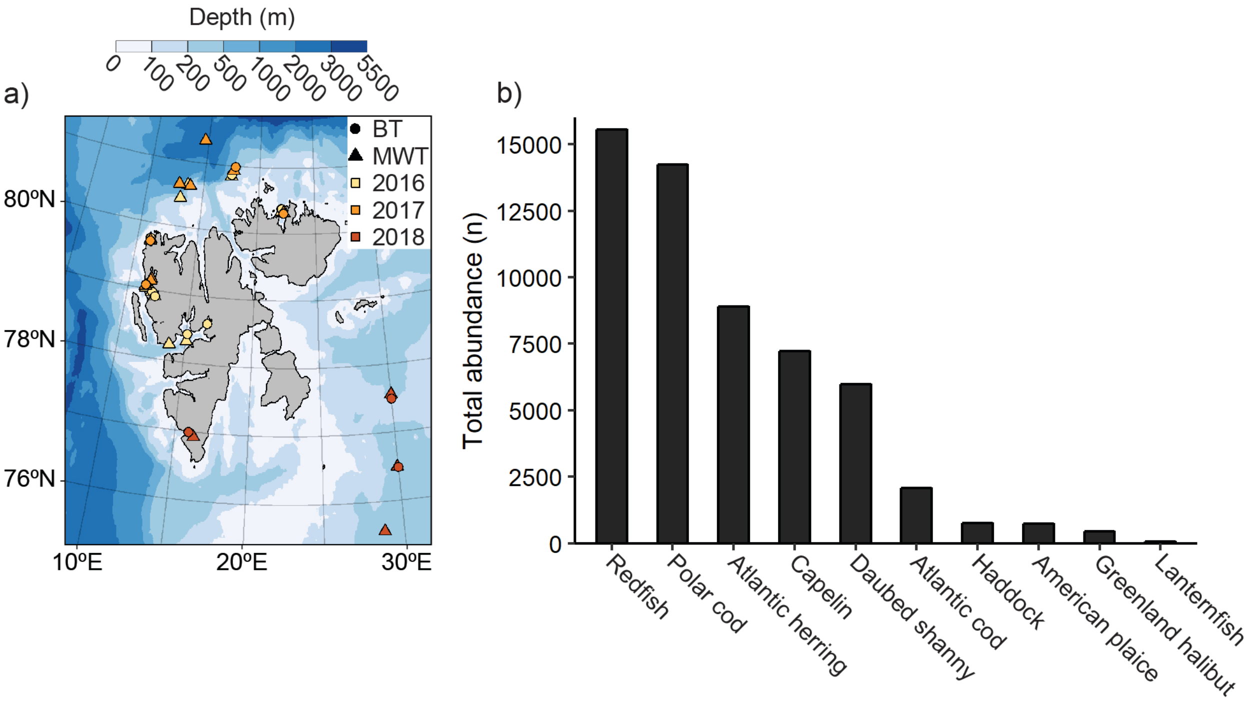

Fig 7.1 (**a**) Map of Svalbard, in the Barents Sea, indicating all stations sampled during the UiT-UNIS Polar Night surveys in January 2016, 2017 and 2018. Stations where bottom and midwater trawls were deployed are indicated. (**b**) Total abundance of the ten most abundant taxa captured in the bottom and midwater trawls during the surveys. Numbers are summed for all nets and all years. Note that herring were mainly captured in coastal fjords and that Myctophidae were generally sampled offshore, below 200 m.

Table 7.1 Details of all species captured in bottom and midwater trawls during UiT-UNIS Polar Night surveys in 2016, 2017 and 2018. Numbers are summed for all nets and all years. The winter ecology of the ten most abundant taxa (highlighted in grey) is discussed in this chapter.

Family	**Common name**	**Latin name**	**Abundance (n)**	**Abundance (%)**
Scorpaenidae	Redfish	*Sebastes* sp.	15,565	27.4
Gadidae	Polar cod	*Boreogadus saida*	14,236	25.1
Clupeidae	Atlantic herring	*Clupea harengus*	8,894	15.7
Osmeridae	Capelin	*Mallotus villosus*	7,232	12.7
Stichaeidae	Daubed shanny	*Leptoclinus maculatus*	5,968	10.5
Gadidae	Atlantic cod	*Gadus morhua*	2,080	3.7
Myctophidae	Glacier lanternfish Lancet fish	*Benthosema glaciale* *Notoscopelus kroyeri*	64	0.1 (1.7)[1]
Gadidae	Haddock	*Melanogrammus aeglefinus*	753	1.3
Pleuronectidae	American plaice	*Hippoglossoides platessoides*	728	1.3
Pleuronectidae	Greenland halibut	*Reinhardtius hippoglossoides*	459	0.8
Liparidae	Gelatinous seasnail	*Liparis fabricii*	194	0.3
Liparidae	Variegated snailfish	*Liparis gibbus*	139	0.2
Cottidae	Atlantic hookear sculpin	*Artediellus atlanticus*	102	0.2
Stichaeidae	Snakeblenny	*Lumpenus lampretaeformis*	57	0.1
Agonidae	Atlantic poacher	*Leptagonus decagonus*	55	0.1
Stichaeidae	Stout eelblenny	*Anisarchus medius*	53	0.1
Cottidae	Moustache sculpin	*Triglops murrayi*	34	0.1
Zoarcidae	Eelpout	*Lycodes* sp.	33	0.1
Zoarcidae	Arctic eelpout	*Lycodes reticulatus*	32	0.1
Anarhichadidae	Atlantic wolffish	*Anarhichas lupus*	25	0.0
Liparidae	Sea tadpole	*Careproctus reinhardti*	14	0.0
Rajidae	Skate	*Amblyraja* sp.	11	0.0
Gadidae	Blue whiting	*Micromesistius poutassou*	9	0.0
Cottidae	Twohorn sculpin	*Icelus bicornis*	7	0.0
Cyclopteridae	Lumpfish	*Cyclopterus lumpus*	3	0.0
Gadidae	Saithe	*Pollachius virens*	3	0.0
Cottidae	Bigeye sculpin	*Triglops nybelini*	3	0.0
Cyclopteridae	Atlantic spiny lumpsucker	*Eumicrotremus spinosus*	2	0.0
Paralepididae	Spotted barracudina	*Arctozenus risso*	1	0.0
Sternoptychidae	Half-naked hatchetfish	*Argyropelecus hemigymnus*	1	0.0
Sternoptychidae	Silvery lightfish	*Maurolicus muelleri*	1	0.0
Zoarcidae	Checkered wolf eel	*Lycenchelys kolthoffi*	1	0.0

[1] When only considering offshore areas

7.2 Fishes in the Arctic: the specialists

A total of 229 marine fish species in 46 families have been recorded in the Arctic Ocean (Mecklenburg et al. 2018). In the Canadian Arctic, 221 marine fish species of 58 families have been listed (Coad and Reist 2018), while ~ 150 species from 52 families inhabit the Barents Sea (Wienerroither et al. 2011). Most Arctic species are purely marine, with less than 35 species exhibiting anadromy, the most iconic and documented of them being the arctic charr, present in both the North American and European Arctic (Coad and Reist 2018). The key species polar cod (*Boreogadus saida,* referred to as arctic cod in North America; Box 7.1) is probably the most widespread and abundant marine fish in the Arctic, on which several fishes, seabird and marine mammal species depend as their main prey (Welch et al. 1992). Polar cod is ubiquitous in Arctic seas and the Central Arctic Ocean (CAO), and has been sampled up to 85°42'N (David et al. 2015). Arctic cod (*Arctogadus glacialis*) is another true Arctic species with a circumpolar distribution reaching at least 88°26'N (Andriashev et al. 1980). Other Arcto-boreal fishes abundant during UiT-UNIS Polar Night surveys in 2016, 2017 and 2018 include the daubed shanny (*Leptoclinus maculatus*) and Greenland halibut (Table 7.1). The winter ecology of these species and that of arctic charr is detailed below. Capelin (*Mallotus villosus*) is sometimes considered an Arcto-boreal species and its distribution reaches the high European Arctic (Gjøsæter 2009), including during the Polar Night. However, it is not abundant in the high North American Arctic and the CAO, and capelin is thus considered a boreal species in this chapter.

7.2.1 Polar cod

The Gadidae polar cod (*Boreogadus saida*) is a key species in the Arctic and can funnel up to 75 % of the carbon between zooplankton and top predators, such as larger piscivorous fish, seabirds, seals and whales (Welch et al. 1992). With *Arctogadus glacialis*, this small fish (< 30 cm) is virtually the only forage species in the CAO and the high Canadian Arctic, where it typically forms > 90 % of the midwater fish assemblage (David et al. 2016; Geoffroy et al. 2016). Knowledge of its winter ecology is thus critical to understand the biology of Arctic fishes during the Polar Night.

Polar cod is associated with a wide variety of habitats including ice-free, nearshore marine waters, brackish lagoons, deeper shelf and slope areas, as well as cracks and channels in ice floes (Gradinger and Bluhm 2004; David et al. 2016; Coad and Reist 2018). This pelagic species occupies the whole water column, from the surface to at least 1,390 m (Chernova 2011). In the Canadian and European Arctic, adult polar cod generally aggregate near the bottom in areas 100 – 500 m deep throughout the year, including the Polar Night (Fig. 7.2). In the western Canadian Arctic, overwintering polar cod show a strong preference for the relatively warm (> 0 °C) and prey-rich Atlantic waters and generally avoid the subzero temperatures of the Pacific Halocline and Polar Mixed Layer (Geoffroy et al. 2011). The upper boundary of the Atlantic layer at 200 m depth coincides with the shelf break, which restricts polar cod aggregations to the continental slope in winter, unless they are being trapped in shallower embayments by currents. In the Svalbard area, polar cod cohabits with several boreal species and is often sampled in coastal fjords, where juvenile polar cod are frequently encountered in kelp forests during the Polar Night (Geir Johnsen; unpublished data). In the Barents Sea, adult polar cod occupies the deeper slope areas during winter, in both Arctic and Atlantic water masses (Renaud et al. 2012; Vihtakari et al. 2018). In all cases, large polar cod (> 15 cm) generally remain near the seafloor, presumably to avoid marine mammal predators, and there is a size segregation with smaller individuals that remain shallower than larger ones (Fig. 7.2). Polar cod larvae stay in the top 20 m with metamorphosis into pelagic juveniles occurring at 2.7 – 3.5 cm. As they grow during their first summer, juveniles start descending and they occupy the top 100 m at the end of the summer. Once they reach 3.5-5.0 cm in length, they descend to depths > 100 m to overwinter. Late hatchers that do not reach the critical size of 3.5 cm at the onset of the sea ice formation in October might recruit under the ice (Fig. 7.2) (Geoffroy et al. 2016). Some individuals recruiting under the ice remain associated with the ice pack (i.e. sympagic) until reaching sexual maturity at age 2 or 3, before descending to depth with their older congeners and migrating back to their spawning grounds. As the ice drifts from coastal regions towards the CAO, so do sympagic polar cod. This process could explain the presence of polar cod under the ice in the Eurasian basin, which would originate from the Laptev and Kara Seas (David et al. 2016).

In the western Canadian Arctic, small polar cod (< 25 g) perform diel vertical migrations (DVM; ; see Chapters 5 and 8) throughout the Polar Night (Benoit et al. 2010). From December to April, they migrate up at night to forage into a cold layer (-1.4 °C) between 90 m and 150 m where the prey to fish ratio is higher as larger individuals stay at greater depths (Fig. 7.3). During the day, smaller cod also remain deeper to avoid predation by seals. This DVM pattern is clearly synchronised with the photoperiod, and the duration and amplitude of vertical migrations increase with irradiance, with an amplitude of < 50 m in December and January to > 150 m in March (Geoffroy et al. 2011). Polar cod can sustain subzero temperatures because of the glycoproteins contained in their blood. In contrast to Antarctic fish which constitutively express antifreeze glycoproteins, the glycoproteins in the blood of polar cod are synthesised when water temperatures diminish below zero. When the water warms up, the synthesis of glycoproteins in polar cod decreases by 35 % (Chen et al. 1997).

The iteroparous polar cod (i.e. which spawns repeatedly over its lifetime) most likely spawns in the lower part of the water column and over the seabed during the Polar Night. The bioacoustic detection of dense winter aggregations of adult polar cod >200 m in the Beaufort Sea suggests that it spawns at depth, in the Atlantic Water mass (Geoffroy et al. 2011; Fig. 7.2). However, it is unknown if polar cod also spawns in shallower coastal areas. Spawning generally occurs under the ice cover and peaks in January and February, but overall spawning events cover a long period including the Polar Night and ranging from November to January in the Canadian Arctic, and from November to March in the Eurasian Arctic (Rass 1968; Craig et al. 1982). In the European Arctic, and possibly elsewhere, gonad development starts around April in females and August/September in males (Nahrgang et al. 2015). Starting in October, mature polar cod migrate to their overwintering grounds to form spawning aggregations. After the Polar Night, these aggregations migrate progressively deeper as light intensity increases, for instance from 220 m to 550 m bottom depth areas in the Amundsen Gulf (eastern Beaufort Sea) (Geoffroy et al. 2011). In the Barents Sea, polar cod can migrate over several hundred kilometres from the northern Barents Sea to one of their known spawning grounds in the south-east of the Novaya Zemlya (Gjøsæter 2009). Exact migration patterns of polar cod are not well described, and it is not clear which proportion of the population spawns on the east coast of Svalbard, in the fjords on the west coast of Svalbard, or in Novaya Zemlya in the southeastern Barents Sea. However, the occurrence of newly hatched larvae in several areas of the Arctic Ocean and of recently spent individuals far from the coast suggests spawning in several areas and habitats (Renaud et al. 2012; Bouchard et al. 2015).

Female polar cod can produce up to 36,000 eggs of 1.9 mm in diameter. Fertilised eggs are buoyant and rise to the ice–water interface (Fig. 7.2) where they are protected from seabirds and larger fishes at depth. They show normal embryonic development between a temperature range of -1.5 ° to 3 °C and a salinity range of 12 to 50 psu. Embryonic development can take as long as 60 to 90 days at the subzero temperatures prevailing under the ice (Nahrgang et al. 2014). The hatching season varies largely between regions. Hatching can start as early as December and January and lasts into July in seas that have a large river discharge, such as the Laptev Sea, Hudson Bay and the Beaufort Sea, but is restricted to April-July where there is little freshwater input, such as the northern Baffin Bay (Bouchard and Fortier 2011). In the Barents Sea, polar cod hatches from February to April (Hop and Gjøsæter 2013). The hatching season persists until the end of June to early August and otolith chemistry of juveniles captured in different Arctic seas indicates an important larval dispersion after hatching. The freshwater thermal refuge hypothesis explains the wide variability in hatching dates. This hypothesis suggests that polar cod hatches earlier in areas with freshwater inputs due to warmer temperature (0 °C vs. -1.5 °C), which maximizes the duration of the growth season and allows a larger size at the end of the summer. Larval survival is limited during the harsh winter conditions, and spring/summer cohorts have better survival rates than winter cohorts. Nonetheless, the latter persist because their larger size in autumn, when the ice cover starts to form, is a survival advantage for their first winter. Recent studies suggest that in the Canadian Arctic, winter hatching might become the rule because a match between yolk resorption in early spring and adequate feeding conditions could become more frequent with an earlier ice breakup (Bouchard and Fortier 2011; Bouchard et al. 2015, 2018).

Larvae hatching in spring and early summer feed on calanoid copepod eggs and nauplii after resorption of the yolk sac. However, the winter cohorts need to start feeding before the emergence of these prey. They presumably prey on the nauplii of small omnivorous copepods that reproduce all year long, such as the small omnivorous *Microcalanus* spp., *Oithona similis* and *Oncaea borealis*, and on the eggs of calanoid copepods that release their eggs in winter such as *Calanus hyperboreus* and *Metridia longa* (Chapter 5). Larvae from the winter cohorts could also feed on other organisms, such as rotifers associated with the brackish waters of river plumes and the microbial food web that remains active in winter in temperate and ice-covered seas (Bouchard and Fortier 2011).

Polar cod is an opportunistic feeder which adapts its diet to spatial and temporal changes in prey availability. In summer and autumn, main prey of small (<15 cm) pelagic individuals are calanoid copepods and amphipods. Gelatinous appendicularians also represent important prey in the northern Bering Sea. In addition, the diet of larger demersal individuals comprises larger prey like euphausiids, amphipods and fishes. In the Svalbard area, the entire polar cod population specialises on *Themisto libellula* in autumn, even when other potential preys are abundant. In contrast, the winter diet, especially that of individuals >15 cm, switches to a strong individual specialisation on teleost fishes, mainly juvenile redfish, daubed shanny and smaller polar cod. Fishes represent up to 24% of the prey of demersal polar cod in January (Cusa 2016).

Its large eyes allow polar cod to detect very low light levels and to forage throughout winter (Box 7.2). However, Cusa (2016) compared stomach contents in January, May, September, and October in the Barents Sea and reported a significantly higher rate of empty stomachs in January and a lower fullness in winter than during other months. This difference could partly result from the more difficult foraging environment prevailing during the Polar Night, with lower visual cues and lower prey abundance, and partly from different seasonal energy requirements. Lower stomach fullness in winter could also result from spawning activities. Although polar cod feeds actively until and right after spawning, it can lose 50 % of its body mass to reproduction and its large gonads (up to 40 % of the body weight) occupy a substantial amount of space in the body cavity which possibly reduces the space available for prey ingestion (Hop et al. 1995).

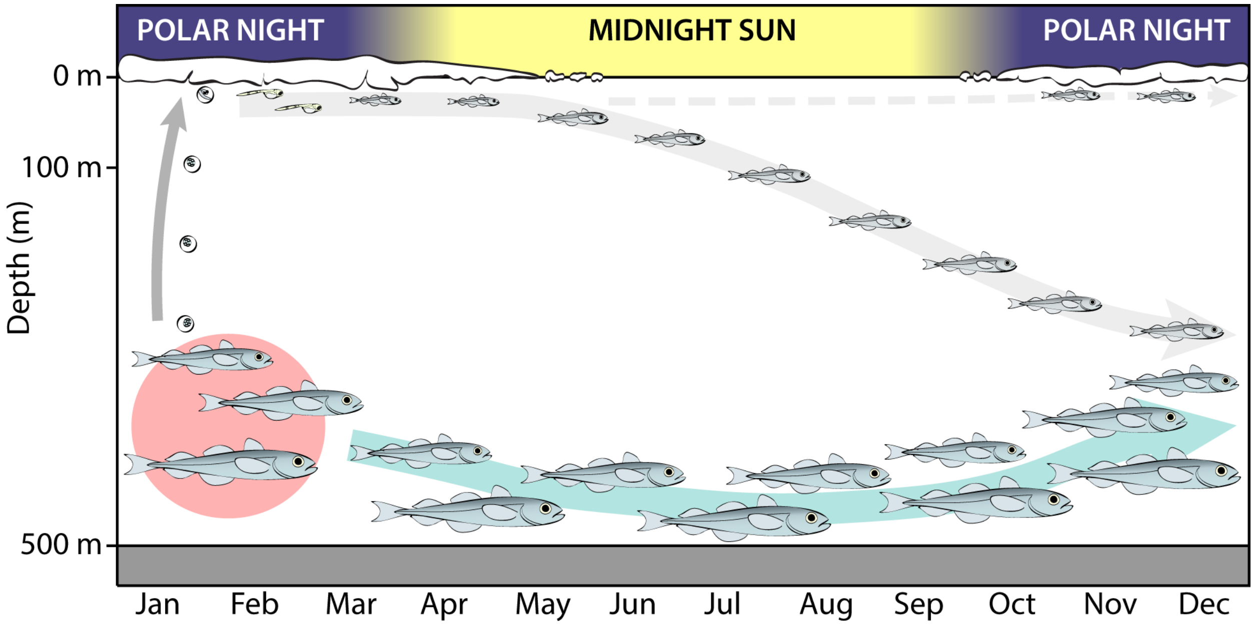

Fig. 7.2 Schematic of the annual life cycle of polar cod deduced from surveys conducted in the Beaufort Sea. The red circle identifies the main spawning aggregations and smaller fishes in the top right corner demonstrate late hatchers recruiting under the ice cover. Note that it is unknown if polar cod also spawns in shallower coastal areas

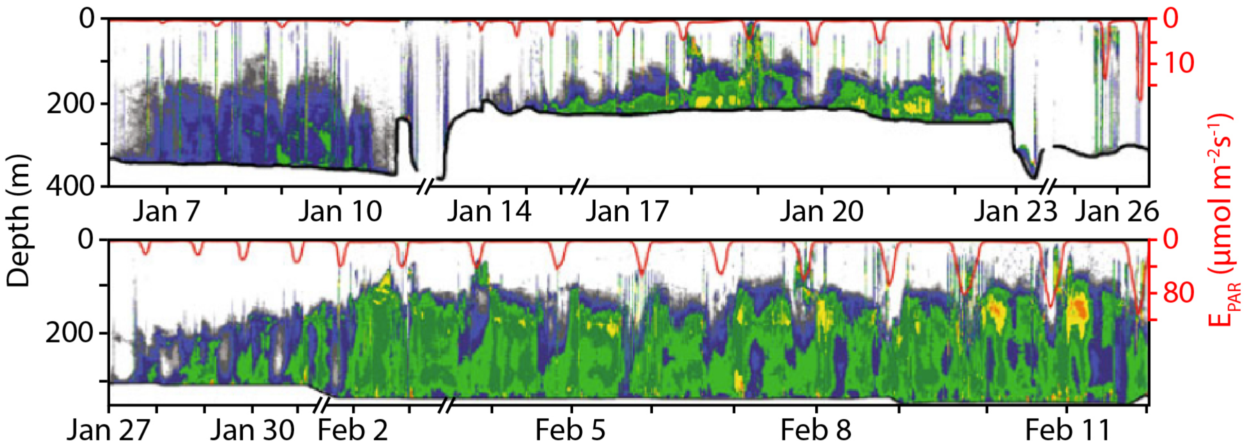

Fig. 7.3 Echogram of volume backscattering strength (Sv) at 38 kHz in the Beaufort Sea in January and February 2008 and showing DVM of pelagic polar cod in relation to irradiance (E_{PAR}, see chapter 3) at the surface (adapted from Geoffroy et al. 2011)

7.2.2 Arctic cod

Arctic cod (*Arctogadus glacialis*), referred to as ice cod in North America (Box 7.1), is a small Gadidae and a sister taxon to *B. saida*. Both species are morphologically similar and sympatric, and juveniles are almost impossible to differentiate morphologically (Bouchard et al. 2013; Madsen et al. 2016). Older individuals of arctic cod can reach 60 cm and weigh 1.5 kg and are generally darker and larger than polar cod (Coad and Reist 2018). Similar to polar cod, arctic cod is a specialist of northern environments with antifreeze glycoproteins in its blood and disproportionally large eyes to detect low light levels in winter (see Box 7.2). Arctic cod is generally less abundant than polar cod and represents ≤ 11% of juvenile Gadidae in Arctic seas (Bouchard et al. 2013).

In the European Arctic, arctic cod was sampled at 155 – 741 m depth with the highest abundance between 300 m and 400 m. Data from the pseudo-abyssal Canadian trench of the Arctic Ocean (80°04′ N – 81°23'N) during the winter period of 1968 – 1969 indicate that *A. glacialis* can also form large swarms under the ice at the end of the Polar Night, in February-March, in the CAO. No under-ice swarms were observed during the core of the Polar Night, from November until February. Arctic cod can inhabit coastal habitats, sometimes in brackish waters, and prefers temperatures between 0.6 °C and 1.5 °C (Jordan et al. 2003; Aschan et al. 2009).

Information about the spawning period of arctic cod is contradictory. The species is generally reported as a winter spawner because a study of the gonads of arctic cod caught in February concluded that spawning must have occurred relatively recently (Andriashev et al. 1980). Süfke et al. (1998) reported low gonado-somatic indices of female *A. glacialis* in August, indicating poorly developed gonads in summer and supporting the idea of winter spawning. However, Borkin and Mel'yantsev (1984) sampled arctic cod in August-September and concluded that spawning must have occurred recently. Furthermore, a ripe female with ovulating eggs was caught in Jan Mayen in July 2008 and fry (26 – 41 mm) were sampled in a bottom trawl deployed in October in the East Siberian Sea (Christiansen 2008). In the Beaufort Sea, a recent study that differentiated arctic cod from polar cod based on genotyping and on the lapillar otolith concluded that both species share the same hatching season from March to July (Bouchard et al. 2013). These observations suggest that both species spawn in winter, during the Polar Night.

Arctic cod larvae (< 15 mm) remain at the ice-water interface, closer to the ice than polar cod larvae, where they feed on cyclopoid nauplii. They have a lower rate of empty stomachs than polar cod larvae and a lower mortality rate, indicating that the capacity to move close to the ice-water interface favours arctic cod, possibly due to higher irradiance to forage (Bouchard et al. 2016). Older individuals continue to feed during the Polar Night (Walters 1961) and their large eyes relative to body size suggest that they can forage under low irradiance conditions (Box 7.2).

7.2.3 Daubed shanny

The Daubed shanny (*Leptoclinus maculatus*), a Stichaeidae with a circumpolar distribution, is highly abundant in the European Arctic. This epibenthic species occupies a wide range of depths ranging from 2 m to ≥ 700 m in the Canadian Arctic and 50 m to 240 m in the Barents Sea. The juveniles are pelagic for the first 2 – 3 years of their life before descending to the bottom, and juveniles contribute a high portion of the fish biomass during the Polar Night in the northern Barents Sea (Meyer Ottesen et al. 2011; Coad and Reist 2018). Daubed shanny composed 10.5 % of the fish assemblage in January 2016, 2017 and 2018 (Table 7.1). As with most polar fish species, its blood contains antifreeze proteins and daubed shanny is usually found in cold water (-1.6 °C to 2 °C) (Christiansen et al. 2012).

Daubed shanny most likely spawns in shallow waters during the Polar Night, and produces less than 1,000 relatively large eggs per female. Spawning occurs in December-January and might extend until late-winter/spring (Murzina et al. 2012, 2013). Early life stages feed during winter (Pekkoeva et al. 2017), and post larval stages possess a unique lipid sac to store large amounts of dietary lipids provided by their calanoid copepod prey during the productive season in prevision of overwintering (Meyer Ottesen et al. 2011; Murzina et al. 2012) (see Chapter 5). Mature daubed shanny continue to feed to a certain extend during the Polar Night, but also likely survive on their lipid reserves during the dark season (Pekkoeva et al. 2018).

7.2.4 Greenland halibut

Greenland halibut (*Reinhardtius hippoglossoides*) is a Pleuronectidae with a circumpolar distribution. It is distributed over a large range of depths (14 m to more than 2,000 m), with larger individuals generally located deeper than smaller congeners (Bowering and Nedreaas 2000). Greenland halibut usually remains between 50 m and 650 m and at temperatures between -1 °C and 3 °C.; colder temperatures can be lethal (Coad and Reist 2018).

This flatfish spawns during the Polar Night, in late autumn and winter. The main spawning period in the Barents Sea starts in November, peaks in December and ends in late January (Albert et al. 1998). There, almost all adults are spent by February. Some males have residual milt after this period which suggests that some spawning may occur several months after the main spawning season, and observation from fisheries suggested spawning concentrations near the coast in early summer (Albert et al. 2001). Greenland halibut spawns slightly later in the Canadian Arctic, with a peak in February and March. The species migrates over long distances to reach spawning areas prior to the spawning season. In the Canadian Arctic, most spawning fish migrate to Davis Strait and Baffin Bay and remain in deep Atlantic waters (Coad and Reist 2018) while some of the eastern Greenland and northern Norwegian sea populations migrate towards Bear Island in the Barents Sea for spawning. Individuals from the Greenland Sea also spawn in Norwegian waters (Albert et al. 1998, 2001). Mature females arrive at the spawning areas in the early autumn and most of them leave in January, while males seem to remain longer. Spawning occurs at depths 600 – 1,000 m in Davis Strait in waters at 4 °C and salinity 34.5 psu, and between 500 m and 800 m in waters ~2 °C along the continental slope between northern Norway and Svalbard in the Barents Sea. Other spawning grounds might not have been clearly identified, for instance in the Beaufort Sea (Albert et al. 1998, 2001; Coad and Reist 2018).

Females produce between 17,000 and 300,000 eggs ranging from 3.7 mm to 4.7 mm in diameter. In January in the Barents Sea, eggs were sampled at depths 100 – 300 m in water masses at 5.6 °C and 35.1 psu. The development time for the fertilised eggs is about 50 days, and larvae and juveniles remain in the pelagic realm for several months after hatching. They settle near the bottom after reaching 80 mm. Eggs and larvae can drift with the currents over hundreds or thousands of kilometres before settling (Ådlandsvik et al. 2004).

Greenland halibut continues to feed in winter, although the percentage of empty stomachs is generally higher during that period. On the continental slope of the Barents Sea, 81 – 94 % of stomachs from individuals sampled during the Polar Night, in December and January, were empty compared to 75 – 79 % in October. However, in western Greenland (62 – 70 °N), only 40 % stomachs were empty in February, which is more than in summer (8 %) but less than in autumn (71 %). Non-spawning and spent individuals have lower rates of empty stomachs and likely continue to feed during the Polar Night (Pedersen and Riget 1993; Hovde et al. 2002). Hence, low feeding activity during spawning, rather than lack of food or difficulty finding prey, may explain higher percentages of empty stomachs in spawning grounds of the Barents Sea in December and January.

Although a bottom dwelling fish, Greenland halibut is capable of energetic swimming in the water column and can forage in the pelagic realm. Smaller individuals likely have a more limited capacity to conduct large-scale vertical migrations and generally feed at greater depths (e.g. > 700 m in the Barents Sea) compared to larger congeners. In the Barents Sea, the diet of Greenland halibut changes with seasons, areas, depths and their size, but teleosts generally dominate the prey assemblage. Juvenile redfish represent the main prey of Greenland halibut in western Greenland in February, and no significant seasonal variations in diet were reported in western Greenland. In the Barents Sea, fish offal and the squid *Gonatus fabricii* dominate the diet of Greenland halibut near Svalbard in January, and herring and capelin dominate the prey assemblage in the southern Barents Sea in autumn. Regional and seasonal differences in diet composition likely result from spatial and temporal variations in abundance and distribution of their major prey species and suggest opportunistic feeding (Pedersen and Riget 1993; Hovde et al. 2002).

7.2.5 Arctic charr

The Salmonidae arctic charr (*Salvelinus alpinus*) remains as freshwater resident or migrate to the ocean in summer to feed. Anadromous individuals usually migrate back to their overwintering ground in freshwater streams, rivers and lakes in late July and August. They spawn in September and October and the eggs rest in the substrate, often in shallow pools below rapids, during the Polar Night. Hatching occurs in spring, around April, and alevins (i.e. newly spawned charr still carrying the yolk) continue to develop in gravel before emerging as free-swimming fry in July (Klemetsen et al. 2003; Svenning et al. 2007).

Measurements of pineal melatonin production in overwintering arctic charr from a high Arctic lake in Norway showed a diel cycle of production, with higher values at night. These results indicate that arctic charr keep track of time during the Polar Night with an endogenous clock (see Chapter 8). Such diurnal cycles of melatonin production were not observed during the midnight sun period (Strand et al. 2008).

In Canada, arctic charr mainly feeds in summer, a period during which they can double their body weight. However, there is evidence that the species also feeds during the Arctic winter (Coad and Reist 2018). In subarctic and high Arctic lakes of Norway, overwintering charr inhabit the littoral zones where they feed on benthic prey. There, arctic charr feeds throughout winter, but its diet is less diverse than during summer and there is a higher abundance of empty stomachs (e.g. 35 % vs. 4 %). Mean stomach fullness is also lower in winter, with an average of 20 % in January compared to 60 % in June. Larger arctic charr (> 15 cm) are mainly piscivorous, including cannibalism. Small charr (<15 cm) are plankton specialists and prey on amphipods, copepods, caddis larvae, chironomid larvae, and plecopteran larvae. Smaller charr also feed on ephippial *Daphnia* when they are present. A lower abundance of preferred prey could partly explain the higher ratio of empty stomachs in winter. Chironomid larvae dominated stomach contents in winter, and a study suggested that high incidence of mud in the stomachs may indicate that arctic charr forage for chironomid larvae in bottom sediments using tactile and chemical senses during the darkest months. In arctic charr, the intake of energy during winter in subarctic lakes of Norway only covers routine physiological maintenance, which suggests that growth and intense foraging activity are limited at that time of the year. Food intake gradually increases with the increasing light (Klemetsen et al. 2003; Svenning et al. 2007).

7.3 Borealization of the Arctic fish community during the Polar Night

Compared to other Arctic seas, the Barents Sea has experienced the fastest rate of borealization (or “Atlantification”) of its fish community (Fossheim et al. 2015). The region is the main gateway to the Arctic Ocean for boreal species. The abundance of North Atlantic fish, such as Atlantic cod and redfish, has increased in the northern Barents Sea since the 1990s. The northern range expansion of boreal species has resulted in lower abundances of the Arctic specialist polar cod in the region, which has retreated towards the cold-water masses of the CAO (Eriksen et al. 2015). There are indications that other Arctic regions have also experienced an increased abundance of boreal species. For instance, over the past two decades capelin has replaced polar cod as the main forage species in Hudson Bay and is becoming increasingly abundant as prey for marine mammals in Baffin Bay (Provencher et al. 2012; Gaston and Elliott 2014). The increase in water temperatures (Chapter 2) is likely the main factor behind the northwards range expansion of boreal species, with boreal species following the increased influx of warmer Atlantic and Pacific waters into the Arctic (Woodgate et al. 2012; Smedsrud et al. 2013; Fossheim et al. 2015; Polyakov et al. 2017).

7.3.1 Boreal species in the Polar Night

Kaartvedt (2008) hypothesised that the extreme dynamics of light regime of polar regions, in particular during the Polar Night (Chapter 3), hinders the positive effects of climate change on the survival of mesopelagic boreal fish at high latitudes by greatly reducing their feeding success (see Box 7.3). Yet, most boreal fish species continue to forage to a certain extent during the Polar Night (Berge et al. 2015a). Moreover, midwater and bottom trawls conducted in the Barents Sea (close to the Svalbard archipelago) in January 2016, 2017 and 2018 yielded high abundances of boreal fish species (63.8 %; Table 7.1 and Fig. 7.4). Of these, the most abundant were juvenile redfish (27.4 %), juvenile herring (15.7 %), juvenile capelin (12.7 %), juvenile Atlantic cod (3.7 %), lanternfishes (1.7 % in offshore areas), juvenile haddock (1.3 %), and American plaice (1.3 %).

Fig. 7.4 Catch from Svalbard in January 2016 comprising polar cod, juvenile redfish, capelin, and northern shrimp (*Pandalus borealis*). Photo: Rolf Gradinger

7.3.2 Redfish

The Scorpaenidae beaked redfish (*Sebastes mentella*) and golden redfish (*Sebastes norvegicus*) are the most common redfish species in the Arctic (Stransky 2005; Cadrin et al. 2010). A third species of *Sebastes* is present in Canada, the Acadian redfish (*Sebastes fasciatus*), but the latter usually remains in sub-Arctic regions. The occurrence of golden redfish in Canadian Arctic waters still requires confirmation. Beaked redfish has the vastest distribution of the three species and the northernmost distribution in the Barents Sea and Canadian Arctic. *Sebastes* spp. are morphologically hard to differentiate. They are long-lived, slow growing, late maturing (6 - 19 years, with 50 % of specimens being mature at age 10 – 11), iteroparous and ovoviviparous (i.e. fertilisation, egg development and hatching occur internally before the larvae are extruded) (Planque et al. 2013). Redfish has strong year classes followed by years with very low recruitment (Drevetnyak and Nedreaas 2009). The high abundance of juvenile beaked redfish from 2016 to 2018 results from strong cohorts and is not necessarily representative of all years.

In the Barents Sea, beaked and golden redfish exhibit pelagic and demersal behaviours, although the beaked redfish is more pelagic and lives in deeper waters than the golden redfish. In general, age-0 redfish are pelagic in deep regions and bottom dwelling in coastal areas (Drevetnyak et al. 2011). For instance, juvenile beaked redfish dominated the offshore pelagic fish community north of Svalbard in January 2016 and 2017, during the Polar Night (89% and 85% of the biomass, respectively; Fig. 7.5) (Geoffroy et al. 2019). In contrast, in Kongsfjorden (western Svalbard) bottom dwelling juvenile beaked redfish were observed at 80 m depth in front of glaciers and in shallow kelp forests (Geir Johnsen, unpublished data). Adult redfish usually live between 300 m to 500 m, and beaked redfish reach depths down to 1,000 m. Redfish remains at temperatures varying from 2 to 8 ºC and prefers slightly warmer temperatures for overwintering (4 – 5 ºC) (Planque et al. 2013).

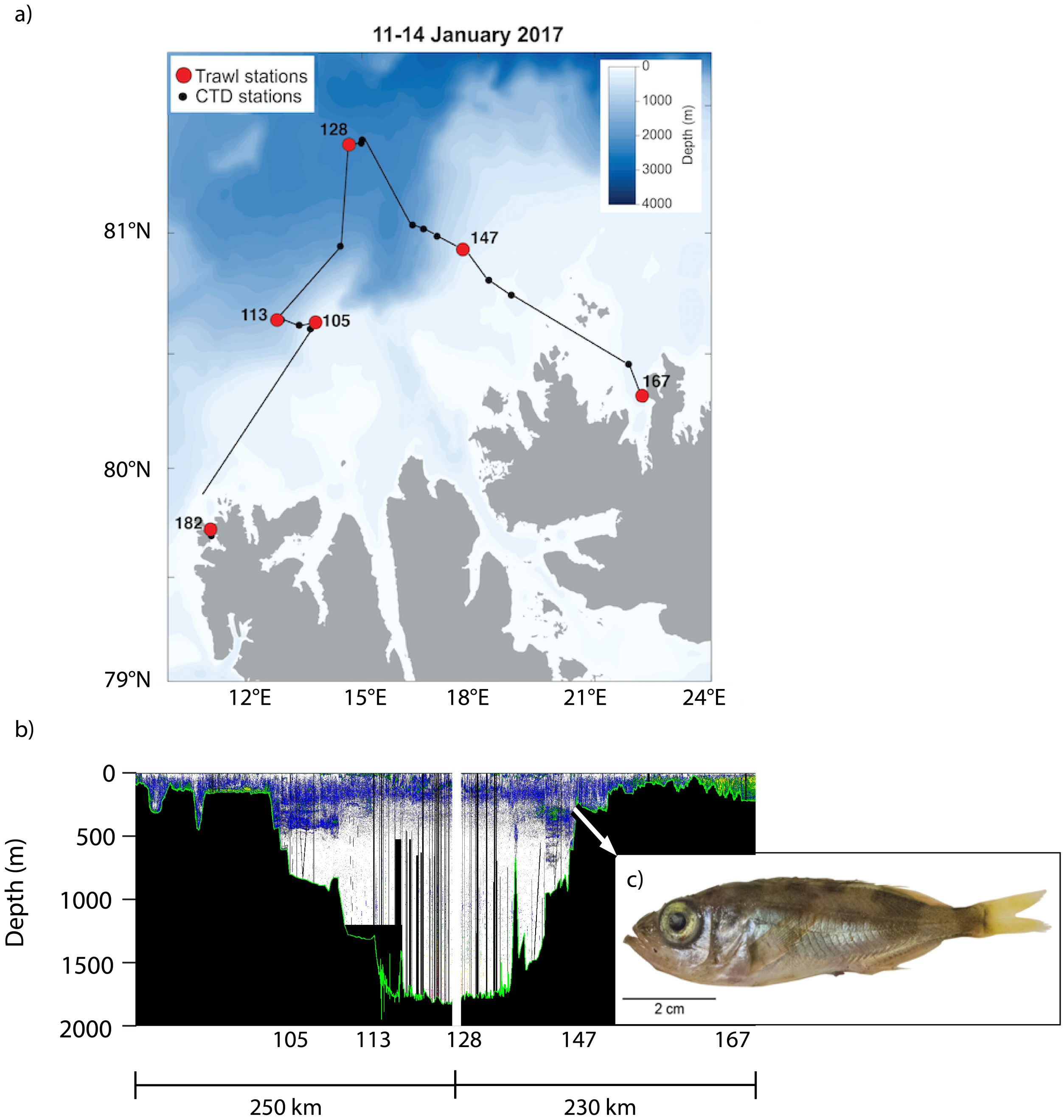

Fig. 7.5 (**a**) Track and trawling stations of the RV *Helmer Hanssen* north of Svalbard in January 2017; (**b**) Corresponding volume backscattering strength echogram of the pelagic layer at 38 kHz; (**c**) Juvenile redfish dominated the pelagic fish assemblage (adapted from Geoffroy et al. 2019).

The spatial distribution of redfish is closely linked to that of relatively warm Atlantic water (Drevetnyak et al. 2011). In the Barents Sea, adult beaked redfish remain in feeding areas (e.g. the deep-water of the western Barents Sea and the continental slope of western Svalbard) during the Polar Night (Drevetnyak and Nedreaas 2009). At the end of winter, they start migrating towards the continental slope of Bear Island and northern Norway where they aggregate for larval extrusion (Drevetnyak and Nedreaas 2009). In the Canadian Arctic, redfish are found in Baffin Bay, Hudson

Strait and further down in the Labrador Sea (Cadrin et al. 2010). Migration patterns in the Canadian Arctic are not documented.

Redfish copulates in the feeding areas between August and November, several months prior to the larval extrusion in March-April. Female beaked redfish release about 12,000 to 80,000 larvae ranging from 6 – 9 mm in length (Drevetnyak et al. 2011). In the European Arctic, larvae ascend to the surface layer (0 – 60 m) and drift with currents into the western and northwestern Barents Sea, and especially towards the Svalbard area where they settle (Drevetnyak and Nedreaas 2009). Juvenile redfish spend the first years of their life in the nursery grounds of the Central Barents Sea and around Svalbard.

Redfish feeds throughout the year, including during the Polar Night, but the mean stomach fullness is lowest in winter and highest in spring (Pedersen and Riget 1993; Dolgov and Drevetnyak 1995, 2011). For instance, the proportion of redfish with empty stomachs in west Greenland reaches 80 % in winter (February), but only 15 – 33 % in spring (Pedersen and Riget 1993). The diet of juveniles is mostly composed of planktonic crustaceans like copepod nauplii and copepodites, hyperiids, euphausiids, and various decapods, but feeding of juveniles is usually low during the Polar Night. Its diet switches in autumn and winter compared to the summer, with less *Themisto* spp. and more teleosts, including cannibalism (up to 43 % of prey biomass). In winter, the stomach contents of redfish in western Greenland is dominated by redfish (for larger individuals 10 – 24 cm) and copepods for smaller individuals (5 – 9 cm). The increased importance of juvenile redfish in the diet of redfish > 9 cm seen in autumn and winter in south-west Greenland was related to an increased abundance of age-0 individuals over the shelf during those months and suggests opportunistic feeding (Pedersen and Riget 1993). Euphausiids, juvenile fish (Atlantic cod, polar cod, capelin, and cannibalism on juveniles), gammarid amphipods, and shrimp make up the bulk of the diet of beaked redfish in the Barents Sea (Dolgov and Drevetnyak 2011).

7.3.3 Herring

Herring is a pelagic, planktivorous, and schooling fish of the Clupeidae family, which is dominated by warmer water species. Atlantic herring (*Clupea harengus*) and Pacific herring (*Clupea pallasii*) inhabit sub-Arctic regions. In the northeast Atlantic, Atlantic herring overwinters in the Norwegian Sea and uses the southern Barents Sea as a nursery ground (Dragesund et al. 1980). Herring also inhabits fjords dominated by warm and saline Atlantic water masses in western Svalbard (Berge et al. 2015b and references therein), which is where herring were sampled in January 2016-2018. In the Canadian Arctic, the northern limit of Atlantic herring distribution is the Labrador Sea and Pacific herring occasionally schools on the shores of the Beaufort Sea. Pacific herring does not perform extensive migrations. Herring prefers temperatures between 0 °C and 11 °C, but can tolerate colder temperatures due to the antifreeze proteins in its blood (Ewart and Fletcher 1990). Atlantic and Pacific herring are usually distributed in coastal areas from the surface to 150 m depth, but they have been sampled down to 364 m and 475 m, respectively. During the Polar Night, juvenile herring in fjords of the west coast of Svalbard aggregate around 50 m depth, halfway through the water column.

Atlantic herring spawns on the Norwegian coastal banks in spring, from February to March (Toresen and Østvedt 2010). Pacific herring spawns in summer, but the timing varies between regions (Hay 1985). For instance, Pacific herring spawns in June in the coastal Beaufort Sea, and from May to September in the Kara Sea. Female Atlantic herring lay between 20,000 and 90,000 eggs (Baxter 1959). The fecundity of Pacific herring in the Arctic is slightly lower with 4,300 to 41,000 eggs per female (Paulson and Smith 1977).

Eighty-four to one hundred percent of herring sampled in Svalbard in January had empty stomachs, indicating little to no feeding during the Polar Night. Individuals that were feeding targeted *Calanus glacialis* and *Calanus finmarchicus*, and some euphausiids like *Thysanoessa* spp. In spring, juvenile herring also feed on capelin larvae and juveniles in the southern Barents Sea and strong year classes of herring can negatively affect capelin recruitment (Gjøsæter and Bogstad 1998).

7.3.4 Capelin

Capelin (*Mallotus villosus*) is an Osmeridae with a circumpolar distribution. This small, pelagic, planktivorous, lipid-rich, and schooling species can be found from the surface down to 1,000 m. Capelin is most abundant in relatively warm waters (1.5 °C to 6.5 °C) but can occasionally tolerate colder temperatures (down to -1.5 °C) without antifreeze proteins by entering a supercooling state (i.e. it can survive temperatures below their body fluid freezing point) (Raymond and Hassel 2000; Dalpadado and Mowbray 2013). However, mass mortality of capelin has been reported at subzero temperatures (Templeman 1965). It is a key species of subarctic ecosystems of the North Atlantic where it funnels the energy between secondary producers and higher predators. On the Atlantic side, capelin is abundant in the Barents Sea and along the coastline of Norway, around Iceland, on both sides of Greenland, from Baffin Island down to Cape Cod, and in Hudson Bay (see figure 1 in Dalpadado and Mowbray, 2013). On the Pacific side, capelin occurs in the Sea of Okhotsk, the Bering and Chukchi Seas, and in the Beaufort Sea. The abundance of capelin has increased in the Arctic over the last 30 years (Gaston and Elliott 2014; Vihtakari et al. 2018). In the Barents Sea, capelin is distributed along the Polar Front (i.e. the area where Atlantic and Arctic water masses meet) during the Polar Night, including the Hopen Deep and the Bear Island Channel, but not on the slope (Gjøsæter 1998; Eriksen et al. 2017). The position of the Polar Front differs between cold and warm years and defines the northern range limit of capelin. During the Polar Night, immature and maturing capelin are vertically segregated by age. Maturing fish are found closer to the seabed and immature fish higher in the water column (Luka and Ponomarenko 1983).

In late winter, mature capelin from the Barents Sea migrate southwards to the North coast of Norway and Russia where they gather in schools to mate and spawn (Gjøsæter 1998). There, spawning usually takes place in March – April but they can also spawn in summer (Hedeholm et al. 2011). Sporadic late spawning events in summer also became more frequent over the last decades. In autumn, capelin migrates northwards and offshore to overwinter in its main feeding grounds in the Barents Sea (Gjøsæter 1998). Capelin populations of the Canadian Arctic also perform extensive migrations towards the shores of Hudson Strait, Baffin Island, and the Beaufort Sea to spawn in summer, usually from June to August, but precise migration routes have not been identified yet (Carscadden et al. 2013)..

Most capelin are semelparous (i.e. they spawn once in their lifetime and most individuals do not survive the spawning season) (Christiansen et al. 2008). Females produce between 7,000 to 60,000 eggs ranging from 0.65 mm to 1.0 mm in diameter (Coad and Reist 2018). They lay sticky eggs on beaches or on the seabed, usually on gravel or sand (Rose 2005; Olsen et al. 2010). Hatching time varies between 25 and 70 days depending on temperature (2 °C and 7 °C, respectively) (Gjøsæter 1998). Fry ascend to the surface layer and, in the Barents Sea, are transported with currents towards nursery grounds in the Central Barents Sea and on the West coast of Svalbard (Gjøsæter 1998).

Capelin forages actively in autumn with > 90 % of individuals feeding during this period. The proportion of empty stomachs drastically increases during the Polar Night (Gjøsæter 1998).

For instance, > 50 % of adult capelin sampled on the continental shelf of the Barents Sea during the Polar Night had empty stomachs in winter. Juveniles do not feed during winter and survive on large lipid reserves built in autumn. Capelin perform DVM and are primarily daytime feeders (Mowbray 2002). In winter, vertical migrations are not common and they stay away from freezing temperatures of the surface layer. Euphausiids, amphipods, and copepods make up the bulk of the diet of adult capelin. Euphausiids (*Thysanoessa inermis* and *Thysanoessa raschii*) is the preferred food item of capelin and supplement 70 – 100% of the energy intake of large individuals. The contribution of amphipods to the diet of capelin increases with capelin size, but varies from one area to the other, e.g. *Themisto libellula* contribution will be more important in Arctic water masses while *Themisto abyssorum* dominates in water masses of Atlantic origin. Capelin also eats the eggs of its own species (Slotte et al. 2006). Feeding habits during winter are not documented in the Canadian Arctic.

7.3.5 Atlantic cod

The emblematic Gadidae Atlantic cod (*Gadus morhua*) is abundant in the North Atlantic and subarctic Seas. Atlantic cod has been fished for more than 3,500 years and is still targeted by important commercial fisheries, in particular in the Barents Sea (ICES 2018). Atlantic cod is benthopelagic and inhabits continental shelves with different types of substrate (rocky and pebbly, gravelly, sandy, or muddy). This groundfish is most abundant between 100 and 300 m in the Barents Sea and found mainly above 150 – 200 m depth in the Canadian Arctic, although it has been recorded down to 700 m (Olsen et al. 2010; Coad and Reist 2018). In the Barents Sea, juvenile and adult Atlantic cod are mostly sampled near the bottom at depths between 88 m and 285 m and represented 3 to 6 % of the fish assemblage in bottom and mid water trawls in January 2016, 2017 and 2018. Cod tolerates a wide range of temperatures (from -2 °C to 20 °C), but usually remains in water masses between 0 and 12 ºC (Drinkwater 2005). Juvenile Atlantic cod tend to occur at wider ranges of temperatures and salinities than adults.

During the Polar Night, Atlantic cod of the Barents Sea are located in ice-free areas south of the Polar Front. Some groups of age 4 cod start migrating towards the Norwegian coastline in late winter to follow the migration of capelin (Olsen et al. 2010). Adult cod start migrating in January towards spawning areas on the coast of northern Norway and return to the Barents Sea after spawning to feed on capelin and herring. Atlantic cod inhabits the western fjords of Svalbard (Renaud et al. 2012), where historical fisheries occurred and where they are frequently observed at depths >50 m as well as in shallow kelp forests (Geir Johnsen, unpublished data). In the Canadian Arctic, Atlantic cod inhabits the Labrador Sea and Baffin Bay. Atlantic cod from Baffin Bay could historically be related to three populations landlocked on Baffin Island. In northern Canada, not all individuals perform extensive seasonal migrations. Those that migrate alternate between offshore areas at 3 – 4 °C during winter and coastal areas in summer where they feed on spawning capelin (Rose 2007).

Atlantic cod is iteroparous and a batch spawner (i.e. females deposit eggs on more than a single occasion throughout a spawning season). The spawning season spans from February to April in Canada and west Greenland, as well as in the Barents Sea (Ellertsen et al. 1989; Rose 2007). Atlantic cod aggregate over the shelf at temperatures between 4 and 6 ºC during the spawning season. Fecundity is related to size and females can produce between 23,000 and 12,000,000 eggs. Eggs are spherical with a diameter ranging from 1.2 mm to 1.6 mm, and are released at depths from 50 m to 150 m. In the European Arctic, eggs and fry are transported from the Norwegian coast by the North Atlantic current and the Norwegian Coastal current into the Barents Sea and the west coast of Svalbard (Helle 1994). Hatching occurs 2 – 3 weeks after fecundation, and juveniles migrate towards the bottom when they reach a length between 2.5 cm and 5.0 cm (Olsen et al. 2010).

Similarly to the other species of Gadidae such as polar cod and haddock, Atlantic cod continues to feed during the Polar Night. In January 2016, 2017 and 2018, 87 % of Atlantic cod had at least one prey item in their stomach. Decapoda make up the bulk (42 %) of the diet of juvenile Atlantic cod during the Polar Night in the Barents Sea. Other common food items comprise *Calanus glacialis* and *C. finmarchicus* (13 %), the benthic amphipod *Anonyx* spp. (11 %) and *Themisto libellula* (8 %). The diet of Atlantic cod is related to size, and the importance of fishes as prey increases with the length of Atlantic cod, with a preference for capelin (Yaragina et al. 2011). During years of low capelin abundance, Atlantic cod can feed on herring, polar cod, redfish, haddock, American plaice, and smaller Atlantic cod. Atlantic cod preys more intensively on benthic organisms during the Polar Night compared to the rest of the year, which could be related to an increased use of tactile senses under low irradiance (Jönsson et al. 2014).

7.3.6 Haddock

Haddock (*Melanogrammus aeglefinus*) is a bottom dwelling Gadidae relatively abundant in the Atlantified regions of the European Arctic, but is absent from the Canadian Arctic (Olsen et al. 2010). It inhabits coastal areas < 250 m deep and prefers temperatures ranging from 2 °C to 10 °C. Haddock is more sensitive to cold than Atlantic cod and usually avoids waters near or below 0 °C (Gjøsæter 2009). Hence, it mostly remain south of the Polar Front. Adult haddock migrate over long distances between their summer feeding grounds in the eastern and coastal waters of the Barents Sea and their overwintering grounds on the western side of the Barents Sea and on the western coast of Svalbard (Russkikh and Dingsør 2011).

In late winter, haddock starts migrating towards the continental slope of Norway where it spawns between March and June, with a peak in late April. Similarly to Atlantic cod, it is a batch spawner with high fecundity (Solemdal et al. 1997). Spawning occurs in the water column over a wide range of depths, usually from 300 m to 600 m and at temperatures between 4 °C and 6 °C (Bergstad et al. 1987). Haddock eggs are pelagic and positively buoyant and ascend towards the surface before hatching at the water-atmosphere interface (Solemdal et al. 1997). The eggs drift with currents from the spawning areas into the Barents Sea and towards the coast of Svalbard (Solemdal et al. 1997). The incubation period lasts about two weeks, depending on the temperature (Gjøsæter 2009).

Haddock continues to feed during the Polar Night, but the ratio of empty stomachs is higher than during summer. Although a bottom-dwelling species, juvenile haddock are pelagic during the Polar Night in the Barents Sea and the eastern part of the Norwegian Sea. Young stages feed on polychaetes and benthic amphipods (52 % in January 2018), pelagic zooplankton (*Themisto libellula*, *Thysanoessa* spp., *Calanus glacialis* and *Metridia longa*; total of 34%), and fishes (14 %). The contribution of fishes to the diet of haddock increases with haddock length. The diet of haddock differs from that of Atlantic cod by the larger contribution of benthic organisms and crustaceans than fish (Gjøsæter 2009).

7.3.7 American plaice

The flatfish American plaice (*Hippoglossoides platessoides*), also known as American dab, long rough dab, or rough dab, is part of the Pleuronectidae family. It is one of the most abundant and widely distributed flatfish in the northeast and northwest Atlantic. American plaice inhabits both sides of the Atlantic, in the Barents Sea on the European side and in Baffin Bay on the Canadian side (Wienerroither et al. 2011; Coad and Reist 2018). American plaice is eurybathic and inhabits a wide range of depths varying from 18 m to 3,000 m, but prefers regions between 50 m and 300 m with temperatures 0 °C – 4 °C and salinities 34.5 – 35.0 psu. It can, however, survive at temperatures from -1.8 °C to 7.8 °C and salinities between 33.3 and 35.2 psu. Antifreeze proteins have not been observed in living individuals, but American plaice possess antifreeze protein genes that could express antifreeze proteins seasonally (Enevoldsen et al. 2003).

In the Barents Sea, American plaice gathers to feed around Bear Island and the Great Bank south of the Polar Front at the beginning of the Polar Night, from October to December. It spends the rest of the Polar Night in wintering areas on shallow banks in the central and eastern Barents Sea and on the West coast of Svalbard. Spawning starts in the western areas in early March and subsequently moves eastward and northwards as the water warms (Dolgova and Albert 2011). In the Canadian Arctic, American plaice forms dense spawning aggregations in the main streams of the warm Atlantic current in April – May, promoting an efficient dispersion of juveniles. Spawning in the Canadian Arctic follows a South to North gradient and starts as early as March and ends in June for the southern populations in the northwest Atlantic and as late as July-August for individuals of the Labrador Sea and west Greenland (Coad and Reist 2018). American plaice shows fidelity to its spawning ground and generally returns to the same area to spawn. The fecundity of female American plaice depends on fish length and they commonly produce between 33,000 and 350,000 eggs, but larger individuals produce up to 2.2 million eggs. In the Barents Sea, fecundity is higher around Svalbard than elsewhere. Spawning occurs at depths of 125 – 250 m and at temperatures of -1 °C to 4 °C. Eggs are 2.8 mm in diameter and positively buoyant (Dolgova and Albert 2011). Larvae hatch after 11 to 14 days of incubation depending on the temperature. Growth is generally slow and is slower in cold Arctic waters. Larvae live pelagically and juvenile settle on the bottom when they reach a length of ~35 mm (Walsh 1996).

American plaice is an opportunistic feeder that can adapt to various ecosystems. There is a seasonal variation in the feeding activity of American plaice, and they tend to mostly feed during the summer and reduce their foraging activities during winter time (Berestovsky and Matishov 2001). Juvenile feed on copepod nauplii and once they settle at the bottom shift to a more benthic diet. The preferred prey items of adults in the Barents Sea are fishes (49.8 % of the biomass), mostly capelin, and benthic invertebrates like ophiuroids and polychaetes (20 %). The diet of American plaice depends on prey availability and interspecific competition (Dolgova and Albert 2011).

7.3.8 Lanternfish

Myctophidae, also called lanternfish because of their photophores that produce bioluminescence (Chapter 3), could represent the greatest biomass of any vertebrate family in the world (Irigoien et al. 2014). During the Polar Night, both glacier lanternfish (*Benthosema glaciale*) and lancet fish (*Notoscopelus kroyeri*) were sampled off the northern coast of Svalbard and represented up to 1.7 % of the fish abundance in offshore areas (Table 7.1). In the Barents Sea, Myctophidae inhabit warm Atlantic water masses and areas > 300 m. In the Canadian Arctic, they are generally caught at depths ranging from 300 m to 1,400 m (Coad and Reist 2018).

The ecology of glacier lanternfish is better documented than that of lancet fish. Glacier lanternfish is ubiquitous in the North Atlantic and inhabits the Svalbard area in the Barents Sea and the northern Baffin Bay in the Canadian Arctic. Glacier lanternfish is a batch spawner and releases up to 5 batches of eggs during a single spawning season. In the Canadian Arctic, spawning occurs partially during the Polar Night, in the early autumn – winter so that larvae appear in spring (April – May) (Coad and Reist 2018 and references therein). On the other side of the Atlantic, in the Barents Sea, glacier lanternfish spawn in June-July. Females produce on average 750 – 800 eggs, but can reach up to 2,000 eggs (Gjøsæter 1973a).

The main prey of myctophids in the Arctic are calanoid copepods and euphausiids. Their feeding activity during the Polar Night is not documented, but *Benthosema glaciale* continues to feed during winter in western Norway and, despite a higher ratio of empty stomachs, 70 % of individuals sampled during that season had at least one prey item in their stomach (Gjøsæter 1973b). Even if they do not feed as much during the Polar Night, this lipid-rich fish possesses large subcutaneous and intramuscular lipid reserves to overwinter (Falk-Petersen et al. 1986).

7.4 On the advantages of spawning during the Polar Night

One of the most striking facts about fish ecology during the Polar Night is the importance of that period for reproduction (Table 7.2). Twenty percent of fish species in the Barents Sea and Svalbard area spawn in winter, including the abundant polar cod, Greenland halibut and daubed shanny (Jakobsen and Ozhigin 2011). Several species of Antarctic fishes, including the abundant Antarctic silverfish, also span during the Austral winter (Di Prisco et al. 1998). Interestingly, most of the winter spawners are polar species, while abundant boreal species like redfish, herring, capelin, Atlantic cod and haddock rather reproduce in spring, summer or autumn (Table 7.2). Hence, the ability to utilise the Polar Night for reproduction, rather than feeding limitations, could be the key adaptation trait limiting boreal species from expanding northwards (Box 7.3).

In contrast with temperate regions which experience spring and autumn blooms, polar regions usually have one quick and intense primary production bloom centred a few weeks before the ice breakup in spring (Chapter 4), which in turn results in a peak in secondary production (Chapter 5). The early life stages of most fish species are planktivorous and need to use the unique and abundant source of energy available during the spring bloom, just after yolk resorption. Fishes that reproduce in winter generally hatch under the ice and first-feeding larvae appear in spring, a period coupled with the peak in production of zooplankton nauplii and eggs, the main prey of most larval fishes (Pepin et al. 2014). According to the match/mismatch hypothesis, first-feeding planktonic larvae are most vulnerable to starvation and fish cohorts with yolk resorption coinciding with the peak production of their prey have better recruitment. Species spawning in winter and hatching in spring thus have a marked advantage in polar regions, and for most of them the cost of initial growth in cold water is counterbalanced by the abundance of prey during larval feeding (Fortier et al. 1995). In addition, species with buoyant eggs hatching under the ice, such as polar cod in the Arctic and silverfish in Antarctica, are protected from predation by seabirds and fishes by hiding at the ice-water interface during the critical embryonic and larval stages. The low irradiance prevailing during winter (Chapter 3) and the light attenuation by the ice and snow cover also offer a dimmed-light refuge against predation by visual predators, such as seals, for spawning fishes (Benoit et al. 2010).

Fishes that spawn during the Polar Night and hatch in winter or early spring maximise the duration of the growth season of larval and juvenile stages and their late-summer size. A large size at the end of the short Arctic summer reduces the vulnerability of juvenile fishes to avian predation, cannibalism, and winter starvation, and thus results in higher recruitment. For polar cod, and possibly other Arctic species, selection pressure pushes hatching to occur as early in winter or spring as possible. Based on these assumptions, the winter thermal refuge hypothesis suggests that in Arctic fishes like polar cod the main driver of hatching under the ice in winter is the need to maximise the size of juveniles at the onset of winter, which in turns minimises mortality during their first winter (Bouchard and Fortier 2011).

Table 7.2 Summary of biological activities during the Polar Night for abundant Arctic and boreal marine species. Note that all species feeding during the Polar Night have a higher proportion of empty stomachs during that period

Origin	**Species**	**Distribution during the Polar Night**	**Spawning season**	**Feeding during the Polar Night**
Arctic	Polar cod	Circumpolar. Pelagic from surface to bottom. Larger individuals are generally demersal.	Polar Night	Yes
	Arctic cod	Circumpolar. Pelagic from surface to bottom.	Polar Night and possibly summer/autumn	Yes
Arcto-boreal	Daubed shanny	Circumpolar. Adults are demersal with pelagic excursions. Juveniles are pelagic. Inhabit a large range of depths.	Polar Night	Yes
	Greenland halibut	Canadian and European Arctic Seas. Adults are benthopelagic with pelagic excursions. Juveniles are pelagic. Inhabit a large range of depths.	Polar Night	Yes
Boreal	Redfish	Baffin Bay and European Arctic. Juveniles are generally mesopelagic and adults are demersal.	Copulation in August-November and larval extrusion in March-April	Yes
	Herring	Subarctic regions of the Pacific and Atlantic. Pelagic from surface to bottom.	Spring for Atlantic herring and summer for Pacific herring	Yes
	Capelin	Circumpolar in low-Arctic seas. Pelagic from surface to bottom.	Summer	Yes
	Atlantic cod	Baffin Bay and European Arctic. Juveniles are pelagic, adults are demersal over a large range of depths.	Spring	Yes
	Haddock	European Arctic. Juveniles are pelagic, adults are demersal over the shelf.	Spring	Yes
	American plaice	Baffin Bay and European Arctic. Demersal over a large range of depths.	Summer	Yes
	Glacier lanternfish	Subarctic and north-Atlantic. Mainly mesopelagic (>200 m).	Polar Night on the Canadian side and summer on the European side	Possibly

7.5 Foraging in the dark of night

Most species documented in this chapter feed to a certain extent during the Polar Night (Table 7.2). However, the stomach fullness is generally lower and the proportion of empty stomachs consistently higher during winter than the rest of the year for all species where seasonal feeding has been documented. This applies to all Arctic (e.g. polar cod), arcto-boreal (e.g. Greenland halibut), and boreal (e.g. capelin and Atlantic cod) species. The reasons behind this reduction, but not complete suspension, of foraging activities in the winter months could be multiple.

First, seasonal metabolic changes might diminish the need for energy intake, for instance for species feeding less during their winter spawning season, such as polar cod (Hop et al. 1995) and Greenland halibut (Pedersen and Riget 1993; Hovde et al. 2002). For species such as polar cod that build up large gonads (up to 40% of body weight), this reduction in energy intake during spawning might in part result from the gonads filling the body cavity, leaving no space for a full stomach. It can also represent a trade-off between the need for energy and the increased risk of being preyed on because the larger the gonads, the more conspicuous an individual is as a prey. Consequently, large spawning individuals remain at depth, were they are less vulnerable to visual predators (Benoit et al. 2010), but where less prey are available.

Second, most species have their highest energy intake in spring and summer and prefer prey available at that period. As the availability of prey changes in winter, it forces fishes to change their diet towards less palatable or easily catchable prey. For instance, small arctic charr change their diet from zooplankton prey in summer and autumn to benthic organisms in winter (Svenning et al. 2007). Polar cod in the Barents Sea changes its feeding behaviour from populations specialised with a preference for amphipods in summer/autumn to a more individualised behaviour focusing on teleost fishes in winter (Cusa 2016). In the Barents Sea, Greenland halibut switches from a capelin-based diet in autumn to a diet focusing on other fish species and squids in winter (Hovde et al. 2002). All these examples strongly suggest a more opportunistic feeding behaviour in winter than during the rest of the year.

Third, the diminution in irradiance during Polar Night (Chapter 3) results in lower fish foraging activities and changes in prey composition at this time of year. Most fishes depend on light for foraging and their visual range is greatly reduced during the Polar Night, as is the probability of detecting their prey (Kaartvedt 2008). The contrast of prey with the background also diminishes under low irradiance. Larger prey, such as fishes, cast a larger shadow than smaller zooplankton and are therefore easier to locate, which could partly explain the change in polar cod diet during the Polar Night. Because larger prey are usually faster, they are generally more difficult to catch, hence reducing foraging success during winter. The ability to select prey might also be reduced by the loss of visual cues like pigmentation under low irradiance conditions and because fish are more opaque than zooplankton (Varpe et al., 2015 and references therein). Overall, the impact of weak irradiance on feeding behaviour is lower for demersal and benthopelagic fishes than for pelagic species because it is easier to detect prey with non-visual senses on the seafloor than in the water column. This likely explains why Atlantic cod and haddock have a higher stomach fullness than capelin, herring and redfish during the Polar Night (Fig. 7.6).

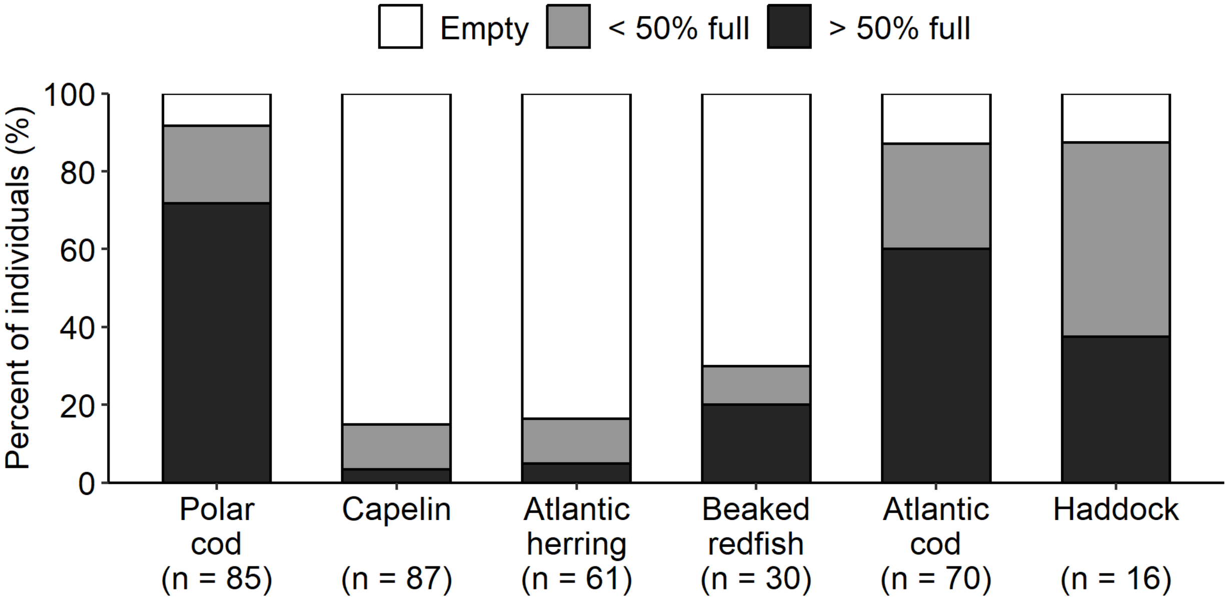

Fig. 7.6 Ratio of individuals with empty, < 50 % full, and > 50 % full stomachs for six abundant species sampled in Svalbard in January 2018.

A portion of all species sampled in January 2018 in Svalbard had stomachs > 50 % full (Fig. 7.6). However, the proportion of empty stomachs of boreal pelagic fishes was high (> 70 %) compared to polar cod (10 %). The discrepancy could partly result from the high sensitivity of polar cod to low light levels compared to boreal species. Polar cod has disproportionally large eyes (Box 7.2) and can use and react to the extremely low light conditions prevailing under the ice in winter, for instance by conducting DVM (Benoit et al. 2010; Geoffroy et al. 2011) (Fig. 7.3). Arctic species like polar cod and arctic cod can thus exploit low light levels from atmospheric irradiance, moonlight, and possibly bioluminescence of zooplankton to continue foraging during the Polar Night (Chapter 3). In contrast, the vision of boreal species is adapted to the stronger day/night irradiance contrast prevailing throughout the year at lower latitudes (Jönsson et al. 2014). Yet, even at lower latitudes where there is no Polar Night, boreal species feed less in winter. For instance, in offshore Newfoundland (< 53 °N), 55 % of capelin stomachs and 57 – 79 % of redfish stomachs were empty in winter (Albikovskaya and Gerasimova 1993; O'Driscoll et al. 2001), while 55 % of herring sampled in western Scotland (56 °N) in winter had empty stomachs (De Silva 1973).These numbers are high, but lower than what was measured in winter in Svalbard, which supports the idea that a combination of seasonal factors and low irradiance explains the high proportion of empty stomachs of boreal pelagic fishes during the Polar Night.

Similar to fishes inhabiting the deep-sea, polar fishes rely on other senses in addition to visual cues to locate and capture their prey during the Polar Night. The olfactory sense can be highly developed in fishes (Hara 1975). Fishes in dim-light environment can also use their mechanosensory lateral line and electrosensory system to guide their activities (La Mesa and Eastman 2012). For instance, the limited vision of Atlantic cod during winter forces them to use their chin barbel and the pelvic fin ray to locate small food items on the seabed, which explains a switch from rather pelagic prey in summer to benthic organisms in winter (Harvey and Batty 2002; Jönsson et al. 2014; Coad and Reist 2018). Reactions to these senses were confirmed in certain boreal fishes and in Antarctic fishes, in particular some notothenioids (La Mesa and Eastman 2012), but remain undocumented for most Arctic species.

7.6 Knowledge gaps and new technology to address them

The winter ecology of the ubiquitous and abundant polar cod is by far better documented than that of other species, which explains the discrepancy in the length of the sections dedicated to each species in this chapter. Yet, in addition to the winter ecology of other abundant and rare species in the Arctic, several general knowledge gaps persist:

1) A high proportion of northern species spawn during the Polar Night, but the migration patterns to spawning grounds and the spawning ground themselves remain at least partly unknown for most of them. Except for the Barents Sea, the winter spatial distribution of fishes in general is poorly documented. This is particularly noticeable in the North American Arctic and the CAO where spatial studies are limited by the heavy ice-cover prevailing in winter.

2) For species inhabiting both coastal and offshore areas, most knowledge on the winter ecology originates from coastal surveys because these areas are often easier to access and closer to permanent research stations. Conclusions drawn from these studies are extrapolated to offshore populations, which might bias our understanding. Future studies should focus on comparing the coastal and offshore ecology of fishes during the Polar Night.

3) The feeding habits of some fish species during winter have been documented, but knowledge on foraging ecology during the Polar Night remains scarce for many species, especially when comparing the diet of juveniles and adults. Knowledge on the preferred prey, feeding strategies and frequency of feeding events in winter would allow better understanding the different life strategies and potential for competition between species.

4) Improved knowledge of the visual capacity of fishes under dim-light conditions is needed to better understand their potential for prey encounter and foraging. In particular, further studies on light perception thresholds and visual adaptation to the Polar Night, especially of pelagic fishes, are needed to better interpret the DVM patterns and seasonal changes in feeding habits and strategies.

5) Seasonal and daily changes in pineal melatonin production is documented for arctic charr, but not for marine fishes. Comparative studies on the daily cycle of melatonin production and clock gene expression during the midnight sun and Polar Night period are needed to understand how the different species modify their circadian rhythm under the unique light regime prevailing in polar environments (Chapter 8).

Studying fish ecology under the unique and harsh conditions prevailing at high latitudes during the Polar Night requires state-of-the art technology. Fortunately, new tools are increasingly available (Chapter 9 and 10). Moored and ice-tethered autonomous acoustic sounders can document the vertical distribution of fishes over complete year cycles (Berge et al. 2016). New broadband acoustic technology installed on these observation platforms or on research icebreakers could result in a better taxonomic resolution than traditional echosounders by providing the frequency-response curve of the targets (Bassett et al. 2016). The new Surface and Under-Ice Trawl (SUIT) can collect under-ice fauna, including fishes and their prey, from research vessels in ice-covered seas (David et al. 2015). In addition, state-of-the-art genetic tools can detect traces of environmental DNA from marine environments to confirm the occurrence of fish species and their zooplankton prey (Valentini et al. 2016). New hyperspectral imagers and other new optical sensors can measure the spectral composition of light (irradiance) at very low light intensities that is apparently dark for the human eye (Chapter 3) resulting in a better understanding of the light field available to marine animals under the ice during the Polar Night. Correspondingly, underwater hyperspectral imagers (UHI) can map and monitor object of interests (habitats or organisms) at very low light intensities (Dumke et al. 2018; Chapter 10). These tools provide improved capabilities to study the ecology and to map and monitor marine organisms under the ice cover during the Polar Night, both in coastal and offshore areas. Building on this technology with acoustics sensors, polar ichthyologists have the possibility to fill several important data gaps in the short-term (see Chapter 9 and 10).

BOX 7.1 Polar cod or arctic cod?

In Europe (and in this chapter), *Boreogadus saida* is usually named polar cod, while *Arctogadus saida* is referred to as arctic cod. In contrast, North Americans usually refer to *Boreogadus saida* as arctic cod and *Arctogadus saida* as ice cod. Hence, a European arctic cod is an American ice cod and an American arctic cod is a European polar cod. What a good tongue twister!

BOX 7.2 The big eyes of Arctic gadids

Compared to boreal gadids, the Arctic specialists polar cod (*Boreogadus saida*) and arctic cod (*Arctogadus glacialis*) have disproportionally large eyes (25.4 – 31.5 % of head length for adult *B. saida* and 17.3 – 39.2 % for adult *A. glacialis*) compared to Atlantic cod (15.5 – 21.7 % of head length for adults) and haddock (20.0 – 28.2 % of head length for adults) (Svetovidov 1948; Methven and McGowan 1998; Jordan et al. 2003). Larger eyes can capture more photons under low irradiance conditions and, in general, relative eye size of fishes increases in deep-sea and polar environments (Eastman and DeVries 1985; Wagner et al. 1998). For polar cod, and most likely arctic cod, DVM patterns and relatively high stomach fullness during the Polar Night suggest that their large eyes are adapted to the dim-light conditions prevailing under the ice during the Polar Night and allow them to continue foraging during the darkest months of the year.

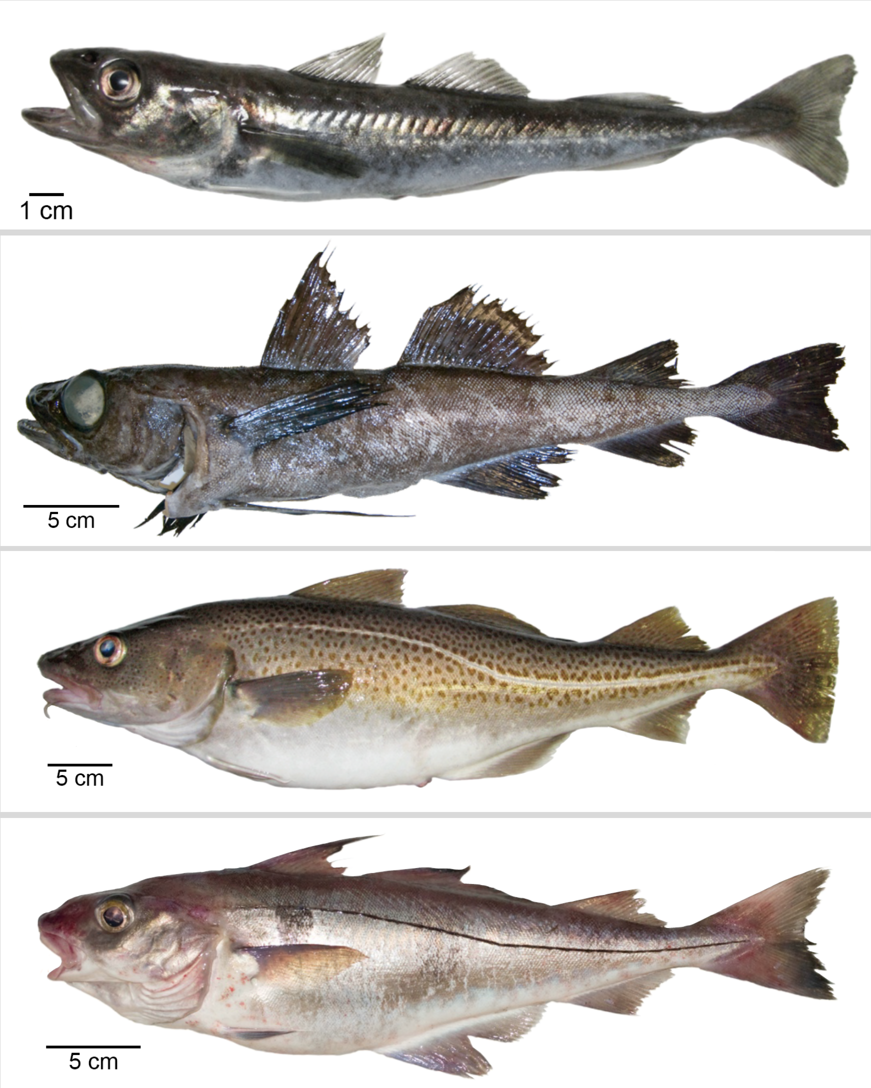

Fig. 7.7 Examples of Arctic and boreal gadids. From top to bottom: polar cod, arctic cod, Atlantic cod, haddock (adapted from Nozères et al. 2010)

BOX 7.3 - Can boreal fishes acclimate to the Polar Night?

Two main characteristics define polar regions, very cold temperatures and a unique light regime of several months of darkness followed by continuous irradiance. Arctic animals, including fishes, are adapted to this extreme environment, but species from temperate regions are not. The borealization of the Arctic, defined as the northward range expansion of boreal species into the Arctic and the retreat of Arctic specialists further north, results from an increase in temperatures (Fossheim et al. 2015). However, the extreme light regime of the Arctic is unaffected by climate change and the photoperiod constraint hypothesis suggests that photoperiod limits the abundance and northwards migration of mesopelagic fishes and their zooplankton prey into the high Arctic (Kaartvedt 2008). This hypothesis has been nuanced by other studies suggesting that the reduction in thickness and extent of the ice cover result in higher irradiance in the water column and that a northward range expansion by visually searching fishes is possible during part of the year (Varpe et al. 2015). Moreover, the abundance of boreal fishes is relatively high during the Polar Night north of Svalbard (Table 7.1) and most of them are foraging to a certain level (Fig. 7.6). The ratio of empty stomachs is higher during winter than the rest of the year, but this is also the case in more southern areas and it is not clear if reduced foraging activities during the Polar Night limit the northward range expansion of boreal species. However, in contrast to Arctic and arcto-boreal fishes that reproduce during winter to benefit from the Arctic spring bloom just after yolk resorption, most boreal species reproduce from spring to autumn which, in the Arctic, results in a mismatch between the apparition of first-feeding planktonic larvae and the production of zooplankton prey. Hence, it was hypothesised that the ability to reproduce during the Polar Night, rather than the ability to feed, might be the key adaptive trait of Arctic fishes and the main factor limiting boreal fishes to colonise the high Arctic (Berge and Nahrgang 2013; Berge et al. 2015c).

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Chapter 8

Biological clocks and rhythms in polar organisms

Kim S. Last, Sören N Häfker, Vicki J. Hendrick, Bettina Meyer, Damien Tran and Fabio Piccolin

Abstract

Biological clocks are universal to all living organisms on Earth. Their ubiquity is testament to their importance to life: from cells to organs and from the simplest cyanobacteria to plants and primates, they are central to orchestrating life on this planet. Biological clocks are usually set by the 'beat' of the day-night cycle, so what happens in polar regions during the Polar Night or Polar Day when there are periods of 24 hours of darkness or light? How would a biological clock function without a time-keeper? This chapter details evidence that biological clocks are central to structuring daily and seasonal activities in organisms at high latitudes. Importantly, despite a strongly reduced or absent day night cycles, biological clocks in the Polar Night still appear to be regulated by background illumination. Here we explore evidence for highly cyclic activity, from behaviour patterns to clock gene expression, in copepods, krill and bivalves. The ultimate goal will be to understand the role of endogenous clocks in driving important daily and seasonal life cycle functions and to determine scope for plasticity in a rapidly changing environment.

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8.1 What are biological clocks?

8.1.1 Molecular underpinnings of biological clocks

Biological clocks are highly accurate molecular machines, continuously adjusting behaviour, metabolism and clock-controlled gene activity (Dunlap 1999). The most commonly studied clock is called the circadian clock and will, under laboratory conditions, generate a rhythm of about 24 hours. It gets its name from the Latin *circa* meaning "about" and *dies* which means a "day", and it measures the time of day much like any watch (Halberg et al. 1960). Although precise, it is usually just a bit fast or slow relative to astronomical time, hence the prefix "*circa*".

The circadian clock is usually located in a distinct part of the brain. In mammals it is close to where the optic nerves cross, a region called the suprachiasmatic nucleus (SCN) (Inouye and Kawamura 1979), and in fruit flies (*Drosophila melanogaster*) it is in the brains' ventral neurons (Rieger et al. 2006). It synchronises a multitude of other clocks in cells, tissues and organs often via hormonal control (in mammals: melatonin) (Foulkes et al. 1999). The clock itself is a molecular machine which constitutes positive and negative feedback between circadian clock genes and the clock proteins they express, primarily entrained by the light/dark cycle (Pittendrich and Minis 1964), for further details see Box 1.

8.1.2 General characteristics and ultimate significance of clocks

The circadian clock has a number of important characteristics. First, it is primarily set by the day/night cycle through *entrainment*, without this the clock gradually desynchronises and rhythmic behaviour is lost (Pittendrich and Minis 1964). Secondly, the clock *free-runs* in the laboratory (Roberts 1960). This means that in the absence of the day/night cycle (or any other cyclic environmental cues) the workings of the clock can be observed through rhythmic expression at the behavioural, physiological or molecular levels i.e. an organism will continue to show rhythmic behaviour such as active/resting phases even in the absence of external signals. This endogenous response is termed a *rhythm* and will eventually decrease or dampen which, depending on the species under investigations, may take from days to months. Any signal which entrains the clock is termed a *Zeitgeber*, from the German word which means 'time-giver' (Aschoff 1979). While the day/night light cycle is a common Zeitgeber, others include food (Stephen 2002) and social cues (Mistlberger and Skene 2004) etc. Finally, the clock is relatively immune to temperature changes, which is especially important in time-keeping in animals which cannot regulate their own body temperature other than by behavioural means (poikilotherms).

The ultimate function of the clock is to allow organisms to *anticipate* rather than simply to *react* to future events, promoting survival and enhancing fitness. This will confer advantages through scheduling of biological functions at the appropriate time of the daily environmental cycle (extrinsic advantage), coordination of internal physiology (intrinsic advantage), and through the role of the clock in responses to seasonal changes. Their importance is illustrated by the effect of fitness of mice with deviant circadian periods in populations living in a semi-natural environment (Spoelstra 2016). Mice with near 24-h rhythms survive longer and reproduced more than mice with rhythms shortened by a mutation in the circadian clock allele. Similarly, in plants with deviant clocks, flowering times are affected with consequent loss of fitness (Green et al. 2002).

Finally it is important to consider that when an organism is studied in the wild, one cannot exclude that it is responding to the exogenous environmental (e.g. day/night) cycle directly i.e. without involvement of the endogenous circadian clock. It is only when organisms are brought into the laboratory and their behaviour or clock genes show circadian rhythms under free-running conditions (i.e. constant light or dark and temperature) that we can say for certain that an circadian clock is extant.

8.1.3 Complex environments require complex clocks

We have seen how the circadian clock is centrally important to synchronising the behavioural and physiological rhythms of organisms and therefore highly adaptive to terrestrial organisms living in a 24-hour world. In the marine environment, however, organisms also experience other cycles of different durations. The Earth and moon spin about a common centre of gravity resulting in various geophysical cycles to which organisms have evolved biological clocks with matched synchronicity (for review of these see: Naylor 2010). Organisms living in tidal habitats may have circatidal clocks (with a ~12.4 h period matching that of the tides), or circasemilunar clocks (with a ~14 day period matching that of the spring/neap tidal cycle). Others synchronise to moonlight and possess circalunar clocks (with a ~29 day period matching the lunar phase cycle) which are often important in synchronising reproductive events. Finally one of the longest types of biological clocks are the circannual clocks (with a ~365 day period matching one year). Although non-circadian types of biological clocks have been well described at the behavioural and physiological levels, our understanding of their molecular mechanisms is still rudimentary (de la Iglesia and Johnson 2013; Raible et al. 2017; Lincoln 2019).

8.1.4 Clock rhythms in Polar Regions

The Polar Day or Night provides two time periods during which solar cycles are difficult to detect or are masked by other external factors. This is because the sun is either permanently above or below the horizon and light from the moon, aurora and stars contribute more or less significantly to the daily light field (as detailed in Chapter 3). When below the horizon, extended periods of civil, nautical and astronomical twilight occur, the effects of which are largely unknown on the circadian clocks of polar organisms. Indeed there is limited information on the irradiance threshold or role of spectral composition in circadian clock entrainment, surprising considering their perceived importance circadian entrainment (Miljeteig et al. 2014, Båtnes et al. 2015, Cohen et al. 2015). Polar organisms therefore not only need to detect the presence/absence of light, but have to use the extreme polar photoperiods (the length of the day or night) and varying light intensities/spectra to entrain any putative circadian clock.

The first evidence of large scale circadian type behaviour in polar marine organisms came from a study in 2008 by Berge et al. which showed that diel vertical migration of zooplankton (DVM) occurred during the Polar Night (as described in Chapter 5). This study challenged the paradigm that DVM did not occur during the Polar Night. Using chronobiological methods, the strength of DVM was determined in different depth layers revealing that DVM only occurred around 50m, as shown in Figure 8.1.

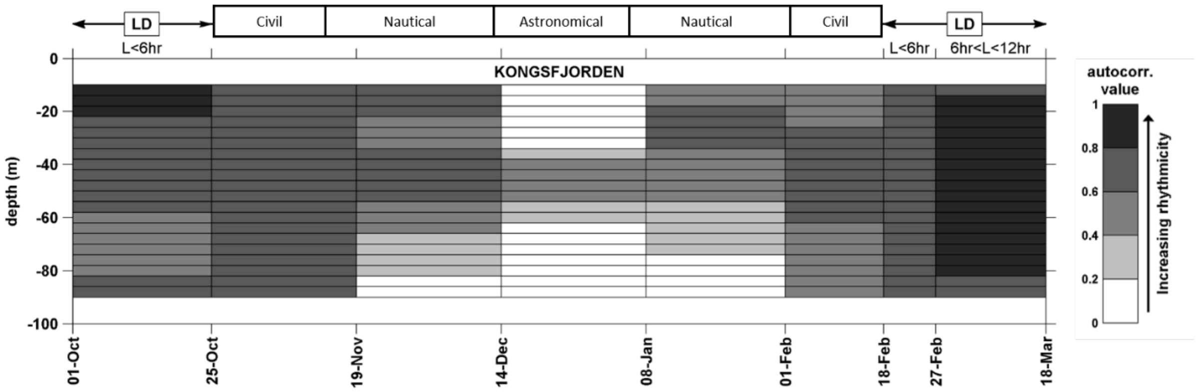


Fig 8.1 DVM signal strength and depth centred during the Polar Night in Kongsfjorden, Svalbard. LD, light dark (difference between day and night in hours) and defined twilight periods (see Table 3.1). Each box represents a specific depth and time interval. Rhythmicity has been calculated using autocorrelation statistics (autocorr.) where the darker the shading at any particular depth, the more synchronized the 24-hour DVM signal. All shaded boxes have a detectable DVM signal that is significant above a 99 per cent confidence interval. White boxes indicate no detectable DVM signal. Adapted from Berge et al. 2008

It was later demonstrated (Last et al. 2016) that although the DVM observed in December was within the circadian range (defined here as within 20 – 28 hours), closer analysis of periodicity at higher temporal resolution revealed the period to be ~24.8 hours, the same as a lunidian day (i.e. the period of one rotation of the earth around its axis with respect to the moon). This response was termed daily Lunar Vertical Migration (LVM-day) and only occurred during December during the full moon period but was shown to be common across the Arctic Ocean as monthly Lunar Vertical Migrations (LVM-month).

Evidence that zooplankton migrate during the Polar Night suggests an ability for detection and response to very low light intensities. However, acoustic data can only reveal migrations at the population level and so it is still largely unknown which organisms respond to moon- or sun- light at this time. The implication that a circadian clock maybe present in migrating zooplankton was tantalising and indirectly resulted in a number of behavioural and molecular studies of polar marine organisms capable of parsing between exogenous responses and endogenous rhythms. Here we build on previous chapters to discuss the underlying mechanisms and entrainment of biological clocks by light (Chapter 3) and their adaptive significance in copepods and krill (Chapter 5) and bivalves (Chapter 6), in an environment which, to the human eye at least, is devoid of clear light signals for large parts of the year.

8.2 Biological clocks in the copepod *Calanus finmarchicus*

8.2.1 Circadian clocks and cycles

The copepod *Calanus finmarchicus*, like many other planktonic organisms, performs DVM. It is very abundant in the boreal, Atlantic and Arctic seas and its life-cycle is well described (as detailed in Chapter 5). Importantly for the study of circadian clock gene expression, molecular resources are available making transcription analysis routines possible (Lenz et al. 2014). Thus in 2017, Häfker *et al.* provided the first evidence of endogenous clock gene cycling in *C. finmarchicus* collected from a boreal fjord in Scotland, UK. In the laboratory and under free-running conditions, *C. finmarchicus* showed circadian rhythms of DVM, respiration, and most core circadian clock genes: clock, period1, period2, timeless, cryptochrome2, and clockwork orange (for details see Box 1). Convincingly most of these genes also cycled in animals taken directly from the wild, though the level of expression was slightly less rhythmic in animals collected from deep water (50–140m) relative to those collected from shallow water (0–50m). The observation that clock gene cycling also occurred in the deeper water was surprising given that light attenuation and scattering in this fjord is extremely high below 20m (Cohen et al. 2019) and so would be completely dark, at least to the human eye. At both depths, peak expression of clock genes generally occurred either at sunset or sunrise, coinciding with peak migration times in the wild. While the mechanistic connection between the circadian clock and behaviour/physiology still remains elusive, the high degree of correlation between clock gene expression and DVM is striking.

Circadian clock control of the behaviour and physiology of *C. finmarchicus* may increase fitness by optimizing the temporal trade-off between feeding and predator avoidance, especially when environmental drivers are weak or absent such as in deep water or during the Polar Night (Häfker et al. 2017). The clock will provide a time-sense so that animals can anticipate the cyclic diel changes of their environment and prepare accordingly, a highly adaptive trait (Sharma 2003). In copepods this includes the accumulation of ATP reserves for the energy demanding ascent to surface waters at sunset; the production of digestion enzymes in advance to process as much food as possible during their limited nocturnal feeding time in surface waters; and, anticipation of sunrise which enables the copepods to return to depth before light levels becomes sufficient for visual predators to hunt.

As circadian clocks are not perfectly precise, but have to be entrained by the diel light/dark cycle on a regular basis, it might be expected that DVM would cease during long periods when there is no more day/night cycle such as during the Polar Day or Polar Night. Studies have shown however, that during the Polar Day when the upper waters layers are permanently illuminated, DVM becomes desynchronized within the population of zooplankton, yet continues at the individual level (Cottier et al. 2006; Darnis et al. 2017). Similarly DVM has been shown to continue during the Polar Night and is either driven exogenously or entrained by the sun (Berge et al. 2015; Hobbs et al. 2018) or the moon (Last et al. 2016), whichever is the stronger signal. DVM of zooplankton has also been documented in the deep sea (as a proxy for another environment without overt solar signals) yet the mechanisms of entrainment are not understood (van Haren and Compton 2013). Noteworthy is that cycling clock gene expression in *C. finmarchicus,* has only been demonstrated during the Polar Day, but not the Polar Night, as shown in Figure 8.2 in animals collected from Kongsfjorden (Häfker et al. 2018a).

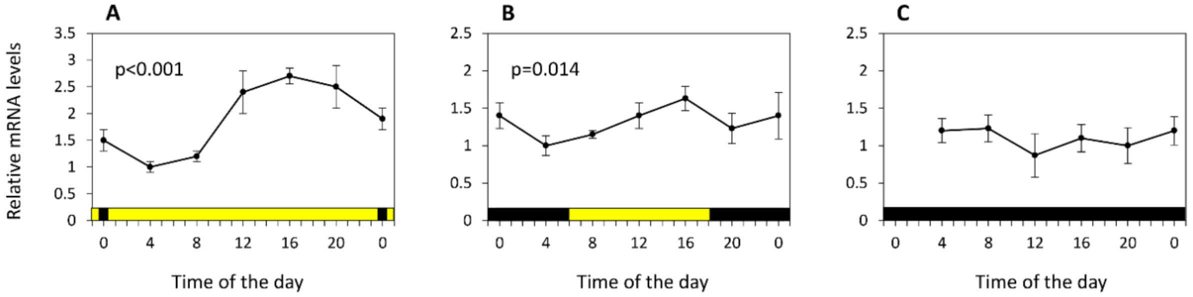


Fig 8.2 Diel clock gene expression of the period1 (*per1*) gene in A: August (active phase), B: September (early diapause) and D: January (late diapause). Color bars indicate day (yellow) and night (black). Expression of *per1* gene was analysed for 24 h rhythmicity with RAIN analysis with significant 24 h cycling ($p < 0.05$) indicated. Adapted from Häfker et al. 2018a

Copepods in early diapause (September; for details see Chapter 5) which were collected below 200m, where light levels were probably below their visual detection limit (Båtnes et al. 2015), still showed clock gene cycling. This indicated that the clock was running endogenously without light entrainment at a time when the copepods had just descended to depth, suggesting that the physiological switch to the diapause state happens after the descent to deeper water layers (Freese et al. 2017; Häfker et al. 2018a,b). The persistent rhythmicity during the Polar Day, at a time when the sun is permanently above the horizon, suggests that changes in spectral irradiance and intensity with solar altitude are sufficient to entrain the clock. Depending on light attenuation in the water column, an organism in the epipelagic may therefore still be able to perceive distinct 'photoperiods', that will vary with depth and with visual sensitivity of the organism (for further discussion see Chapter 3).

Whilst the mechanism of photoperiodic detection and circadian clock entrainment during the Polar Day is still unknown, the observation of endogenous gene cycling at this time suggests that clock functioning requires only subtle changes in solar irradiance. However during the Polar Night *C. finmarchicus* showed no clock gene cycling (Figure 8.2). This may be attributed to the lack of sufficient light intensity/spectrum at this time or to the physiological state of diapause which could actively switch off clock gene cycling (Häfker et al. 2018b). Where DVM or LVM is observed during the Polar Night using acoustics (Berge et al. 2008; Last et al. 2016), we suggest the behaviour is primarily exogenously driven by sun- or moonlight respectively, although light strong enough to evoke a direct response may also have the potential to entrain a biological clock although this would require testing.

8.2.2 Seasonal clocks

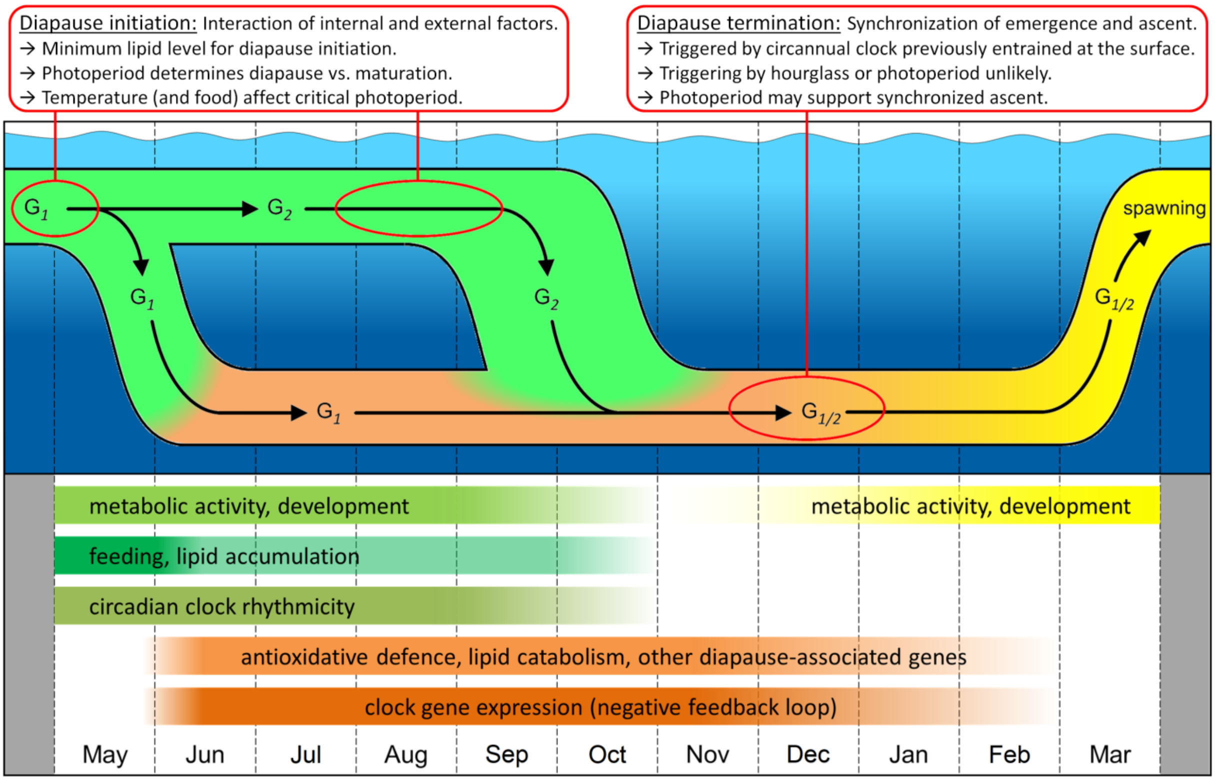
For a large part of the year, the majority of the population of *C. finmarchicus* migrate to deep water undergoing a form of hibernation, or diapause. At this time they are inactive, show reduced metabolic activity, and survive on their lipid storages without feeding (noteworthy however is that not all copepods do this, for details see Chapter 5). Diapause has been investigated for more than a century, but the factors controlling the initiation and termination of this important life phase remain elusive (Baumgartner and Tarrant 2017). Since circadian clocks are intrinsically linked to photoperiodism (Schultz and Kay 2003; Goto 2013), and diapause in *C. finmarchicus* occurs at a specific time of year depending on location, we suggest the potential of circadian clock involvement and diapause regulation via photoperiod measurement.

Classically, the lipid stores of copepods have been considered to have a major role in diapause with the expectation that diapause is initiated once the animals reach a certain lipid threshold, enabling them to survive the foodless time of diapause at depth (Rey-Rassat et al. 2002). Conversely, the gradual depletion of the lipid stores over time is expected to result in the triggering of emergence of diapause once reserves fall below a critical value. Diapause 'lipid-threshold' hypotheses do, however, struggle to explain why, particularly at lower latitudes, some animals at the copepodite CV stage (for details see Chapter 5) either enter diapause, or mature and produce another generation (cohort). If the lipid stores were the factor triggering diapause, all animals should descend to depth. Similarly, a gradual depletion of lipids cannot be considered a precise timer for diapause emergence, conflicting with the observations that the ascent from diapause in winter/spring is often strongly synchronized within a given *C. finmarchicus* population (Baumgartner and Tarrant 2017).

As copepods typically overwinter at depth where light or other seasonal cues are unavailable or reduced, an argument is made in favour of seasonal/circannual clocks in regulating diapause timing as has been described for various insects (Meuti and Denlinger 2013). The circadian clock of *C. finmarchicus* remains functional during extremely long photoperiods in summer (Häfker et al. 2018a), and it is likely that the same is true for the polar-adapted species *C. glacialis* and *C. hyperboreus*. Thus, the circadian clock could be used to determine the seasons based on photoperiod and the use of a critical day length in diapause initiation. As sufficient lipid storages are still crucial to survive diapause, it is probable that a certain lipid threshold has to be reached before photoperiod induction takes place (Häfker et al. 2018b).

For diapause emergence triggers however, photoperiod is an unlikely cue due to the lack of light at diapause depth which is usually, in *C. finmarchicus*, >200m. The synchronized emergence in the absence of any seasonal cue points towards the existence of an endogenous circannual timing mechanism. Indeed very early studies on *C. hyperboreus* and another *Calanus* species showed that animals collected from the field and kept in constant darkness in the laboratory still emerged from diapause in synchrony with their conspecifics in the field several months later (Conover 1965, Fulton 1973). Although the mechanism of this is still unclear, circannual rhythms have been described in several terrestrial species maintaining time with astonishing precision (Goldman et al. 2004). It has been suggested that for the boreal *C. finmarchicus* and its Arctic congener species, photoperiods perceived during the summer when the animals are near the surface of the ocean, may entrains their circannual clock (Häfker et al. 2018b). This would provide a temporal cue to trigger emergence in winter in the midst of the Polar Night in readiness of moulting and reproduction.

Aside from the physiological changes associated with diapause (Chapter 5) this phase of the *C. finmarchicus* seasonal cycle is also characterized by distinct changes in gene expression patterns as detailed in Figure 8.3.



Diapause initiation: Interaction of internal and external factors.
→ Minimum lipid level for diapause initiation.
→ Photoperiod determines diapause vs. maturation.
→ Temperature (and food) affect critical photoperiod.

Diapause termination: Synchronization of emergence and ascent.
→ Triggered by circannual clock previously entrained at the surface.
→ Triggering by hourglass or photoperiod unlikely.
→ Photoperiod may support synchronized ascent.

Fig 8.3 Seasonal life cycle and gene expression of *C. finmarchicus*. Exemplified for a boreal habitat where copepods produces two generations per year (G_1 & G_2). Red boxes summarize possible mechanisms of diapause initiation/termination. Bars in the lower panel indicated seasonal gene expression patters. Figure adapted from Häfker et al. 2018b

Copepods active in surface waters and those that recently descended to diapause depth show high expression of genes related to metabolic activity, development, digestion and lipid accumulation, reflecting migration to phytoplankton rich water, growth and accumulation of lipid stores for overwintering. This is also the phase when circadian clock genes show diel expression rhythmicity matching the DVM that occurs at this time. At depth, copepods show major changes in gene expression, which mark the start of diapause. While the expression of the genes active in surface waters decreases, so clock gene rhythmicity ceases. Genes involved in oxidative stress responses and lipid catabolism are upregulated, reflecting the often hypoxic conditions in deep waters with behavioural inactivity fuelled by the gradual depletion of lipid storages.

Another interesting, yet unexplained, observation over the seasonal cycle of *C. finmarchicus*, is the overall upregulation of several clock genes despite the lack of diel rhythmicity (Häfker et al. 2018a,b). Towards late autumn/early winter, there is a shift in gene expression, which signifies the start of the diapause emergence phase. Although animals still remain at depth, the expression of diapause-related genes decreases while genes associated with metabolic activity and development increase. The initiation of the emergence phase is synchronized within the population and happens in deep waters, without any known seasonal cues and well in advance of the ascent to surface waters in spring, clearly showing 'anticipation' for a future behaviour/physiological state. These observations suggest that emergence is triggered by an endogenous timing where the mechanism may represent a putative circannual clock. While the mechanistic nature of such a clock is unknown, in could be related to lipid storage status and photoperiod measurement at diapause initiation (Häfker et al. 2018b). Such a mechanism, which works independent of light for certain times of the year, could ensure precise seasonal timing even under the extreme light conditions in polar marine habitats.

8.3 Biological clocks in krill *Euphausia superba*

8.3.1 Circadian clocks and cycles

Krill are very abundant in the polar oceans and are one of the preferred prey species for many marine predators throughout the year. Whilst the most common krill species in the Arctic is *Thysanoessa* spp (Fig. 11.9), the Southern Ocean is dominated by its much larger cousin the Antarctic krill, *Euphausia superba* (Fig 8.4). Krill generally are exceeding agile and fast swimmers, frequently congregating in large swarms making them a prime target for higher trophic predators such as fish, baleen whales and birds. From echosounder data and net hauls they are also considered the dominant group undergoing highly synchronised diel vertical migrations (DVM).

Figure 8.4 The Antarctic krill *Euphausia superba*, an important food source for the majority of Southern Ocean higher trophic levels. Photo: Carsten Pape

Whilst very little is known of the physiology and behaviour of *T. inermis,* the converse is true of *E. superba*. Studies have revealed that its success is hinged on a life-cycle perfectly matched to the annual variations in day length (photoperiod), sea ice cover and food supply. Krill show highly orchestrated annual patterns of metabolic activity, sexual maturity and lipid utilization with recent studies further revealing daily rhythms in behaviour, metabolism and gene transcription (Meyer et al. 2010). Its position as a model organism for the study of a high latitude biological clocks has, therefore, made it worthy of discussion here although the species neither lives in the Arctic nor is exposed to permanent darkness because of Southern Ocean latitudes. However, its vertical distribution is deeper than in those of its northern cousin, with corresponding increased light attenuation, and therefore parallels may be drawn between these polar habitats.

As is the case with many other pelagic organisms, *E. superba* undergo DVM, swimming to surface around sunset and retreating to deeper waters around sunrise. This predator avoidance behaviour changes seasonally with more pronounced DVM in spring and autumn when compared to the summer. In the spring and autumn migrations are predominantly in the upper 200m, whilst during summer, when the sun rarely dips below the horizon and food availability is high, no clear DVM pattern is observed. Instead, multiple shallow individual migrations occur in a similar manor as those seen in Arctic copepods (see Chapter 5), referred to as unsynchronized DVM. During winter, when days are exceedingly short and there is thick sea-ice cover, krill move to deeper water where they perform extensive DVM postulated to support foraging at the seafloor (Taki et al. 2005; Siegel et al. 2005; Bernard 2017).

The seasonal changes in krill DVM are not just a reflection of changing photoperiods, but are also influenced by the ontogenetic developmental of the krill. During winter, the larval stages Furcilia III to VI, which are mainly associated with the winter sea ice, show reverse DVM, rising to the surface during the day rather than at night. In the day the larvae are closely associated with the sea-ice, whereas after sunset they are dispersed in the upper 50m of the water column. Such behaviour has been suggested to increase the chances of finding food in patchy environments and reduces predation from visual hunters which come to the surface waters during the night (Meyer et al. 2017).

Clearly there are adaptive advantages to changing foraging behaviour with season and developmental stage and it follows that physiological processes also show seasonal cycles. For instance, laboratory experiments show that the response of *E. superba* to high food concentrations during winter is dependent on appropriate changes in light regime with only long days stimulating increased feeding activity (Teschke et al. 2007). Long days also result in advancement of sexual maturity whilst sexual regression could only be induced under short days. Photoperiodic entrainment of metabolic processes and feeding activity, growth, and time of maturity have all been interpreted as part of a comprehensive over-wintering strategy to save energy during the food-depleted season (for more details see Chapter 5). The observation that daily and seasonal behavioural / physiological cycles are so overt have led to the hypothesis that they are regulated by an endogenous timing system entrained by the seasonal Antarctic light regime (Meyer et al. 2010).

Free-running circadian clock gene activity was first described in krill during the Antarctic summer at a time when the sun is permanently above the horizon (Mazzotta et al. 2010; Teschke et al. 2011). Mazzotta et al. (2010) showed that at this time 8% of the transcriptome of krill displayed daily oscillations with either 12 h or 24 h periods. Associated with this was a progression of biochemical and physiological events throughout the day. Breakdown of energy-yielding nutrients and energy storage pathways were specifically activated in the early morning whilst glycogen mobilization, gluconeogenesis and fatty acids catabolism was activated in the evening and throughout the night. The implication was that a significant component of the transcriptome cycling is involved in the circadian clock, at least during the summer (De Pittà et al. 2013). More detailed investigations followed, which showed that the DVM, oxygen consumption and expression of the core-clock genes correlated with the light/dark cycle again persisting under constant darkness, demonstrating that the response was due to an endogenous circadian clock (Piccolin 2018). However, rhythmicity of these physiological processes was only 30% and inter-individual variation between krill was large, suggesting possible differences at the molecular level between animals with different clock genes alleles or variation in the regulation of circadian input/output pathways.

A comparison of the principal clock components in krill and their role within the circadian feedback loop with known circadian models in mammals, insects and crustaceans have shown that the krill clock exhibits both mammalian and insect features, presumably contributing to an evolutionary strategy to cope with polar environment challenges (Biscontin et al. 2017). The krill clock proteins CLK and CYC were identified as the putative positive elements of the principal feedback loop, as described for *Drosophila* (see Box Figure 8.9), whereas the krill clock proteins PER, TIM and CRY2 were identified as the putative negative elements, as described for the monarch butterfly *Danaus plexippus* in sun compass orientation (Merlin et al. 2009).

8.3.2 Seasonal clocks

Seasonal changes in the activity of the circadian clock and the regulation of daily metabolic output rhythms in *E. superba* were studied in a one-year experiment in which krill were exposed to simulated seasonal photoperiodic cycles of the Southern Ocean (66°S) and to constant darkness in the absence of other environmental signals (Piccolin et al. 2018a). Food was provided *ad libitum* and temperature was kept constant. In simulated early-autumn conditions, with 16 hours of light and 8 hours of darkness (LD 16:8), clock gene activity was rhythmic as seen in Figure 8.5 B showing *per* gene (the role of *per* in the circadian clock is described in

Box Figure 8.9). At the same time the metabolic output was synchronized with the light/dark cycle, with up-regulation of key metabolic genes occurring during the dark phase. Conversely, in simulated mid-summer (LD 24:0) and mid-winter (LD 3:21) conditions, clock gene activity was arrhythmic as shown in Figs. 8.5 A and C respectively, and with up-regulation of key metabolic genes occurring at different times of the day.

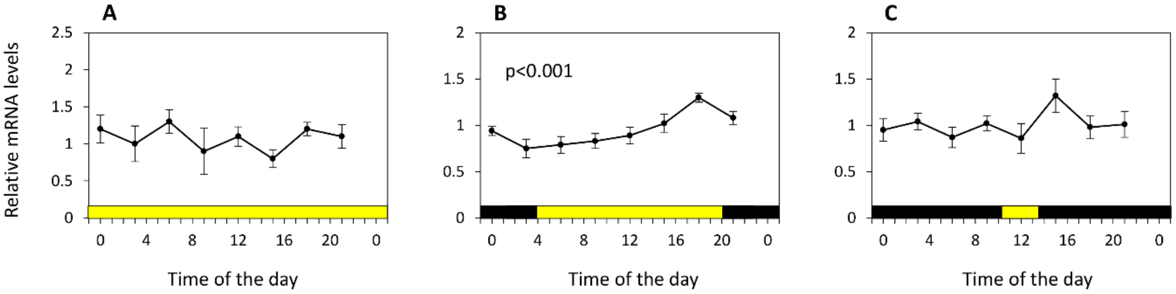


Fig 8.5 Daily patterns of expression of the period (*per*) gene in A: mid-summer, B: early-autumn and C: mid-winter. Data points represent means ± SEM (N = 6). Colour bars indicate simulated day (yellow) and night (black) phases. Expression of *per* gene was analysed for 24 h rhythmicity and RAIN analysis with significant 24 h cycling ($p < 0.05$) is indicated. Adapted from Piccolin et al. 2018a

The results suggest that only overt day/night cycles are able to entrain the circadian clock and promote the synchronization of metabolic output functions such as changes in growth, enzyme activity and oxygen consumption, much like in *C. finmarchicus* (see previous section). However, both rhythmic clock gene expression and transcriptional output was observed in wild krill caught during Polar Day in the Southern Ocean and hence there may be important clock entraining cues missing in the laboratory (Piccolin et al. 2018a).

Interestingly, under constant darkness, seasonal rhythms of growth, enzyme activity and gene expression were observed, suggesting the possible involvement of an endogenous circannual clock. However, oxygen consumption, which represents the sum of multiple physiological processes including basal metabolism, swimming activity, growth, and feeding activity, did not display a seasonal rhythm (Piccolin et al. 2018b), which was in contrast to another study by Brown et al. (2013). These differences may be explained by the timing of the experiments. Brown et al. (2013), initiated DD in early autumn (February), whereas Piccolin et al. (2018b) initiated the treatment earlier, in the austral December (early summer). It is likely that to achieve effective entrainment, the circannual clock might require exposure to a specific portion of the seasonal photoperiodic cue in phase with the endogenous circannual cycle, to provide the “correct” seasonal response, as in rainbow trout, *Oncorhynchus mykiss*, and detailed with a circannual phase response curve (Randall et al. 1998). The implication here, is that there is a critical photoperiodic entrainment period of the circannual clock that occurs between mid-summer and early autumn. Indeed, experiments under simulated natural light conditions at 66°S revealed that oxygen consumption only started to decrease after the light-phase duration had been reduced below 16 h, corresponding to simulated early autumn in February (Piccolin et al. 2018b). However, in krill exposed to constant darkness, the krill clock genes *clock*, *cryptochrome*2 and *timeless*, showed up-regulation under such conditions, suggesting a specific link between clock-related activity and the light-regime at that time of year. It therefore appears likely that a circannual clock is involved in structuring the physiological processes of krill irrespective of the exogenous seasonal light regime.

8.4 Biological clocks in bivalves

8.4.1 Measuring bivalve shell gape cycles

As suspension-feeders, bivalves play important roles in coupling benthic-pelagic interactions, seafloor biogeochemical processes, and modification of near-bed hydrodynamics. Like zooplankton, bivalves are photoperiodic, but unlike zooplankton, they are either completely sessile or only have limited capability to move. Their response to changes in light is to modify the duration and the amplitude of their valve opening. Thus bivalve behaviour is typically studied using valvometers consisting of pairs of electrodes which are glued to the animals' shells (see Figure 8.6). The valvometers provide a means to measure electrically, and at high frequency, the distance between the valves providing both gape activity patterns and shell growth data as the electrodes are incrementally pushed apart over time.

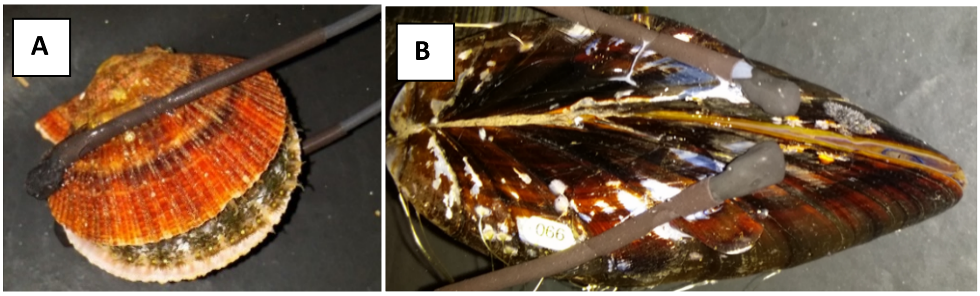


Fig 8.6 Arctic scallop *Chlamys islandica* (**a**) and the blue mussel *Mytilus edulis* (**b**) equipped with lightweight electrodes of the high frequency non-invasive (HFNI) valvometer biosensor to record valve activity behaviour. Photo: D. Tran

Monitoring valve gape behaviour is used as a proxy for gill filtration which is necessary for respiration and nutrition or, as a response to environmental stressors such as pollutants (Andrade et al. 2016) or harmful algae (Tran et al. 2010). Uniquely, the valvometer system provides a means of measuring the gape activity of bivalves in their natural ecosystem over long time scales (days to years).

This approach has been applied to fan mussel *Pinna nobilis* shell gape behaviour in the Mediterranean Sea (Garcia-March et al. 2008) and to oysters *Crassostrea gigas* (Tran et al. 2011) in the Atlantic revealing different rhythms correlated to moon-sun cycle interactions. In *P. nobilis* a daily rhythm (~24 h) of shell gape activity is evident, modulated by a moonlight rhythm (~29.5 d) with a complete absence of tidal oscillations, presumably due to the limited tides in the Mediterranean. In contrast, the dominant rhythm for *C. gigas* is that of a tidal cycle (~12.4 h), even in subtidal conditions, with modulation of intensity by the neap-spring tidal cycle (~14.7 d) and the anomalistic moon cycle (~27.6 d). A weaker daily rhythm is also apparent, but changes seasonally, from nocturnal in autumn and winter to diurnal in spring and summer (Payton et al. 2017a). Indeed Payton et al. (2017a) clearly showed that the tidal, moonlight and daily rhythms are all modulated on annual time-frames suggesting an interaction with a putative circannual rhythm.

Several recent long-terms studies have been made possible by real time communication with valvometers providing remarkable insights into the behaviour of some ecologically important Arctic bivalves, specifically: the ocean quahog clam, *Arctica islandica*, considered as the longest-lived non-colonial animal on earth with a longevity > 500 years (Ballesta-Artero et al. 2017); the native Arctic scallops, *Chlamys islandica,* and; the blue mussel *Mytilus* spp. which is classified as a non-native species in Arctic waters.

8.4.2 Seasonal clocks

A three-year study was conducted on *C. islandica* in Kongsfjorden, a high Arctic fjord (Spitsbergen, Svalbard, 78° 56'N) to determine daily cycles of valve gape during the Polar Day, the Polar Night and equinoxes (Tran et al. 2016). Results revealed that the percentage of scallops within the population exhibiting a cyclic pattern in gape behaviour within the circadian range was highest during the Polar Night (76%) and lowest during the Polar Day (50%) with intermediate numbers during the equinoxes (67%). During the periods centred on the spring and autumnal equinoxes the scallops exhibited a cycle with a period very close to 24h, synchronized by daily light-dark alternations. During the Polar Night and Polar Day, the daily cycle was less synchronized to the exact 24h period. It is unclear whether the scallops reacted exogenously to light, or if a functional and robust endogenous circadian clock initiated rhythmic behaviour during times when light/dark cycles were muted during the Polar Night and Day.

To better understand seasonality and potentially the role of circannual rhythmicity in shell gape behaviour and growth, a comparative assessment was made between *C. islandica* and *M. edulis* during two years of monitoring (2016-2018) in Svalbard (78°56'N). Figure 8.7 (upper panel) shows a typical, double-plotted actogram of an individual profile of a *C. islandica* illustrating that the scallop remained mostly open (for details see Figure 8.7 caption) with an opening amplitude near the maximum throughout the two years. In contrast, the behaviour of a blue mussel, *M. edulis*, shows a different annual pattern of valve behaviour with strong seasonal components. The valve opening amplitude was maximal since the beginning of the Polar Day until to the beginning of Polar Night where the activity strongly decreased until to the next Polar Day.

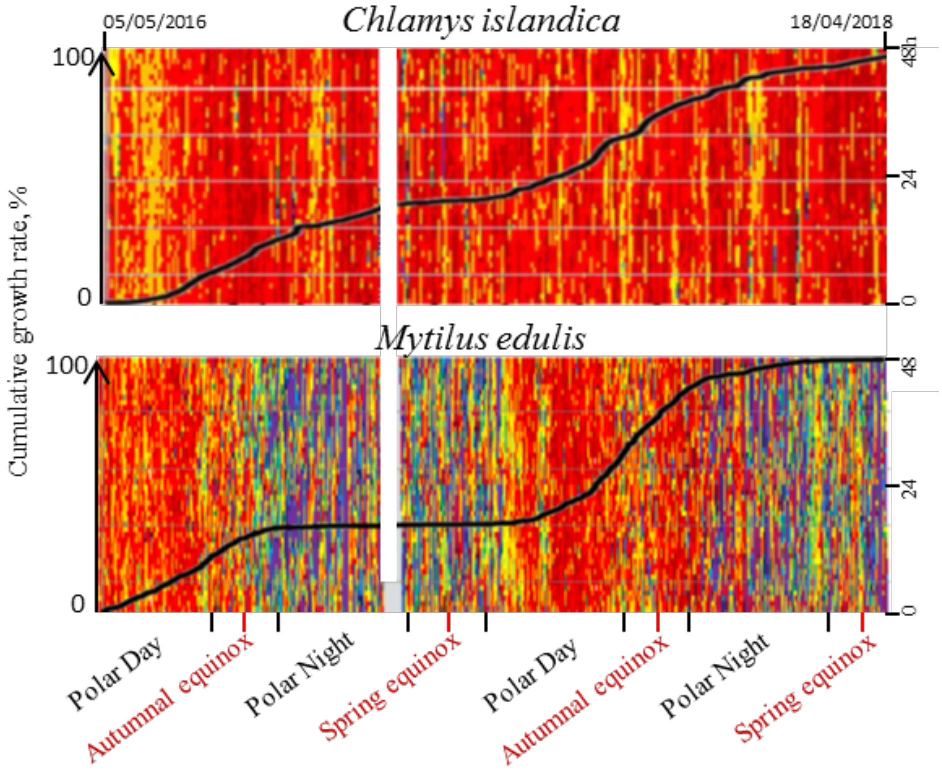


Fig 8.7 Annual behaviour (gape activity) of Arctic bivalves. Double-plotted actograms of individual hourly Valve Opening Amplitude (VOA) behaviour (right y-axis) of a *C. islandica* and a *M. edulis*. The behaviour was recorded by HFNI valvometer biosensors over two years (2016-2018) in the Kongsfjorden (Spitsbergen, Svalbard, 78° 56'N). Dark red and blue colours correspond to 100 % and 0 % of VOA, respectively. Black lines correspond to the profile of the shell growth. Left y-axis correspond to cumulative growth, 100% correspond to the maximal of growth shell at the end of the two-year experiment. Unpublished data

Even at this high latitude *M. edulis* followed a seasonal cycle of gape activity like in other bivalves such as *A. islandica* (Ballesta-Artero et al. 2017), where shell gape activity is well correlated with food availability and, to a lesser degree, photoperiod and water temperature. There are subtle differences in behaviour however; whilst *M. edulis* valve opening was maximal during the Polar Day corresponding to the summer, in *A. islandica* this occurred during the spring. Conversely, *C. islandica,* tended to keep its valves open continuously, irrespective of season, and the valve opening amplitude exhibited only a very narrow range of variation (75-80 % of maximal amplitude), with no significant daily/seasonal rhythms (Tran et al. 2016). This highlights that in the scallop at least, there is an absence of any seasonal or potentially circannual cycle/rhythm of valve activity.

Since HFNI valvometry, measured by the use of a high frequency non-invasive valvometer, also provides a measure of shell growth from daily incremental increases between the minimum distances of electrodes when the shells are closed, seasonal patterns of growth may also be investigated. In Figure 8.7, two typical profiles of shell growth are shown in the two species, superimposed over the valve activity behaviour. In *M. edulis*, a seasonal/circannual cycle of growth correlates to the behavioural rhythm of shell gape. The slope of shell growth rate was maximal when the valve opening amplitude was maximal during the Polar Day. In contrast, shell growth rate was minimal during the Polar Night, when valve opening amplitude was also decreased.

In *C. islandica* the growth pattern at the annual scale was similar to *M. edulis*, but with less marked variation and therefore not correlated with a circannual rhythm of valve activity. The reduced growth in the Polar Night in these both bivalves' species is in concordance with sclerochronology studies done on the Iceland cockle, *Clinocardium ciliatum,* in Greenland showing a reduction of shell growth during Polar Night (Sejr et al. 2009).

8.4.3 Circadian clocks

The somewhat surprising finding that the highest percentage of cyclic activity in *C. islandica* was during the Polar Night warranted further investigation, specifically to understand circadian clock involvement in this response. Thus the strength of the scallop daily gape cycle over three successive Polar Nights was assessed according to changes in light irradiance (as twilight) over the Polar Night period (Tran et al. 2016). Five periods were investigated for each of the three Polar Nights: 2 civil twilights, with decreasing or increasing light irradiance; 2 nautical twilights, with decreasing or increasing light irradiance and; astronomical twilights, the darkest twilight of the Polar Night (see Chapter 3 for twilight definitions).

The results revealed that for the population of scallops monitored, a robust daily/circadian cycle was found during the decreasing civil twilight (Fig. 8.8). Decreasing light levels during nautical twilight, however, resulted in no significant daily/circadian activity. Surprisingly, during astronomical twilight, the scallops recovered significant daily/circadian activity but out of the circadian range (here between 16h and 33h). At an individual level, animals often had a daily/circadian cycle at both increasing/decreasing civil and increasing, but not decreasing, nautical twilights. Other than during nautical twilight, a correlation was revealed between increasing light intensity in the twilights and the percentage of cyclic scallops in the circadian range. Moreover, the cycle of activity became increasingly more synchronized to 24 hours with higher irradiance during twilight.

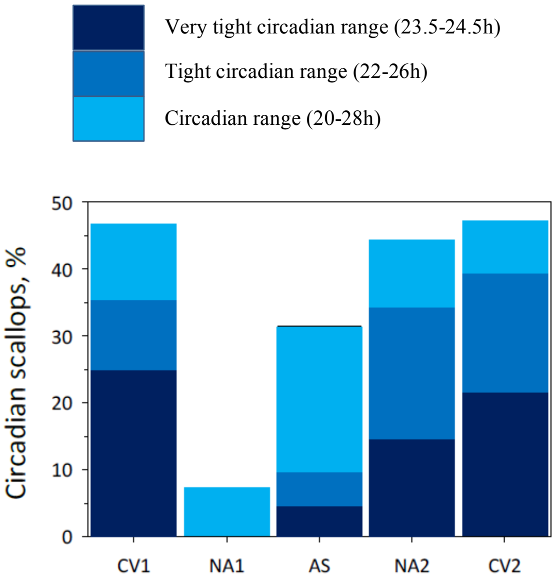


Fig 8.8 Circadian activity of *C. islandica* (n=14) during the Polar Night in Kongsfjorden (Spitsbergen, Svalbard, 78° 56'N). Percentage of scallops with valve behaviour in different circadian ranges according to the different twilight periods during three Polar Nights studied (2012-2015). Each Polar Night was sub-divided into five periods that corresponded to different twilight periods of increasing and decreasing levels of light irradiance: the civil twilight periods (CV1, CV2); the nautical twilight periods (NA1, NA2); and the astronomical twilight periods (AS). The mean percentage represents an average for the three Polar Nights studied. Modified from Tran et al. 2016

At this stage it was still unknown if the daily cycle of activity in *C. islandica* was simply due to an exogenous response to extremely low levels of light during the Polar Night, or an actual endogenous circadian rhythm of activity? To address this question, core clock genes were sequenced from *C. islandica* which revealed close homology with those found in temperate bivalve species. To measure the clock gene expression of *C. islandica*, two field experiments were performed in Kongsfjorden during the Polar Night (January 2017) and during the autumnal equinox (September 2017). Sampling of different tissues was carried out every 2 hours during a 24 hour cycle. The results showed that the level of the clock gene expression was very low. In both periods of sampling, some clock genes were oscillating in a circadian range and were tissue-specific. During the equinox experiment, the genes *period* and *ror* in the adductor muscles, *cryptochrome 1* in the mantle and *clock* in the gills revealed cycling circadian gene expression. During the Polar Night, no clock genes were observed to oscillate in muscles but cycling was apparent in *clock* and *ror* in gill tissue as well as *ror* in the mantle edge. The lack of cycling gene expression in some tissues challenge the role of clock genes in entraining all physiological and behavioural activities, especially when compared to temperate species, such as the oyster *C. gigas*, which demonstrates circadian cycling in all the core clock genes when exposed to a light-dark regime (Payton et al. 2017b).

In conclusion, recent studies in the Arctic show that bivalve molluscs are able to maintain rhythmic behaviours at daily and annual scales similar to bivalves at lower latitudes (Garcia-March et al. 2008, Tran et al. 2011, Payton et al. 2017a). Those in the Arctic appear to have adapted their behaviour to the specific light climate presumably to take advantage of the seasonal cycle of food availability. Although the molecular circadian clock machinery is present, its function at high latitudes remains to be elusive and should be the focus of further research.

8.5 Climate change effects on biological clocks in Polar regions

By measuring photoperiod, the circadian clock synchronises the timing of seasonal life cycle events in response to annual cycling changes in light conditions. However, climate change induced geographical population shifts towards higher latitudes, such as those already seen in *C. finmarchicus* (Falk-Petersen et al. 2007) and the blue mussel *M. edulis* (Berge et al. 2005), is resulting in animals experiencing a mismatch between the thermal and the photoperiodic environments to which they are adapted (Reygondeau and Beaugrand 2011). Consequently, as the oceans warm and become more illuminated following sea ice melt, there will be trade-offs between latitudes of favourable temperature and potentially unfavourable photoperiod. Such trade-offs will be particularly pronounced in the Arctic with rapid photoperiodic change over short latitudinal ranges and increases in sea temperature predicted to be large (Beaugrand et al. 2019).

Thermal-photoperiodic mismatch due to climate change may be most evident in the seasonal life cycles of *Calanus* spp.. If diapause initiation is promoted via photoperiodic time measurement then a critical photoperiod would induce the animals to switch from one seasonal physiological state to another. However critical photoperiods may be affected by temperature as well as sequence variants (alleles) of circadian clock genes (Watson and Smallman 1971; Paolucci et al. 2013). While the strong selective pressure for optimal seasonal timing suggests rapid spread of “favourable alleles”, at least for terrestrial insects (Bradshaw and Holzapfel 2001; Tauber et al. 2007), it is completely unclear how such adaptation processes could work in marine habitats affected by large scale displacements via ocean currents.

While all three species of *Calanus* rely on the spring phytoplankton bloom, the boreal *C. finmarchicus* does so the most (for details see Chapter 5). Since increasing ocean temperatures are leading to earlier sea ice breakup and earlier phytoplankton blooms (Søreide et al. 2010) the negative consequences to *C. finmarchicus* may be large if its phenology is reliant on an inflexible circadian/circannual clock. Generally, the inter-annual variability of the timing of the bloom is high in polar habitats due to the variability in the timing of sea ice breakup (Kahru et al. 2010). *C. glacialis* and *C. hyperboreus* are probably better adapted than *C. finmarchicus* to this heterogeneity (reflected in their multi-year life-cycles) and *C. finmarchicus* may not, therefore, be able to fill a gap created by the pole-ward retreat of its polar congeners. Either way, any reduction in fitness and recruitment of *C. finmarchicus* because of thermal/photoperiodic constraints would severely affect higher trophic levels and biogeochemical cycling (Falk-Petersen et al. 2007; Jónasdóttir et al. 2015). Similar ecosystem consequences might be expected in loss of fitness in krill and, to a lesser extent, bivalves.

Copepods, krill and bivalves have adapted to the extreme polar photoperiods and their behaviour and circadian clock expression is highly modulated by seasons and physiological state. Quite how circadian clock entrainment works during much of the Polar Night twilight periods, however, and its function in maximizing fitness, remains completely unexplored.

BOX 8.1 Molecular interactions of clock genes and proteins

The underlying molecular mechanism of the circadian clock is highly conserved between species and consists of autoregulatory feedback loops where gene products (proteins) switch off their own gene transcription. In invertebrates the best studied model for the circadian clock is *Drosophila melanogosta* (Zeng et al. 1996). Here the two principle clock genes (*per* and *tim*) are located in the nucleus of the cell (except in mitochondria) and are "switched on" or activated via clock proteins (CLOCK/CYCLE) using promoter regions (E-boxes) as depicted in Figure 8.10.

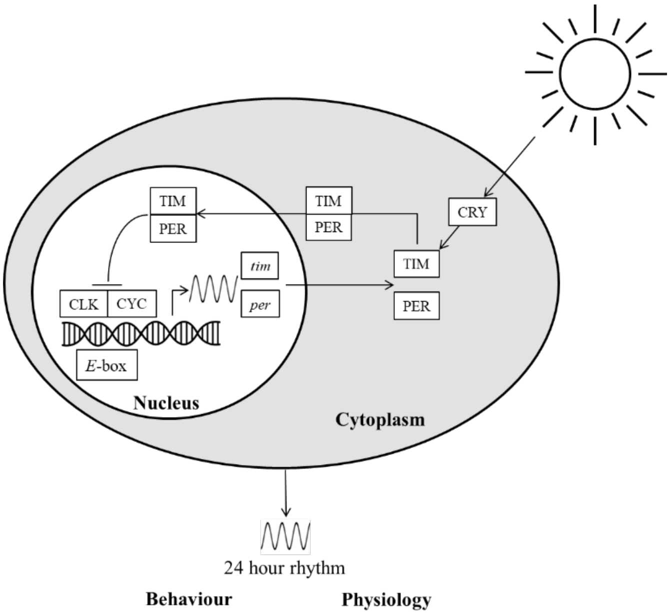


Fig 8.9 Simplified *Drosophila* circadian clock showing molecular interactions of clock genes and proteins. Entrainment of the clock is by the day/night cycle and the final output is a 24 hour rhythm of behaviour and physiology. The mechanism of the clock is similar between species although different genes may be recruited.

Per and *tim* messenger ribonucleic acid (mRNA) are then used to generate clock proteins (PER and TIM) in the cell cytoplasm where another clock protein (CRY) can alter the phase of the circadian clock since it is light sensitive. CRY has the potential to degrade (phosphorylate) TIM, either slowing or speeding up the circadian clock since PER/TIM can only re-enter the nucleus if they have coupled together in a special way (they need to have formed a heterodimer). Once in the nucleus they then interact with the activator clock proteins CLOCK/CYCLE, essentially "switching them off". This then also switches off *per* and *tim* gene expression. Eventually after about 24 hours the inhibitory proteins PER/TIM are depleted and this is when the whole cycle starts again (for detailed overview of the molecular circadian clock in *Drosophila* see: Dubowy and Sehgal 2017). Quite simply the clock is an unseen evolutionary marvel, ticking with peaks and troughs of clock gene mRNA and their proteins, cycling through the day. The molecular machine and gene expression pathways remain largely unchanged between species, apart from a few tweaks, and a simplified proto-clock has even been documented in the earliest protozoa which first appeared in the Earth's history over a billion years ago (Tauber et al. 2004).

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Chapter 9

Sensor Carrying Platforms

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Abstract

Information and communication technology, autonomy and miniaturization in terms of e.g. microelectromechanical systems are enabling technologies with significant impact on the development of sensors, sensor carrying platforms, control systems and data gathering, storage and analysis methods. Sensor carrying platforms are grouped in stationary devices such as landers and moorings to dynamic platforms such as marine robotics, ships, aerial systems and remote sensing satellites from space. Lately, the development of low-cost small-satellites with customized payload sensors and accessible mission control centers has opened for a democratization of the space for remote sensing as well. The mapping and monitoring strategy may be carried out by each type of sensor carrying platform suitable for the mission. However, we see a quantum leap by operating heterogenous sensor carrying platforms for the most efficient mapping and monitoring in spatial and temporal scales. We are facing a paradigm shift in terms of resolution and coverage capabilities. There have been several research efforts to improve the technology and methodology for mapping and monitoring of the oceans. Today, we see that the mapping coverage may be 100-1000 times higher than the state-of-the-art technology six years ago. The entailed increase in data harvesting does also create new challenges in handling of big data sets. It is an increasing need to update the oceanographic and ecosystem numerical model capabilities taking full benefit of the ongoing shift in technology. The Arctic can truly be characterized as a remote and harsh environment for scientific operations and even more demanding during the Polar Night due to the darkness. During winter operations extreme coldness may also be a challenge dependent on the weather conditions. Enabling technology and proper operational procedures may be the only way to reveal and understand the processes taking place there. The spatial scale is enormous, and as several research campaigns have already taught us, the variability is huge not only during the seasons but also over the years. This clearly also tells us the importance of prolonged presence. In this chapter we will briefly present the various sensor carrying platforms and payload sensors. We will also describe the philosophy behind integrated operations using heterogenous platforms and why and how to bridge science and technology being successful in the development of autonomous systems for efficient and safe operations. Examples and experience from Arctic missions will also be presented.

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Keywords Marine robotics • Small-satellites • Autonomy • Sensors • Integrated operations • Safe job analysis

9.1 Introduction

The understanding and corresponding management of the oceans including Arctic areas is crucial for a sustainable use of marine resources. However, a large part of the oceans is still unknown. This may be even more pronounced in Arctic areas where the dynamic processes and seasonal variability are high. The environment is extreme, challenging to access, and dangerous for humans to operate in. During the Polar Night with darkness and coldness the operations become even more demanding. The possible undesired side-effect of light pollution from ships and other infrastructure on the marine ecosystem has recently been documented by Ludvigsen et al. (2018, see also Chapter 5). Here, it was shown that artificial light changes the behaviour and abundance of zooplankton, some escaped while others where attracted by light. Hence, the missions must be carefully planned subject to the objectives.

Exploring extreme environments calls for superior and reliable technology, robust and adaptable operational procedures, acceptance of risk yet the ability to manage it. New instruments and sensor carrying platforms are contributing to reveal the dynamic processes taking place across spatial and temporal scales. Heterogenous robotic systems (Fig. 9.1) such as autonomous underwater vehicles, surface ships to aerial and satellites have been an enabler for research in areas such as acoustic and optic sensing, inertia platforms, control and autonomy, risk management, big data analytics, and ocean modelling. In order to operate efficiently the science and technology need to be bridged, and for autonomous systems, interdisciplinary is crucial in planning and execution of operations and for the development of adaptive mapping strategies. Here, the on-line re-planning of the mission will be optimized subject to rewards concerning improved data harvesting, and associated risk considerations for e.g. collisions with sea bottom, ice and moving objects, and possibly loss of vehicle (see Chapter 10).

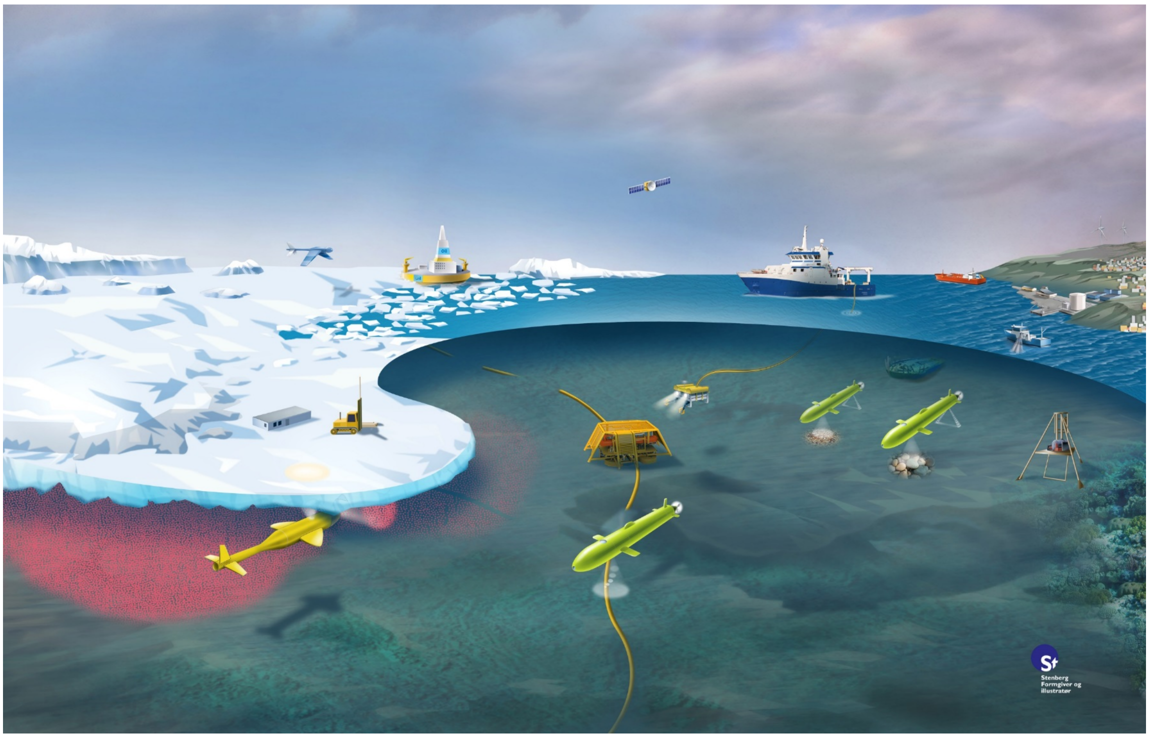

Fig 9.1 Heterogenous sensor platforms for ocean mapping using satelittes, aerial vehicles, ships, underwater vehicles and landers, illustration by NTNU AMOS/Stenberg.

We will in this Chapter address various aspects of sensor carrying platforms. The Chapter is organized as follows: Section 9.2 presents the main characteristics of sensor carrying platforms. Sections 9.3-4 are about payload and navigation sensors, respectively. In Section 9.5 we present how the various platforms perform with respect to coverage and resolution in spatial and temporal domains. Autonomy aspects are discussed in Section 9.6. Examples from field campaigns are shown in Section 9.7, while an introduction to safe and efficient operations are discussed in Section 9.8.

9.2 Characteristics of Sensor Carrying Platforms

The sensor carrying platforms (Fig. 9.1) may be grouped into:

- Underwater: Landers and buoys, remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs), gliders and profilers.
- Sea surface: Ships, and unmanned surface vehicles (USVs).
- Air and space: Satellites, unmanned aerial vehicles (UAVs) and air planes.

Developments in sensor carrying platforms, sensors, control methods, autonomy, communication and networked vehicle systems have been driven by the needs in marine sciences as described in Singh et al. (2001), Pizarro and Singh (2003), Moline et al. (2005), Ludvigsen et al. (2007), Bingham et al. (2010), Berge et al. (2012), Williams et al. (2012), Seto (2013), Bellingham (2014), Nilssen and Ødegård et al. (2015), Williams et al. (2015), Ludvigsen and Sørensen (2016), Johnsen et al. (2018) and the references therein.

Each sensor carrying platform has its own characteristics with pros and cons as listed in Tables 9.1-2. Dependent on installed payload sensors they also have different capabilities in terms of spatial and temporal resolution and coverage as indicated in Figure 9.2 and Tables 9.3-4. For many operations it may be enough to consider only one of the platforms at a time. However, as shown in Nilssen et al. (2015) integrated operations with heterogenous robotic systems and swarms may be more efficient. For Arctic operations there will be additional challenges related to harsh environments including icing and low temperature, remoteness, darkness (during the Polar Night), and not at least that the operations take place in an environmental sensitive area. Under such circumstances proper planning regarding logistics and operation including health, safety and environment impacts (HSE) must be seriously dealt with.

9.3 Payload Sensors

Payload sensors are measurement units that are carried by a sensor carrying platform for collecting data and images, either by remote sensing or by direct measurements in the habitat (*in situ*). The objective of the sensor carrying platform is to position the sensor or instrument at a specific location or trajectory at a given time. If the biological or oceanographical process subject to the investigation is dynamic, there may also be temporal constraints that the platform needs to fulfill. Moving towards more autonomous vehicles with scientific mission objectives, rather than a pre-programmed behavior, may require that these instruments are no longer passive payloads, but that their measurements are forwarded to the mission planning layer and the guidance and optimization system in the operations control for mission optimization, see Figure 9.4.

Table 9.1 Characteristics, pros and cons of underwater sensor carrying platforms

Platform	Characteristics	Pros: +	Cons: -
Landers, and buoys	• Main components: instrument platform either standing on the seabed (lander), or suspended in the water column moored to the seabed or tethered to floating device at the surface • Offline or online communication by cable or satellite/radio • Powered by solar power, batteries or cable	• High payload capacity • Low cost operation when installed • If online, access to real-time data • Possibility for synoptic measurements along vertical profile	• Bio fouling and corrosion degrade the sensors and data quality • High risk for offline systems with uncertainty regarding data recording and quality • For online systems high cost for installation of power and communication systems • Lander and cables for online systems exposed for damage due to e.g. trawling
Remotely Operated Vehicles (ROVs)	• Main components: vehicle, umbilical and control stations • Delivered in different sizes, depth and thrust ratings, functionality, manipulator and sensors • Power supply and communication by umbilical • Navigation by means of acoustics, inertial navigation systems (INS), doppler velocity log (DVL), camera • ROV is normally launched from crane on dynamic positioning (DP) ship	• High payload capacity • Umbilical gives almost unlimited electrical power and high bandwidth communication • Manipulator arms for sampling and intervention • Collection units (water masses and seabed) • Online video and sensor readings to human operator	• Umbilical limits spatial coverage and is exposed to current loads/drag forces. Increasingly problems for deep water. • Expensive operation due to day rates of ships with DP systems for station keeping • Weather window: Operation of ROV is sensitive to waves and current giving reduced availability • Data quality could be degraded by large ROV motions and forces induced by the umbilical
Autonomous Underwater Vehicles (AUVs)	• Main components: vehicle, control station, acoustic navigation and for bigger AUVs launch and recovery system • Delivered in different sizes, depth and thrust ratings, functionality, and sensors • Carries its own power supply • Navigation by means of global navigation satellite systems (GNSS), acoustics, compass, INS, DVL, camera • Operates untethered • Operates supervised or autonomously with limited communication ability	• High payload capacity (however less capacity compared to ROV) • 3D (long, lat and depth) mapping capabilities are unique • New research on autonomy improves AUV intelligence and ability to operate in an unstructured environment • Allows operations in areas that have limited or no accessibility with other platforms such as under ice	• Risk of operation – loss of data and vehicle • Limited power supply on-board • Today: Need for competence on AUV crew for launch and recovery, planning of operation and troubleshooting during different operational scenarios • Possible limitations in operation due to ship traffic and risk for collision with e.g. ice • Different water layers (e.g. salinity, temperature, turbidity) increase risk for poor navigation and control
Gliders	• Components: vehicle, satellite communication sender/receiver and control station • Carries its own power supply • Operates autonomously with intermittent piloting commands when surfaced • Deployed from boats • Navigation by dead reckoning and surface GNSS fixes supplemented by acoustic navigation when under sea ice • Buoyancy driven propulsion by variable ballasting of water • Hybrid gliders with propeller available for operation in areas of strong current	• Water column coverage (200-6000m) over long distances • Few personnel involved during the daily operation • Follow large ocean current systems • Large suite of sensors are available to fit • Spatial and temporal resolution of data is high • Data transmitted in near-real time reducing risks of data loss	• Low payload capacity for multiple, high-power sensors • Slow speed operation – 0.2 m/s average. • No capability for benthic (seabed) mapping due to control concept • Limited power, payload, control and navigation accuracy • Risk of operation – loss or damage of vehicle • Limited online control • Possible limitations in operation under ice and due to ship traffic and risk for collision • Requires significant technical team for pre and post-deployment servicing • The data are not trivial to analyse due to significant space-time aliasing

Table 9.2 Characteristics, pros and cons of surface and air & space sensor carrying platforms

Platform	Characteristics	Pros: +	Cons: -
Unmanned Surface Vessels (USVs)	• Components: vehicle, propulsion system, navigation, payload module, control station • Delivered in different sizes with various principles for propulsions (combustion engines, batteries, sun, wind) • Carries its own power supply • Navigation by means of GNSS, compass, INS • Operates supervised or autonomously if limited communication ability	• 2D mapping capabilities are unique • Can operate well on shallow water • Less dependent on ship during operation • Sensors: Wide payload capacity • Perfect to aid AUV operations by serving as communication hub	• Risk of operation – loss of data and vehicle • Weather window: Operation of USV is sensitive to ice, waves and current giving reduced availability and quality of data • Today: Need for competence on personnel for operation, troubleshooting. Autonomy may be improved • Possible limitations in operation due to ship traffic and risk for collision
Ships	• Components: hull, deck space, crane, power, thruster and propulsion system, DP system, sensors • Control centre for other sensor carrying platforms	• Very large payload capacity • Efficient mobility and deployment of ROV, AUV, USV, USV • Conduct and handle samples from any gears and sensor platforms	• Ship-based sensors will have limited spatial resolutions for increasing water depth • Costly operation
Unmanned Aerial Vehicles (UAVs)	• Main components: fixed wing, multi role, or combined, control station, GNSS navigation, launch and recovery system • Delivered in different sizes with different range, wind and endurance capabilities, functionality, and sensors • Carries its own power supply • Operates supervised with or beyond line of sight	• 2D (long., lat.) mapping capabilities are unique • New research on autonomy improves UAV intelligence and ability to operate in an unstructured environment • Allows operations in areas that have limited or no accessibility with other platforms • Efficient platform both as sensor carrier as well as communication hub	• Currently, limited payload capacity • Endurance • Icing • Sensitive to wind speed • Risk for loss of vehicle
Small Satellites	• Main components: Hull, antennas, payload sensor, control system, space control centre • Delivered in different sizes with different range, functionality, and sensors • Operates 3-5 years in 450-500 km orbit • Launched from dedicated space rockets or as appendices on bigger space launches	• 2D (long., lat.) mapping coverage is unique • Operation with customized sensors and communication equipment	• Dependent on visibility • Cost of deployment • Loss of unit and data • Low resolution

Also, for mapping of almost static systems, i.e. the seabed topology, archeological sites, etc. with increased autonomy the sensor carrying platform will have to consider findings and react on them in order to optimize the survey operation. Besides improved methods for online risk assessment (risk vs. reward) considering e.g. risk for collision against improved data quality operating closer to objects of interest (OOI) should be addressed. For dynamical processes, the development of the process must be considered along with their driving parameters. Sensor range and resolution vary with the technology and corresponding configurations, and greatly depend on how the platform navigates in relation to the feature or process to be measured. When appropriate range and resolution have been determined, it is possible to consider efficiency of the sensor and platform combinations for a given mission purpose (Table 9.3).

9.3.1 Underwater Optics

Optical imaging of the seabed provides high resolution qualitative information about shape, colour and texture of the seabed. To identify objects on the seafloor, optical imaging is still the most reliable method due to the high resolution of the colour and texture information. However, to obtain quantitative data from optical imaging is challenging (see examples in Chapter 10).

Camera and Video: Underwater photogrammetry has experienced considerable advancements the last few years, driven by the developments in computer capacity and computer vision software (Nornes et al. 2015; Yamafune et al. 2017). Seawater and its optically active constituents (inherent optical properties, IOP, see Chapter 3), e.g. phytoplankton, coloured dissolved organic matter (CDOM) and total suspended matter (TSM), alter the spectral light absorption and backscatter limiting the range for the optical cameras constraining the distance between camera and OOI and the corresponding area coverage (see Chapters 3 and 10). Optical imaging by use of still images or video cameras can be relevant for measuring e.g. geological conditions, archaeological features, and biological identification and behaviour. In addition, regular cameras and videos obtain a low spectral resolution, combining three colour bands in red, green and blue (RGB), similar to the spectral sensitivity of the human eye (Johnsen et al. 2013).

Underwater Hyperspectral Imaging (UHI): Applying hyperspectral imagers, the colour information can be quantified at all wavelengths of the visible light as presented in Johnsen et al. (2013, see seafloor mapping example in Chapter 10). By measuring the full visible light spectrum (400-700 nm), the light absorption of the seabed and the seawater can be quantified and characterized. Using knowledge of the spectral distribution of the light applied, many substances can be characterized by their reflection spectrum, after correction of IOPs. The hyperspectral imager can hence be used to estimate presence of substances like chlorophyll a (Chl a) or optical fingerprints of other pigments. The UHI technology opens up for fast processing of data for automatic identification of any OOI at the seafloor (Chapter 10). As for camera and video, the optical properties of the water column affect the sensor range and data quality.

The spectral characteristics of optical backscatter and light attenuation measurements can be used for characterizing the seawater with instruments like fluorometers, turbidity sensors and light scattering sensors. Monitoring the biological and chemical properties in the water masses, such as oxygen concentration and saturation can be measured by an *in situ* optodes. These data can be used to distinguish between water bodies, but also to investigate the bio-chemical development in the water by combining measurements of *in situ* temperature, salinity, nutrient concentration, current speed and direction, CO_2 concentration, Chl a concentration (indication of phytoplankton biomass, detailed in Chapter 4) and zooplankton biomass using acoustical sensors such as ADCP (acoustic doppler current profiler), AZFP (acoustic zooplankton fish profiler (detailed in Chapters 5-7).

9.3.2 Acoustics

Active sonars are devices that use transducers which generate sound waves of specific frequencies and listen for the echoes of these emitted sound waves reflected from objects on the sea-bed or in the water column. Active sonars have a large variety of applications, ranging from underwater navigation to sea-bed mapping. Different sensors that use active sonar technology are discussed below (see also Chapter 10).

Acoustic Doppler Current Profilers (ADCP) provide vertical and horizontal velocities of the ocean currents. The instrument measures the Doppler shift of the scattered acoustic signal, and from this, the velocity of the instrument relative to the scatters can be calculated (RDI 2011). ADCPs can be used to estimate a three-dimensional ocean current velocity vector by assuming that the planktonic scatters in the water column are drifting passively with the same speed and direction as the currents. Typical planktonic scatterers are copepods, euphausiids (krill), and pteropods (sea butterflies). The acoustic backscatter collected by the ADCPs provides information about the distribution, relative abundance, and vertical velocity of planktonic organisms in the water column (Deines 1999). Previous studies have used ADCPs mounted on moorings (e.g. Berge et al. 2009) or on autonomous platforms such as AUVs (Geoffroy et al. 2016) to study Diel Vertical Migrations (DVM) and patchiness of zooplankton in the Arctic. Ocean currents are dynamic processes influenced by tides, lunar cycles, climatic variations, weather, and many other environmental factors. Therefore, current velocities as measured by ADCPs will vary on all timescales from sub-hourly to decadal.

Multi-frequency echosounders are sonars using one or several transducers pinging at different discrete narrowband frequencies to detect zooplankton or fish in the water column. Frequencies can be customized for a specific scientific mission, but generally vary between 18 kHz and 769 kHz. Common models used for marine research in the Arctic are the Simrad EK60 and the Acoustic Zooplankton and Fish Profiler (AZFP; ASL Environmental Sciences; ASL 2016). Simrad EK60 mounted on research vessels and operating at 18, 38 and 120 kHz (RV *Helmer Hanssen*, Norway) or 38, 120 and 200 kHz (CCGS *Amundsen*, Canada) have been used to study fish and zooplankton during the Polar Night (e.g. Benoit et al. 2010; Geoffroy et al. in press). A similar instrument mounted on a REMUS 600 AUV (Moline et al. 2015) mapped the distribution of mesopelagic organisms (600 – 1200 meters depth). The AZFP is typically used for zooplankton or fish surveys (as suggested by its name) and has been operated on moorings (Darnis et al. 2017) and from Autonomous Surface Vehicles (Ludvigsen et al. 2018) to investigate DVM of zooplankton during the Polar Night, as well as on gliders to study spatial and temporal distribution of biomass (Chave et al. 2018).

Broadband echosounders are progressively replacing narrowband echosounders in marine research. Instead of emitting at a discrete narrowband frequency, each transducer of the broadband echosounder emits a chirp centered around a nominal frequency. The bandwith increases with the nominal frequency of the transducer. For instance, Simrad's 38 kHz transducer emit a chirp between 34 and 45 kHz, and their 333 kHz transducer emits between 283 and 383 kHz. Compared to narrowband echosounders that use the difference in Mean Volume Backscattering Strength between narrowband frequencies to classify scatterers into functional groups (Korneliussen et al. 2018), each animal detected by a broadband echosounder produces a frequency response curve, which could improve the taxonomic resolution of acoustic signals (Bassett et al. 2016). Main models of broadband echosounders used in marine research are the Simrad EK80 and Wideband Autonomous Transceiver (WBAT). Narrowband and broadband echosounders have very high temporal resolution (seconds) and can be used to monitor changes in vertical or horizontal distributions of fish and zooplankton in the order of minutes to months.

Active sonars can also be used to measure range to objects on the sea-bed by measuring the time from transmit to the reflected acoustic signal arrives back the sensor (two-way travel time) and multiplying it by the speed of sound. *Multibeam echo sounders* (MBE) transmit fan shaped acoustic pulses (pings) to cover across-track swaths of the seabed. Using directional receivers to determine angle and two-way travel time of each received beam, a MBE can measure hundreds of directions and ranges for each ping reflected off the seabed surface, resulting in a dense point cloud of the bathymetry of the sea-bed (L3 Communications 2000). *Side-scan sonars* (SSS) measure the surface reflectance of the seabed and reveals information about the sea-bed material composition due to different sound absorption characteristics (L3

Communications 2000). A side-scan sonar operates by sending out a ping, and by measuring the time of flight and intensity of the reflected signal. From this, an image of the seabed's acoustical reflectivity can be produced. From these images, it is possible to identify for example ship wrecks since wood and steel have significantly different reflectivity than the sea-bottom. Initially, only time and intensity are measured, and a flat seabed assumption is necessary to provide an image. However, modern interferometric sonar systems also estimate the direction of the signal and produce bathymetric data. *Sub-bottom profilers* (SBP) produce information about the sub-seabed structures. The system transmits low frequency, high power acoustical pulses to penetrate the seabed. Measuring the intensity of the reflected signal, the sub seafloor conditions are recorded in 2D in the along-track direction of the sensor.

During the last decade, synthetic aperture sonars (SAS) have been implemented on AUVs and other platforms. By constructing "false" arrays, considerably longer than the physical arrays, these systems use multiple pings simultaneously to map each seabed point. This method is independent of frequency and therefore provides significantly increased seabed resolution compared to conventional SSS at the same ranges (Hansen 2011). Interferometric SAS can produce high resolution bathymetry data that are co-registered with the intensity-based imagery, and also enables coherence calculations for data quality estimations.

9.3.3 Other Sensors

In addition to optical and acoustic sensors, other instruments are used to provide important measurements to describe environmental characteristics or other properties relevant for the mission purposes.

CT sensors measure conductivity and temperature. Salinity, speed of sound and seawater density are calculated from these fundamental parameters. Salinity and density are key parameters for oceanography, while speed of sound is essential for all sonar applications such as seabed mapping and acoustic navigation.

Magnetometers can be used for localizing ferrous man-made objects like anchors and cannons in historical ship-wrecks (Ballard 2008). They are also used to measure the magnetic characteristics of seabed rocks (Tivey et al. 1998). Magnetometers measure the strength, direction and relative change of magnetic fields. For such measurements to give meaningful spatial representations of seabed features, appropriate sampling rate and navigation of the sensor platform must be selected and planned in compliance with the mission purpose.

Table 9.3 Sensor and platform characteristics for seabed mapping purposes

Sensor	**SAS[1]**	**SSS[2]**	**Video**	**LIDAR[3]**	**MBE[4]**	**SBP**	**Photo**	**HI/UHI**
Efficiency	2 km^2/h	0,58 km^2/h	7200 m^2/h	>15 km^2/h	0,5 km^2/h	7200 m^2/h	7200 m^2/h	7200 m^2/h
Technology	Acoustic	Acoustic	Optic	Optic	Acoustic	Acoustic	Optic	Optic
Bathy. Res.	8 cm	>10 cm	na	1 m	> 5 cm	na	0,5 cm	na

SAS: Synthetic aperture sonars; SSS: Side scan sonars; LIDAR: Light detection and ranging; MBES: Multibeam echo sounders; SBP: Sub-bottom profilers; HI/UHI: Hyperspectral imaging/underwater hyperspectral imaging

[1] Based on data from HiSAS 1030
[2] Based on data from Quinn et al. (2005)
[3] Based on data from Doneus et al. (2013)
[4] Based on 120 degree swath @ 2 kts, max depth 40 m

9.4 Underwater Navigation Sensors

Acoustic baseline sensors: For several decades, acoustic baseline sensors like *long baseline* (LBL) and *ultra-short baseline* (USBL) have been the preferred positioning sensors for underwater operations. These systems measure the time of flight for the signals, and by applying the speed of sound, the range between the vehicle and a transducer is calculated. For LBL navigation, lateration using ranges to two or more transponders are used to determine the vehicles horizontal position (Kinsey et al. 2006). USBL also measures the phase-shift of the incoming signal to determine the transponder bearing. The result is a XYZ-position (3D) derived from range and phase angles. An important advantage of acoustic navigation is that the errors are observable and bounded, at the cost of additional infrastructure. LBL navigation requires two or more transponders to be deployed in the operational area, while USBL navigation depends on ship-presence in the operational area for the full duration of the mission. For ROV operations this might be acceptable. However, one of the primary arguments of utilizing AUVs has been to decrease cost through lower dependence on pre-installed infrastructure and ships.

An ADCP can be employed as a *Doppler velocity log (DVL)*, which measures the Doppler shift in the incoming acoustic signal reflected off the seabed (called bottom-track mode) or acoustic scatterers in the water column (called water-track mode). A DVL uses several transducers pointing in different directions to measure velocities in all three axes (typically four transducers in a so-called Janus configuration) (RDI 2011).

Pressure sensors: Depth is related to pressure through knowledge of the density of seawater. Both are easily observable with high precision, and therefore the pressure sensor is typically the main sensor for depth even when acoustic navigation is available. Depth is a fundamental measurement for underwater vehicles and is necessary both for control and for referencing collected data.

The heading sensor will provide a measurement of the heading of the vehicle. There are three main concepts of measuring the orientation of the vehicle around the vertical axis; gyro-compassing by extracting the earth's rotation, using a magnetic compass, or by determining the heading vector from the relative position of two or more points (Gade 2018). The former is the most common and accurate for underwater applications, albeit it relies on expensive and power-hungry sensors. The accuracy of both gyro-compassing and magnetic compassing will rapidly deteriorate when moving close to either of the poles, and alternative methods must be used when operating in these areas.

Inertial sensors form the basis for most dead-reckoning systems. By integrating the acceleration and linear and angular velocities, an inertial navigation system (INS) provides estimates of the position, orientation, and velocity of the vehicle. Integrating the acceleration and rate of changes of the orientation angles in the time domain an observer provides state estimates for position, orientation angles, velocities and accelerations. The error component in the inertial system will cause the position estimates to drift unbounded (Gade 2018). To limit this drift, the INS is typically aided by auxiliary sensors such as DVL and pressure sensors. However, to bound the error, an external positioning system must be used, such as LBL, USBL or GNSS.

9.5 Spatial and Temporal Resolution and Coverage

Nilssen et al. (2015) proposed a concept for integrated environmental mapping and monitoring (IEMM) based on a holistic environmental monitoring approach adjusted to purpose and object/area of interest. The proposed IEMM concept describes the different steps in such a system from mission of survey to selection of parameters, sensors, sensor platforms, data collection, data storage, analysis and to data interpretation for reliable decision making. In addition to measurements of essential parameters, the quality of the data interpretation is dependent on the spatial and temporal resolution and coverage. Hence, the dynamics in both space and time have to be considered in the mission planning process. The order of magnitudes for temporal and spatial resolution and coverage capabilities of relevant technology platforms are shown in Figure 9.2. The spatial and temporal coverage and resolution mapping needs will vary dependent on the mission purpose (e.g. processes, organisms of different sizes), and the different decision-makers such as scientists, authorities, and industry may have individual needs and requirements. The sensor carrying platforms' capabilities and limitations (summarized in Tables 9.3-4), mission purpose, and object/area of interest are of importance.

The process accuracy and scale define both the sensors precision required and the navigation accuracy necessary. Processes with time constants more than ten years can be considered constant in this context. When the time constant is between 10 years and 1 week, it can be documented using repeated surveys for a time series, and for when the time constant is lower than one week it can be attempted resolved within a single operation. Lower time constants require higher temporal resolution, possibly requiring multiple vehicles, or may even landers.

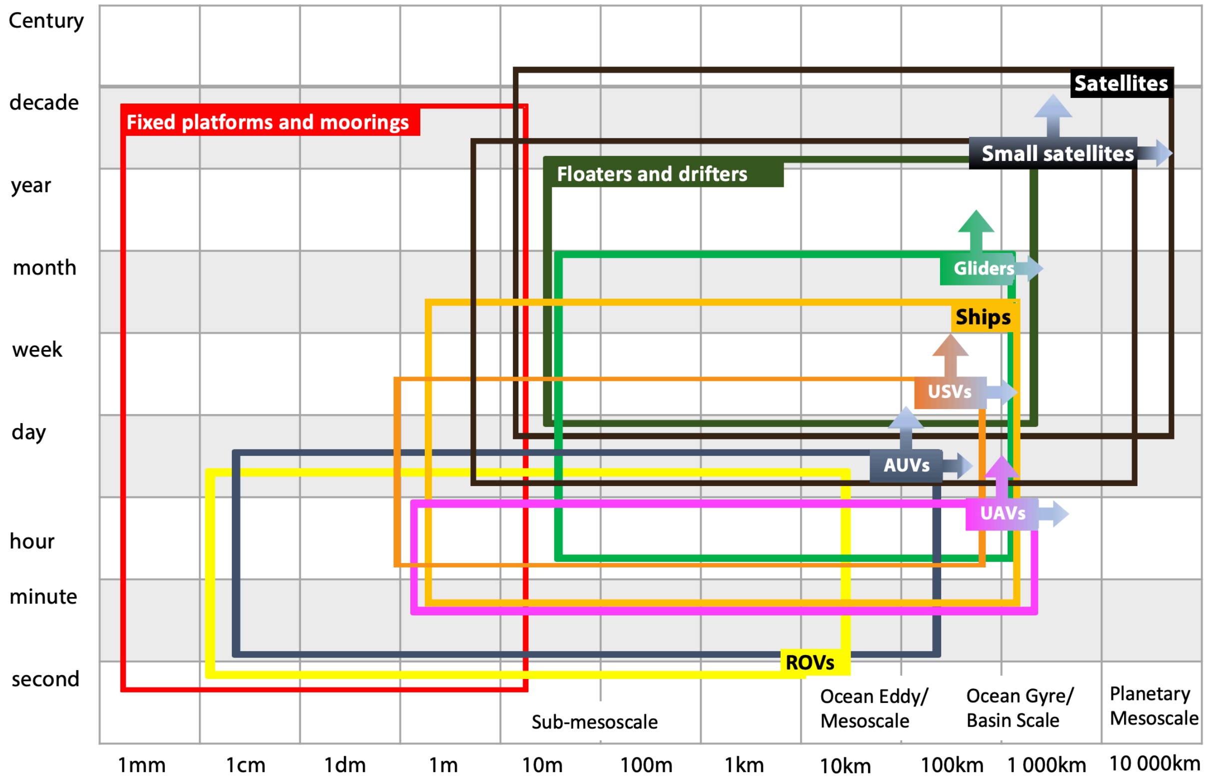

Fig 9.2 Spatial and temporal resolution and coverage of different instrument carrying platforms (based on Nilssen et al 2015 and Haury et al 1978). Note that satellites equipped with optical imaging sensors are dependent on sun light and cannot be used during the Polar Night. Abbreviations: ROVs: Remotely Operated Vehicles; AUVs: Autonomous Underwater Vehicles; USVs: Unmanned Surface Vehicles; UAVs: Unmanned Aerial Vehicles

Table 9.4 Spatial and temporal resolution and coverage for sensor carrying platforms

Platform	**Spatial**		**Temporal**	
	Resolution	**Coverage**	**Resolution**	**Coverage**
Landers and moorings	• High • Accuracy: [mm-cm] • Dependent on sensor accuracy only	• Low • Range: [1-100 m] • Area: [1-100 m^2] • Dependent on sensor	• High • Dependent on sensor performance only	• High: [1-24$^+$months] • Dependent power supply, sensor fouling and data capacity
Remotely Operated Vehicles (ROVs)	• High • Accuracy: [cm-dm] • Dependent on sensor & control performance	• Low • Range: [100m-1$^+$km] • Area: [0,01-0,1$^+$$km^2$] • Dependent on ROV control performance, access to open waters	• High: [0-2$^+$m/s] • Dependent on sensor and ROV control performance	• Low: [8-24$^+$hours] • Dependent on ship operation
Autonomous Underwater Vehicles (AUVs)	• High • Accuracy: [dm-m] • Dependent on sensor and AUV control performance	• High • Range: [1-100$^+$km] • Area: [0,1-10$^+$$km^2$] • Dependent power supply	• Medium: [1-2$^+$m/s] • Dependent on sensor and AUV control performance	• Low: [8-24$^+$hours] • Dependent on AUV power supply and consumption
Gliders	• Medium • Accuracy: [0,1-1km] horizontally, [1-2 m] vertically • Dependent on Glider control performance and current system and ice	• High • Range: [10-1000$^+$ km] • Area: [1-100$^+$$km^2$] • Dependent on Glider power supply	• High: [0,1-1$^+$m/s] • Dependent on sensor and Glider control performance	• High: [1-100$^+$days] • Dependent on Glider power supply and consumption
Unmanned Surface Vessels (USVs)	• High • Accuracy: [0,1-10m] • Dependent on sensor and USV control performance, vessel size, waves, wind, current and ice	• High • Range: [10-1000$^+$ km] • Area: [1-100$^+$$km^2$] • Dependent on USV power supply and consumption, ice	• High: [0,1-4$^+$m/s] • Dependent on sensor and USV control performance	• High: [1-100$^+$days] • Dependent on USV power supply and consumption
Ships	• High • Accuracy: [1-10$^+$m] • Dependent on water depth, sensor and ship control performance, waves, wind, current and ice	• High • Range: [10-1000$^+$ km] • Area: [1-100$^+$$km^2$] • Dependent on ship operation, ice	• High: [0-10$^+$m/s] • Dependent on sensor and ship control performance	• High: [1-30$^+$days] • Dependent on ship and crew
Unmanned Aerial Vehicles (UAVs)	• High • Accuracy: [0,1-10m] • Dependent on sensor and UAV control performance, wind, fog and snow	• High • Range: [10-1000$^+$ km] • Area: [1-100$^+$$km^2$] • Dependent on UAV power supply and consumption, wind, fog, snow	• Low: [10-30$^+$m/s] • Dependent on sensor and UAV control performance	• Low: [8-24$^+$hours] • Dependent on UAV power supply and consumption, wind, snow and fog
Small Satellites	• High • Accuracy: [10-100 m] • Dependent on sensor and control performance, visibility	• High • Range: 100 000$^+$ km • Area: [10-1000$^+$$km^2$] • Dependent on power supply, visibility	• Low: 3-5 cycles/day	• High: [2-5$^+$years] • Dependent on power supply, visibility

9.6 Autonomy Aspects

The field on autonomy is complex and multi-disciplinary. Important aspects to consider are sensing, control theory, optimization, situation awareness, cognitive science as well as risk assessment and management. Autonomous systems are often referred to as intelligent systems due to their ability to manage unexpected events in unstructured and unknown environments. More than mimicking a human operator, this means integrating mathematical models with real-time data from sensors and instruments and allowing algorithms optimizing responses realized by embedded computer systems.

9.6.1 Autonomy Levels

There are different definitions of autonomy levels; defining the steps from manual or remote control, teleoperation, semi-autonomous to fully autonomous vehicles. The levels of autonomy are characterized subject to the level of human-robot interaction (HRI), mission complexity and environmental complexity.

1. *Automatic operation (remote control)* means that even though the system operates automatically. The human operator directs and controls all high-level mission planning functions, often preprogrammed (human-in-the-loop/human operated).
2. *Management by consent (teleoperation)* means that the system automatically makes recommendations for mission actions related to specific functions, and the system prompts the human operator at important points in time for information or decisions. At this level the system may have limited communication bandwidth including time delay, due to i.e. distance. The system can perform many functions independently of human control when delegated to do so (human-delegated).
3. *Semi-autonomous or management by exception* means that the system automatically executes mission-related functions when response times are too short for human intervention. The human may override or change parameters and cancel or redirect actions within defined time lines. The operator´s attention is only brought to exceptions for certain decisions (human-supervisory control).
4. *Highly autonomous*, which means that the system automatically executes mission-related functions in an unstructured environment with ability to plan and re-plan the mission. The human may be informed about the progress. The system is independent and “intelligent” (human-out-of-the loop).

For more details see e.g. NIST (2015), National Research Council (2005), Ludvigsen and Sørensen (2016), and Utne et al. (2017).

9.6.2 Control Architecture

Three control levels are defined:

- *Mission planner level*: Here the mission objective is defined, and the mission is planned. Subject to contingency handling, any input from payload sensor data analysis and any other input from the autonomy layer, the mission may be re-planned. This means that the payload data should be analysed in near real-time aboard the sensor carrying platform..
- *Guidance and optimization level* handles waypoints and references commands to the controller.
- *Control execution level*: at this level the plant control and actuator control take place.

If the data collected are not in accordance with the data request, a new adjusted data request can be made automatically and be a feedback for the controller to adjust the sampling area, sampling frequencies, range until the request is satisfied. Such a strategy will be pursued by the following to enable increased levels of autonomy. In Section 9.7.3 an example of adaptive sampling/measurement using AUV is shown.

Mathematical modelling may be achieved through a systems perspective integrating models and knowledge from the different domains such as oceanographic, ecosystem and vessel models. Models at different fidelity will be used for mission design, simulation, real-time monitoring, decision and control. In particular, fast low-fidelity models may be used in conjunction to the real-time control systems while high fidelity models may be used in offline studies. The states and parameters of the models may be updated using the measurements following established methods from state estimation and system identification. Hence, states and parameters may be estimated using real-time data in order to adaptively update models in order to detect normal and abnormal changes in the systems or their environment.

Data gathering including sensor fusion for perception of the environment and any OOI will include integration of imaging sensors such as radar, optics, and acoustics with inertial and navigation sensors for accurate detection and tracking of objects and environmental parameters. For many autonomous sensor carrying platforms energy is a limiting factor, where power demands for the sensors are in the same order as needed power for propulsion. Hence, proper strategy for enabling and disabling the payload and navigation sensors will be important both for receiving good data, precise and robust control as well as wanted endurance of the operation.

By combining various control and risk assessment methods such as nonlinear optimization, hybrid control, Bayesian networks and probabilistic reasoning, and machine learning the control execution level will be able to accommodate autonomy requirements. Risk and reward are closely related. For example, in order to record high quality data, the robot may operate closer to the seabed or OOI still avoiding collision within reasonable risk margins. In case of networked systems with simultaneous operations, robotics, and mobile sensor networks another level of agent control needs to be considered. Integrated guidance and path-planning with high-level mission planning may be achieved using numerical optimization where data, decisions, rules and models are represented as constraints, as well as discrete search algorithms and computational intelligence.

9.6.3 Risk Aspects

Risk management is crucial for successful operation of sensor carrying platforms. Increasing the level of autonomy calls for a more systematic approach where more of the risk handling is transferred from the operator to the sensor carrying platform itself. We may categorize risk for autonomous systems (NIST 2015, National Research Council 2005, Utne et al. 2017) according to three dimensions (Figure 9.3):

1. Mission complexity
    - Complexity of mission tasks and subtasks and corresponding decision mechanisms and rules.
    - Organization and collaboration between various actors involved in the operation.
    - Needed performance including quality of payload sensor data, control accuracy of sensor carrying platform.
    - Knowledge about operational area and environmental and operational conditions.

- Situation awareness capabilities breaking down into three separate levels; Level 1: Perception of the elements in the environment; Level 2: Comprehension of the current situation; and Level 3: Projection of the future situation. It is obvious that situational awareness is crucial for the sensor carrying platform to achieve needed control performance for satisfactory data gathering as well as acceptable risk management, e.g. collision avoidance, loss of sensor carrying platform and failure handling.

2. Environmental complexity
    - Variability in the environment due to e.g. shifting weather conditions (see the trawler "Northguider" accident in Chapter 10).
    - Terrain variation in the areas of interest – flat, steep, etc.
    - Risk for collisions with possible static and moving objects. Object frequency, density, and intent are important to consider.
    - Particular climate risk due to e.g low temperature, darkness and icing.
    - Mobility constraints of the sensor carrying platform.
    - Communication dependencies between platforms and with operator. Underwater operations with acoustical communication are normally far more limited with respect to bandwidth and range compared to radio communications in air.
3. Human independence / Level of autonomy
    - Frequency and duration of robot-initiated interactions with the operator.
    - Operator workload and skill levels.

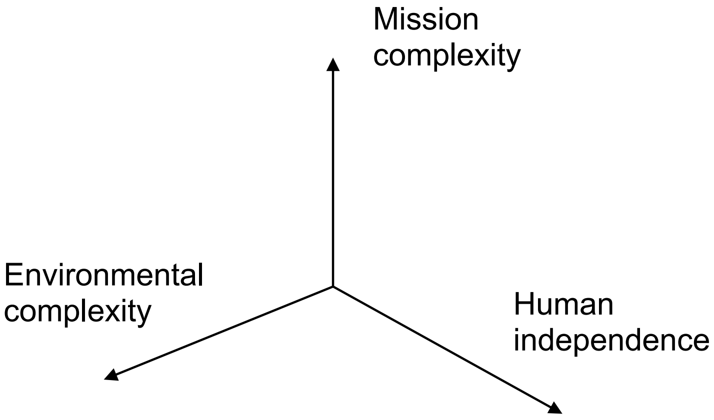

Fig 9.3 Risk models for autonomous systems

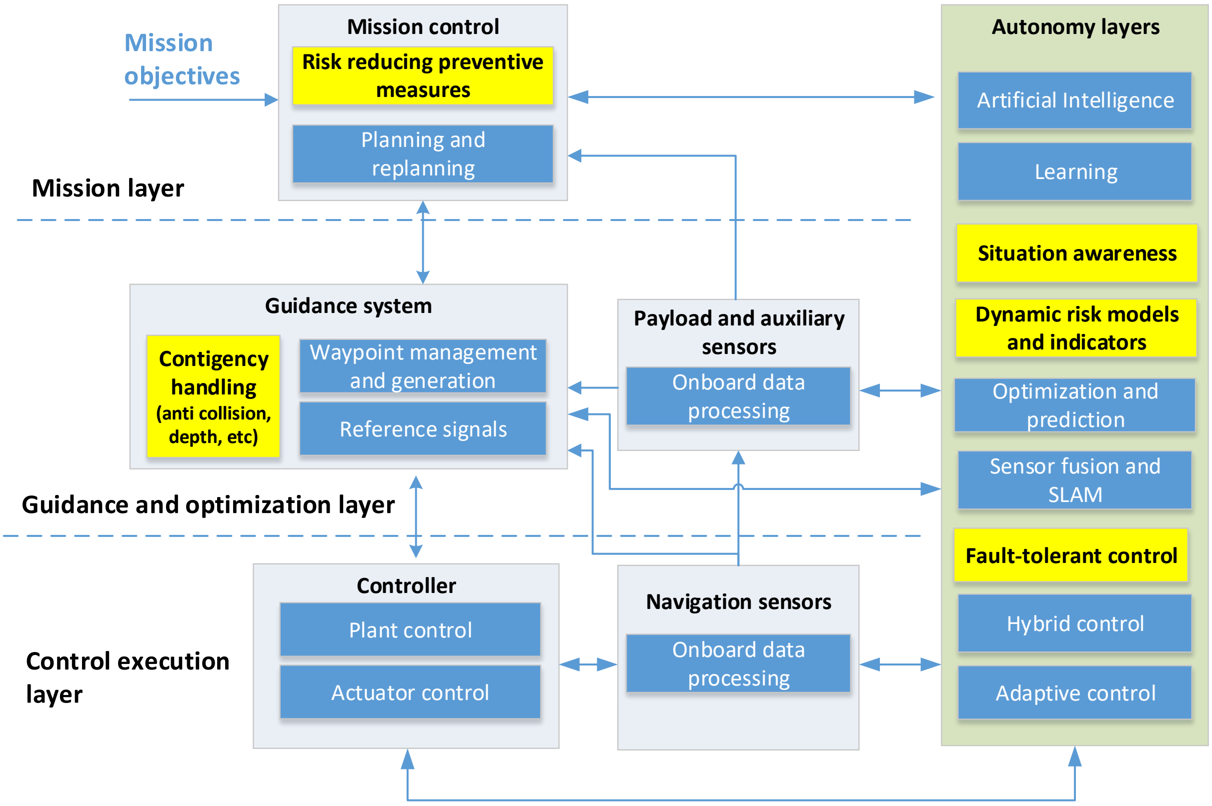

Fig 9.4 Autonomous control architecture exemplified for unmanned underwater vehicles.

9.7 Case studies

9.7.1 Under-ice and Polar Night AUV Operations

The sea-ice extent in the Arctic has been severely reduced in the last decades, with a record low in September 2012, with all subsequent years among the top ten lowest sea-ice extents (NSIDC 2018) (see Chapter 2). The mean sea-ice thickness has also been reduced significantly, from 3.64 meters in 1980 to 1.89 meters in 2008 (Farmer and Cook, 2013). The changing Arctic environment not only influences how the Arctic is used by humans, but it also impacts the Arctic ecosystem and marine life. For example, the under-ice algae and phytoplankton blooms which are important for the Arctic food chain, are hard to detect using remote sensing, and therefore these processes are poorly understood (Johnsen et al., 2018) and suffer from under-sampling.

AUVs are an especially interesting sensor platform for sea-ice data collection, due to its autonomous and untethered nature. In addition to collecting data about the biological processes described above, an AUV can be customized with a diverse sensor suite. For example, an AUV can be used for ice-monitoring, and provide detailed under-ice topography data using MBE mounted up-side down, which is important input to decision making in Arctic marine operations (Norgren 2018). Upwards-looking MBE data can also be used as input to the navigation system when performing ice-relative navigation under drifting sea-ice or icebergs using a technique called Simultaneous Localization and Mapping (SLAM) (Norgren and Skjetne 2018).

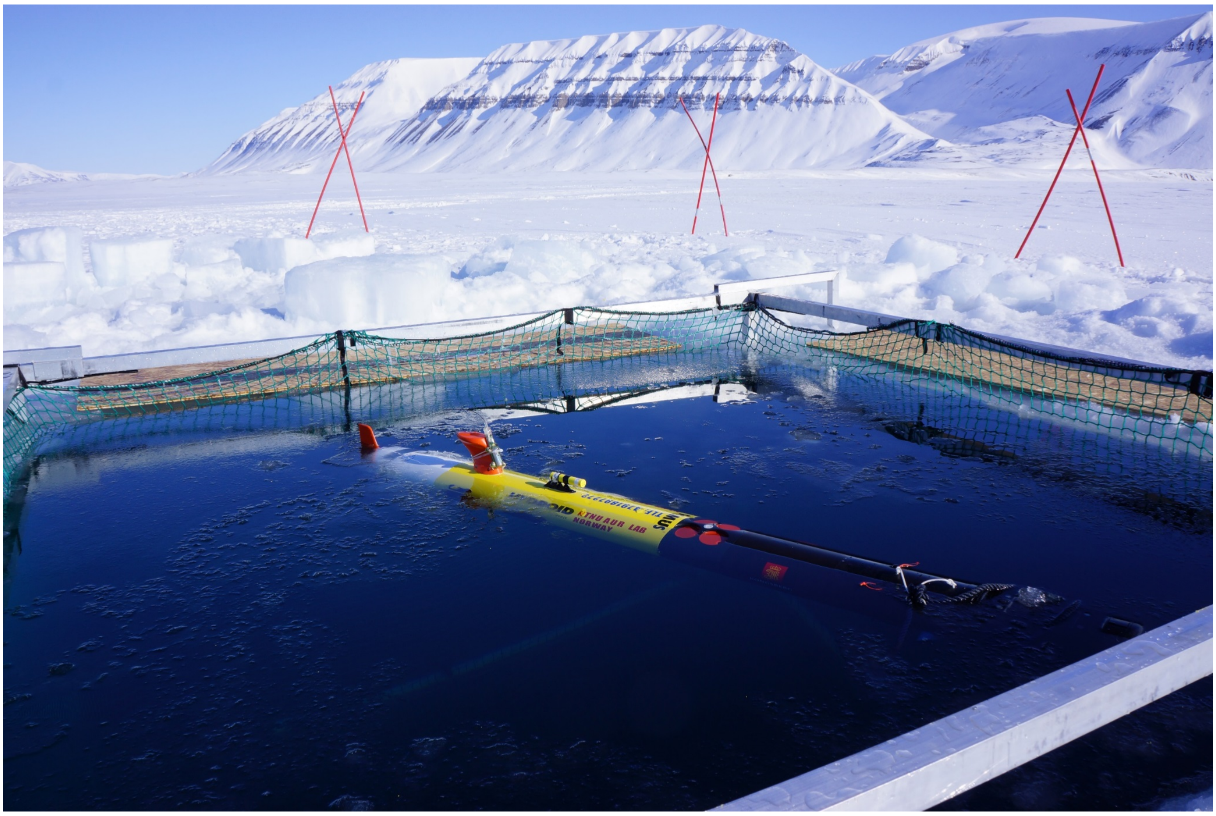

Fig 9.5 AUV (Remus 100) ready for an under-ice mission

Deploying an AUV under-ice greatly increases the risk of losing the vehicle in the event of failure. Not only does the vehicle itself require specialized support systems and sensors, the operators require special experience and knowledge. Working towards operations under drifting and rotating sea-ice, an important first step is operations under land-fast sea-ice in real Arctic conditions. In the spring of 2017, the REMUS 100 (Figures 9.5-6) was deployed under the ice in Van Mijenfjorden, outside the mining village Svea in Svalbard. The scientific objectives of the campaign were to collect oceanographic data for a related field campaign, as well as to assess the ice-monitoring capabilities of small-size AUVs.

The REMUS 100, originally developed by Woods Hole Oceanographic Institute (WHOI), is a low-logistics, small size AUV. The vehicle can easily be deployed and operated by two persons. The vehicle is rated for 100 meters depth and has a typical endurance of about 6 hours at 1.5 m/s velocity. The REMUS 100 was chosen for this operation because of its robustness and prior track list in under-ice operations, including operations under coastal sea-ice offshore Barrow Alaska (Kukulya et al. 2010; Plueddemann et al. 2012) and operations under ice for mapping phytoplankton blooms (Johnsen et al. 2018).

The payload sensor suite consists of up- and down-looking ADCP/DVL, SSS, fluorometer, oxygen sensor, and Neil Brown CTD (for full specifications, see Norgren 2018). For the purpose of ice-monitoring, the AUV was fitted with an up-looking Imagenex DeltaT MBE. For navigation, the AUV used Honeywell HG1700 IMU with ring-laser gyros for accurate inertial navigation using an aided inertial navigation system (AINS). External positioning was provided through GPS before launch, and through LBL during the missions. To obtain as accurate positioning as possible, the LBL transponders were placed out using an accurate GPS base station providing a fix with accuracy of ~0.5 meters. For safety purposes, the AUV was also equipped with an acoustic tracker with standalone battery, so the AUV could be located even in the event of a critical power failure.

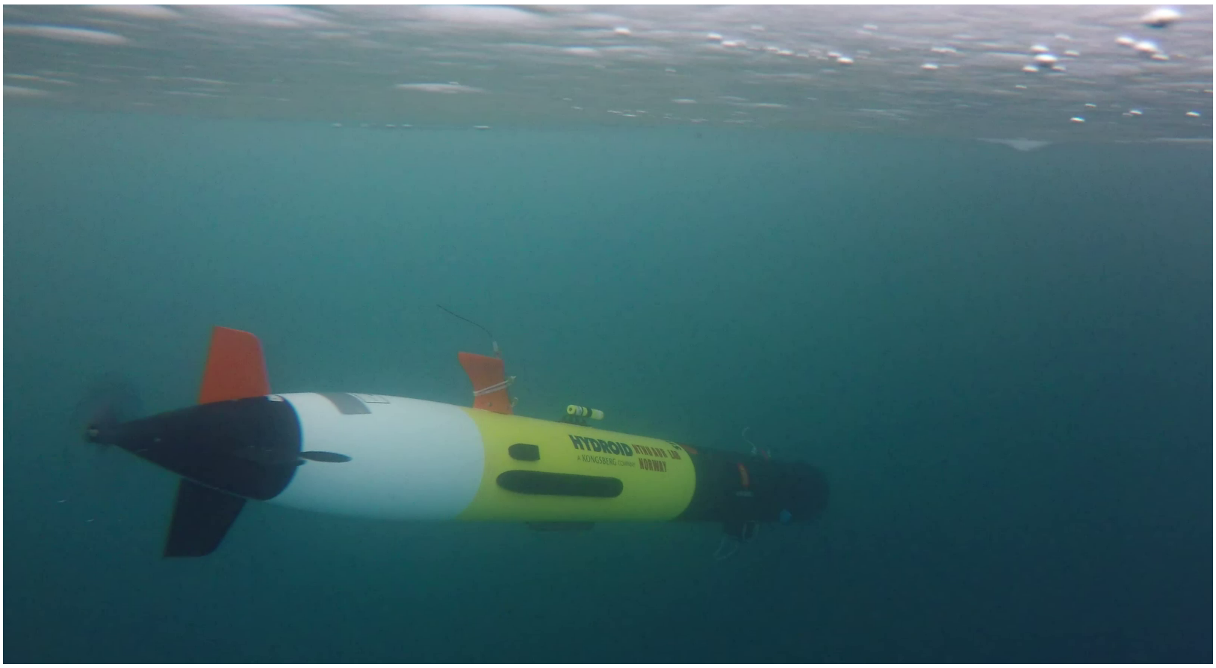

Fig 9.6 AUV launced under sea-ice. The under-ice environment is normally dark as for the Polar Night operations in open waters

Looking towards long-range missions under drifting sea-ice, the main lesson learned was the need for a robust and fail-safe navigation system, specialized towards Arctic under-ice missions. Robust navigation is especially important in these operations, due to the risk of loss of the vehicle during surface and recovery phases. Figure 9.7 shows the collected sidescan imagery from the recovery phase of one of the under-ice missions, and the recovery frame is clearly visible 17.5 meters from the centreline. The intention was for the AUV to surface in the recovery frame, but due to a failure in the DVL, the quality of the navigation system was reduced significantly. Furthermore, due to multipath and noise from the sea-ice, the LBL system was unable to provide accurate navigation fixed during the recovery phase due to the AUV's proximity to the ice.

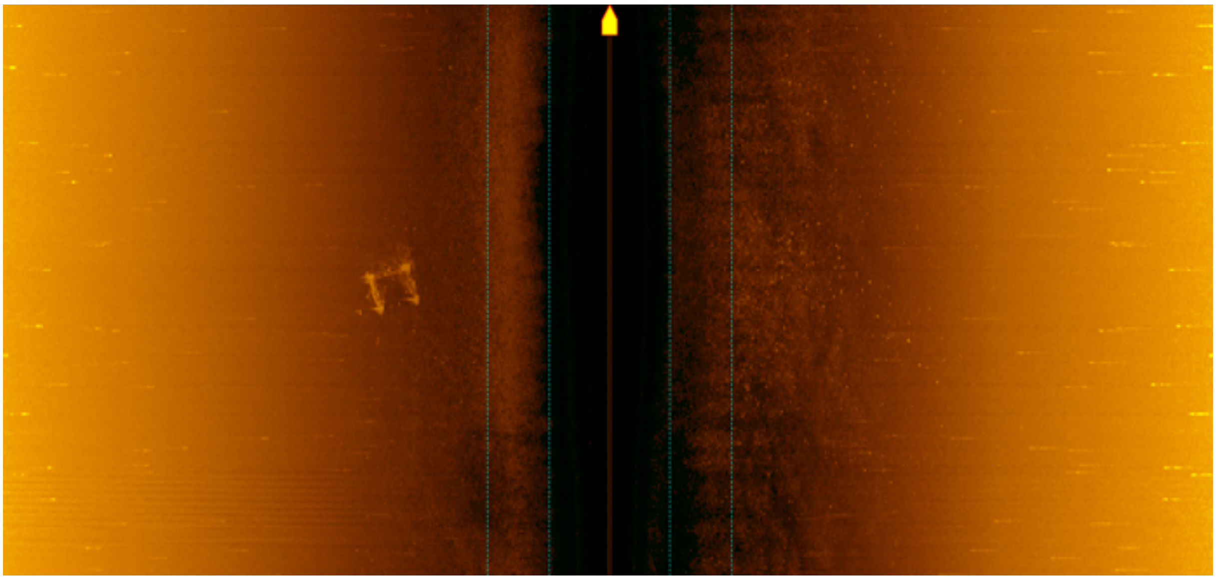

Fig 9.7 Under-ice sidescan imagery using Remus 100 AUV. The recovery-frame is clearly identifiable in the sidescan data 17.5 meters from the centerline (which indicates the AUV's position).

9.7.2 Marine Archeology

Marine research missions in the Arctic are often in initiated by and strongly coupled with knowledge gaps that are critical to fill for knowledge-based ocean management. Often it may be an advantage to operate during the fall and winter seasons (including the Polar Night), as the visibilty in the water normally is better due to less fresh water run off bringing sediments into the water. Ecosystem based management models are necessary for understanding and predictions of complex and interconnected processes that span different disciplines as well as great temporal and spatial scales. An integral part of marine ecosystems are the so-called cultural services, including underwater cultural heritage. One of the greatest impacts on marine Arctic ecosystems until the climate changes we have seen in recent decades, is the commercial exploitation of marine mammal resources that started with European whaling in the early 17th century (Hacquebord 2001). During peak intensity more than 300 ships hunted whales, walrus and seals in the areas surrounding Svalbard and Greenland every year (Hacquebord 2010) until the resources neared depletion at the end of the 19th century, and the enterprises moved to Antarctic waters for even larger scale industrial whaling activities. The Arctic whaling industry represented huge profits for European investors, however, entailed great operational risks. More than 1000 historical wrecks from many western European countries are estimated to lie on the seabed between Greenland and the Svalbard archipelago, the majority of which are related to whaling expeditions that abruptly ended in unkind encounters with crushing ice and harsh weather conditions, often with tragic outcomes (Garcia et al. 2006). The underwater cultural heritage that can be found on the Arctic seabed represents not only direct evidence and knowledge of the profound anthropogenic impact on marine ecosystems but is also a unique and important source of insight into European history. Every ship with its crew must be seen as isolated miniature societies reflecting economic, political and cultural conditions in contemporary Europe, and as such have great value as complementing sources of historical and archaeological knowledge of their period.

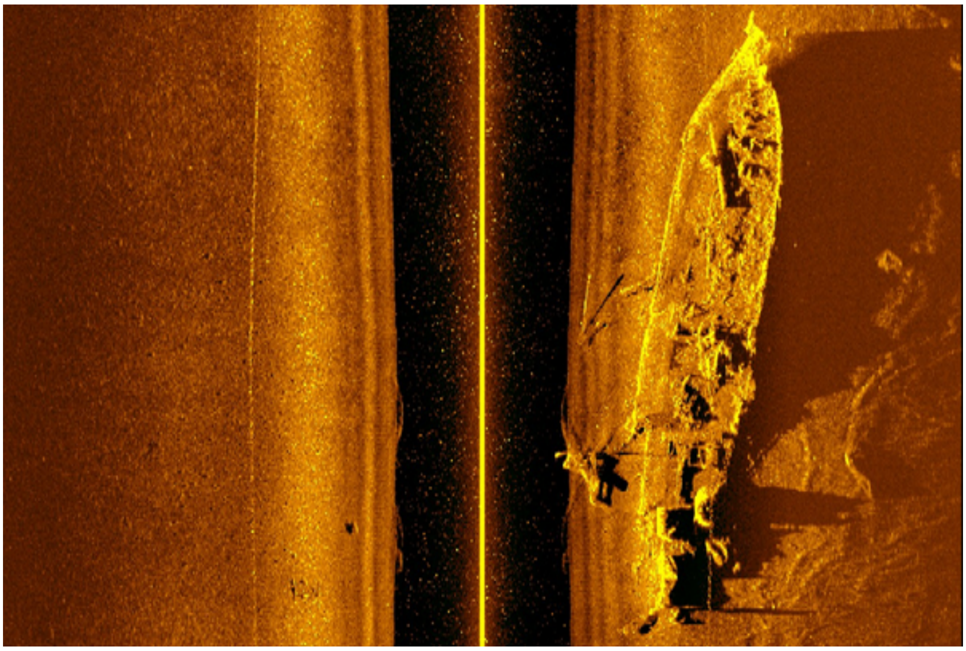

Fig 9.8 Sidescan Sonar image of the floarting whaling station *Figaro* using a Remus 100 AUV

In collaboration with UiT The Arctic University of Norway, UNIS and other partners, NTNU AMOS and AUR-Lab have integrated marine archaeological activities into the scientific scopes of several research campaigns and other field activities. In 2015 and 2016, the wreck of

Figaro was investigated with underwater robotics (Fig. 9.8). *Figaro* was a wooden hulled bark built in 1879 that sunk in 1908 while being used as a floating whaling station. Preliminary mapping of the wreck site was conducted with a portable AUV (Hydroid REMUS 100 with SSS) and a mini-ROV (Seabotix LBV 200 with HD Video and scanning sonar) during a UNIS/NTNU student course in 2015, and provided baseline knowledge of the site for detailed investigations and full mapping with a work class ROV (Sperre Subfighter 7500) with several sensors (HD Video, Stereo camera and UHI) during a visit to the site with RV Helmer Hansen on the scientific Polar Night Cruise in January 2016. The results from both investigations are currently being used in a research project on the *Figaro,* and its role as an example of transitional technology between traditional whaling methods used in the Arctic, and the highly specialized factory ships that characterize the Antarctic whaling in the first half of the 20th century. Traditional diver based marine archaeological methods are seldom serviceable at these latitudes, for both logistical and HSE reasons. Access to, and hence the ability to investigate wrecks in such environments depends on adaptation and design of underwater robotics and sensors to both archaeological purposes and Arctic conditions. This is a novel research field that has seen focused attention at NTNU AMOS over the last five years. To our knowledge *Figaro* is currently the world's northernmost, and in Svalbard so far, the only underwater cultural heritage site to be scientifically investigated by archaeologists.

Fig 9.9 Wood devouring organisms found on a log of Sibarian larch during the Polar Night (January 2016) in Rijpfjorden (Fig. 1.2) at 250m depth. Photo Geir Johnsen

The 2016 Polar Night Cruise represents a major step forward in demonstrating the operational capabilities of underwater robotics in demanding environmental conditions. An AUV SSS seabed mapping mission in the Dane's Gat in Smeerenburg fjord was successfully executed with launch and retrieval from a small open boat in darkness and sub-zero temperatures. Likewise, the full ROV-based mapping of the *Figaro* wreck site was undertaken in January, with the sun mostly lower than 12 degrees below the horizon. In addition, the limited runoff from glaciers during mid-winter entailed a significant improvement in visibility, and in turn optical imaging capability, compared to the preliminary ROV inspection in early September 2015 (see Chapter 3).

During the same 2016 Polar Night Cruise, biologists and archaeologists made an alarming discovery of wood devouring organisms present on the seabed in Rijpfjorden, an Arctic fjord at 80 °N on Nordaustlandet (Kintisch 2016, Berge et al, in prep). Shipworms (Fig. 9.9) and other similar organisms are by far the greatest threat to *in situ* preservation of historical shipwrecks, and the unexpected finding could indicate that the general assumption that the freezing cold Arctic waters are benign and stable environments for underwater cultural heritage is wrong or possibly being invalidated by changing properties in the marine ecosystem (Kortsch et al. 2012). The finding therefore accentuates the importance of and the need for more widely scoped trans- and interdisciplinary research efforts in these areas. Underwater robotics and advanced sensors are enabling technologies that can be adapted and tailored to such efforts, providing knowledge for a better holistic management of marine ecosystems (Nilssen et al. 2015).

9.7.3 Adaptive Mapping of Plankton Using AUV

As seen in Sections 9.5-6, the design of proper mapping or measuring/sampling strategies to be implemented in the mission layer (Fig. 9.4) may be complex in order to achieve a proper reconstruction in time and space of the dynamic processes taking place in the oceans. Generally speaking, the dynamic processes may be regarded as under sampled even when using highly dynamic capable sensor carrying platforms such as AUVs. Hence, the sampling strategies need to be optimized in order to make sure that the samples (measurements) are taken where the information value is the highest. See Figure 9.10 as an illustration of mapping plankton biomass using AUVs with an adaptive or non-adaptive adaptive strategy. The latter will not automatically adjust the trajectory of the AUV to the area of interest. In order to conduct an adaptive mapping strategy, the AUV must be able to analyse the data on-line and accordingly update the trajectory of the AUV to the high concentration areas of biomass. As seen in Figure 9.4 the AUV will be subject to a re-planning action. To address the need for improved observations in oceanography, adaptive sampling and numerical ocean modelling have been coupled (Fossum et al. 2018). By combining Gaussian Process (GP) modeling with onboard robotic autonomy, volumetric measurements of phytoplankton can be made at fine scales, informing studies of patchiness in phytoplankton biomass, biogeochemical processes, ands primary productivity.

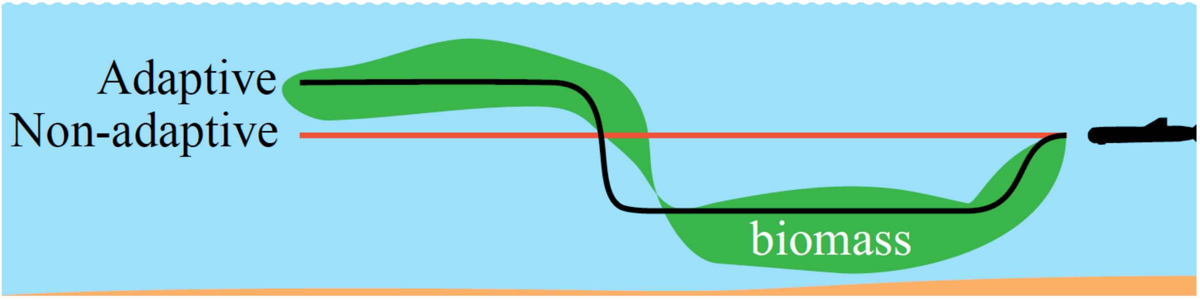

Fig 9.10 Adaptive AUV sampling strategies can react to immediate changes in the environment and adjust data collection, accordingly. This will increase the resolution and coverage of important features in the water column. Graphic by Trygve Olav Fossum

To autonomously map spatial distribution of phytoplankton biomass in 3D using AUVs, GP models and robotic sampling were employed to provide efficient adaptive sampling strategies. The method estimates and track layers of high Chl a concentration, focusing sampling efforts and increasing accuracy along essential biological features such as the sub-surface Chl a maxima (SCM). Using spatial modeling and interpolation it becomes possible to reconstruct the distribution in 3D. Comparison of in-field data shows correspondence between AUV data and behavior, providing a broad and extensive perspective of the pelagic activity.

The method for adaptive mapping in Fossum et al. (2018; 2019) combines marine data from: autonomous underwater vehicles (AUVs), model forecasts, remote sensing satellite, buoy, and ship-based measurements, as a means to cross-validate and improve ocean model accuracy. Numerical ocean models (e.g. SINMOD, SINTEF Ocean) are connected to *in situ* models to provide basis for a sampling strategy, using ocean temperature. Using hindcast data from the SINMOD ocean model, a stochastic proxy model, based on GP, is used for assimilation of in-situ measurements. The sampling algorithm, being both data- and model-driven provides input for an online sampling algorithm and runs onboard the AUV enabling the vehicle to optimize its path and strategy in real time. Figure 9.11 illustrates the concept. The numerical ocean model system SINMOD, buoy data (temperature, salinity and biological measurements), research vessel (biological and physical measurements), remote sensing (temperature and Chl a), autonomous surface vehicle (temperature, salinity and weather data), and an AUV (biological and physical measurements).

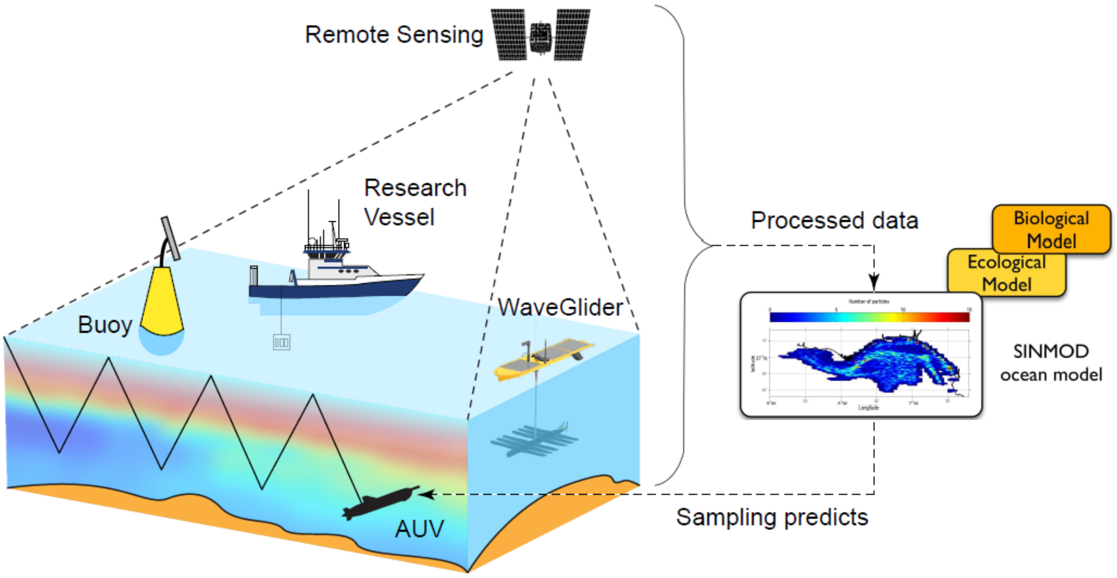

Fig 9.11 Adaptive sampling strategies, Fossum et al. 2018 and 2019

In January 2016 UiT, UNIS and NTNU deployed an autonomous surface vehicle (ASV) to measure the light response of zooplankton at 78° N in Kongsfjorden, Svalbard (Ludvigsen et al. 2018). To be able to collect data without anthropogenic light and a larger part of the water column, an autonomous surface vessel was introduced. The Jetyak (Kimball et al. 2014) was first deployed by the WHOI and was based on a commercially available polyethylene single person kayak and is fitted with a petrol engine and water jet propulsion. A control system is fitted to the vehicle to enable the vehicle to operate autonomously or remotely controlled. Low-bandwidth communication is provided by a radio frequency modem at ranges up to 20 km. An AZFP (Acoustic Fish Zooplankton Profile, ASL) multi frequency echosounder mounted downward facing provided acoustic data at 125, 200, 455 and 769 kHz. Only the three lower frequencies had enough range to be used in this study. Due to the very low draft, the Jetyak provided shallower echosounder readings compared to the research vessel. A fiber optic spectrometer (Ocean Optics QE Pro) was also mounted on the vehicle to provide diffuse sky spectral irradiance. The light levels in the water column were modelled for this study.

During the experiment, the ASV Jetyak was programmed to patrol a predefined transect, and the vehicle was running a total of 54.7 km of survey lines. The system was deployed for three days aiming to collect data during the solar noon of Polar Night. The solar inclination was in the range 8° - 9° below the horizon at noon, and the acoustic data showed a 6 – 8 meters vertical movement of zooplankton detected by the AZFP. The sensitivity to light pollution from the research vessel and from headlights worn by researchers in small work boats indicated high sensitivity to artificial light seen clearly in acoustics readings. Light avoidance was shown down to 80 meters depth. As the zooplankton community appeared very sensitive to varying levels of illumination, great care was taken not to introduce artificial light disturbing the natural activity of the zooplankton under ambient light conditions.

ASVs do not require facilities for crew and can hence be made smaller than conventional research vessels lowering their human footprint. Also, avoiding artificial light, the platform may be used to examine processes in natural ambient light conditions (see Chapter 3). But the Arctic does also present special challenges for unmanned vehicles; logistics for operational support is far sparser and communication infrastructure is less developed. The ASV benefits from the facilities of research vessels and operations as represents a useful complement and for the described research campaign the introduction of ASV in the operation revealed knowledge hardly obtainable from manned platforms. The architecture of ASV systems further encourage the usage of autonomous and data drives sampling behaviors (Fossum et al. 2019).

9.7.4 Winter Observations in the Barents Sea Using Gliders

An example of the consideration of spatial and temporal scales in the selection of an observational technology for a scientific application can be seen when comparing the methods for making standard ocean sections from a ship or using ocean gliders. Historically, ships have been the workhorse of oceanography and still play a primary role in the collection of ocean data. However, the use of ships has limitations, particularly related to operations in high sea states, endurance to enable measurement on seasonal scales, spatial resolution to resolve small-scale features of the ocean (<1 km) and cost per day. Ocean gliders appear to occupy the same operational space as ships (Fig. 9.2) but are increasingly seen as capable of addressing many of the limitations of ships (Rudnick, 2016; Testor et al. 201) giving greater horizontal resolution and longer endurance with the capacity to operate in winter. In addition, gliders are able to operate close to and underneath sea ice (Lee et al. 2017) at low risk to ships and/or personnel. Therefore, these platforms are well-suited to oceanographic observations during the Polar Night.

A program of field campaigns in the Barents Sea during 2018 (Fig. 9.12) aimed to investigate the changing oceanic properties in this critical Arctic inflow region (Chapter 2) from the Polar Night through to summer in relation to stratification, fronts and phytoplankton blooms. Standard ocean sampling was conducted from a research vessel during three cruises in January, April and June but observations between these cruises were made with a Slocum Glider (Webb et al, 2001). The sensor package on the gliders comprised CT and concentration measurements of dissolved oxygen, Chl a, cDOM and total suspended matter (Chapter 3). The glider was able to dive to 200 m and the mission plan was to observe along north-south transects in the region of open water in the southern Barents Sea.

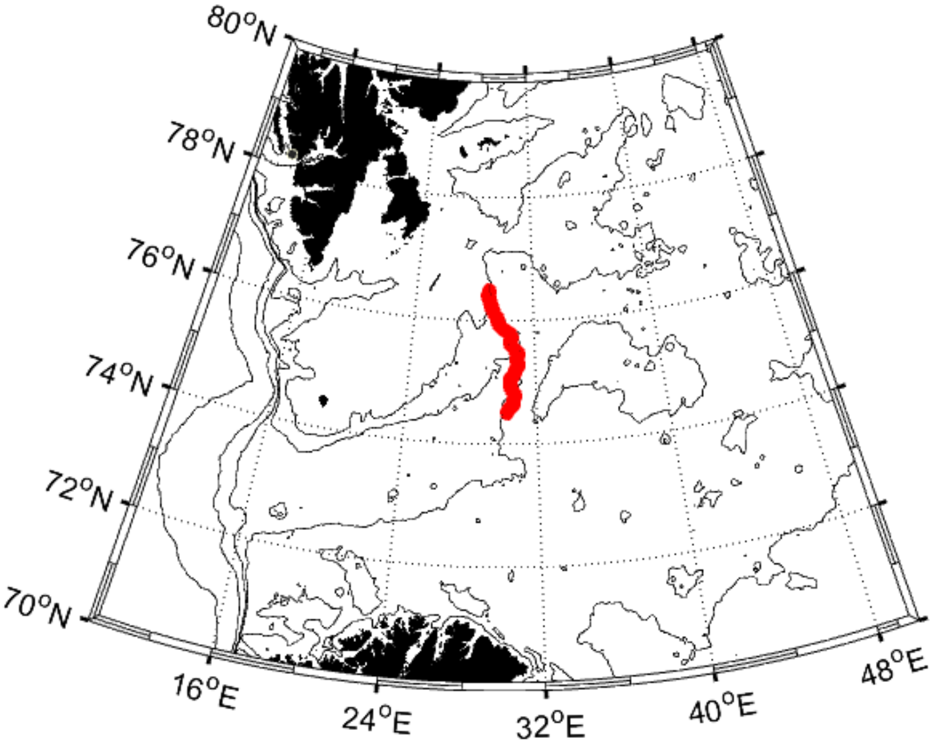

Fig 9.12 Map of the Slocum glider transect in the Barents Sea between 11th - 26th January 2018

Figure 9.13 shows one north-south section collected from 11-26th January 2018. Glider profiles are typically spaced at 1 km intervals and the entire section comprises about 470 dives. From the data we can see remnant stratification by salinity in the southern part of the section with a more uniformly mixed water column to the north. We also see a south to north gradient in temperature as the glider approaches an oceanographic structure called the Polar Front which separates the warmer, more Atlantic waters to the south from the colder, fresher Arctic waters to the north. Data from the fluorometer shows that the phytoplankton community is below detectable levels along the entire transect. The detail that is revealed in horizontal and vertical density gradients is far greater than can be obtained with a ship and allows the relationship between ocean structure and biological response to be investigated thoroughly along repeatable sections over seasonal timescales.

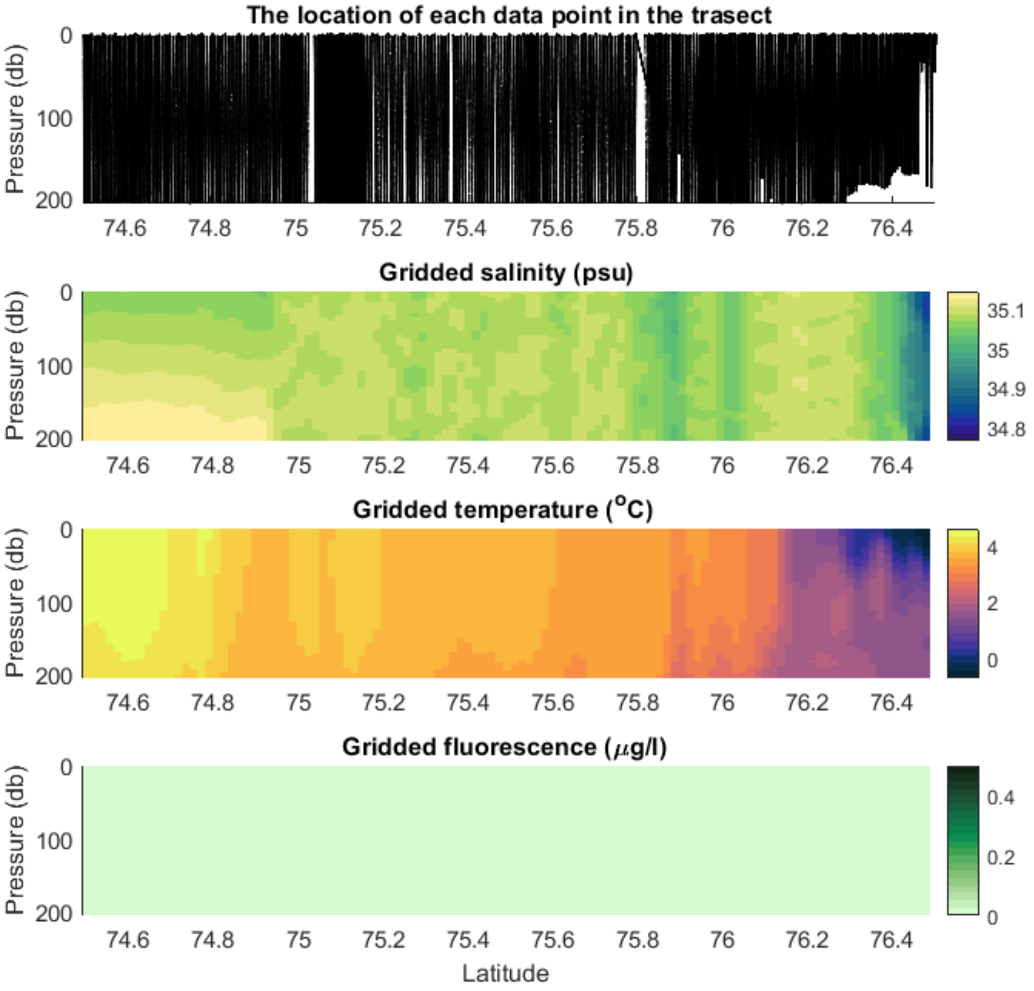

Fig 9.13 Vertical sections of salinity, temperature and Chl-a concentration based on fluorescence measurements obtained from a glider in the Barents Sea between 11-26th Juanuary 2018. Depth represented as preassure.

9.8 Safe and Efficient Operations

The Arctic environment is characterized by lack of infrastructure and harsh environment. Any incident in the Arctic will potentially result in a higher consequence than comparable incidents in more developed areas because all responses assets have longer time constants and higher costs. For medical incidents, support will be far away requiring long distant travels, and for technical incidents, challenging logistics makes it hard to provide instruments, tools or spares for situations that are not planned or foreseen (see Chapter 10). The harsh environment provided tough requirements for operational support.

A well-defined mission objective is important defining a data acquisition operation. The mission objective should contain a research question to be addressed. Performing natural science in Arctic area – the investigation site if often given by the process and objective of the research. Together these form the base for determining parameters and variables of interest in the operation and associated entities to the parameters and variables like required accuracy, spatial and temporal resolution, spatial and temporal coverage, timing requirements and required position accuracy (Nilssen et al 2015). From these, one can determine and derive an appropriate platform and instrument suite.

In the further planning one will consider the research location in terms of bathymetry, current and weather conditions and marine traffic. Prior information of the area and the research subject is taken into account and implemented into the plan. An operation procedure is laid out including sequential steps like *mobilization, testing, transiting, launch, map, recover and demobilization.* The level of fidelity of the plan will be adjusted according to the operation complexity and risk. High risk and complex operations require a more detailed operation procedure. Before the operation can commence there should be a clear plan for data processing and analysis as this often forms important premises for the data acquisition.

Having established the operational procedure, the five step risk management methods can be applied to reduce risk (DNVGL 2001 RP-H101 Risk management in marine and subsea). Risk is defined and the product of probability of occurrence and consequence. This includes HSE, project and operational risks. The first step is to establish a process plan the contains an HSE philosophy. An example of such a strategy can be: "Plan for safe and efficient operations, maintain focus on feasibility and optimize planning of the marine operation by reducing delay, improve ship time utilization and minimize cost". A goal can be to perform marine operations with no incidents, accidents or losses. This should be reached through systematic risk identification and reduction, planning according to recognized standards, good coordination of involved operations and presence of qualified personnel.

To be able to manage the risk in the operation, an acceptance criterion should be established in step two. This includes defining categories of consequences and compiling this into risk categories. Common criteria would be to comply with the ALARP principle (As Low As Reasonable Practicable). In step three the risk of the operation is categorized and assessed often by using a method called HAZID (HAZard IDentification). Based on a principle description of the planned operation, undesirable consequences and hazards in the operation are identified and listed in a risk register.

Table 9.5 Conceptual set-up for Safe Job Analysis

No	Basic steps	Hazard	Potential consequence	Measures	Responsible
1.	Plan the operation	Overestimate energy capacity and navigation accuracy	Loss of vehicle, time and data	Perform checks and mission verification	Vehicle operators
2.	Mobilize the vessel	Falling equipment	Personal injury, loss of equipment	Clear area while lifting	Crane operator
3.	Deploy the vehicle	Collision vehicle and vessel	Loss of equipment	Clear communication and plan	Vessel master and vehicle operator
4.	Carry out AUV mission	Lose vehicle	Loss of vehicle	Monitor vehicle – keep low response time	Vehicle operator
5.	Recover the vehicle	Collision vehicle and vessel	Loss of equipment	Clear communication and plan	Vessel master and vehicle operator
6.	Demobilize the vessel	Falling equipment	Personal injury, loss of equipment	Clear area while lifting	Crane operator

Step four concerns risk identification and is based on a detailed procedure of the planned activities and common tools applied are SJA (Safe Job Analysis) and HAZOP (HAZard and Operability Analysis). The SJA is used to analyses activities systematically and to establish risk management and preparedness, see Table 9.5. The final step to risk management is the risk reducing activities including a feasibility assessment.

Acknowledgement

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Chapter 10

Operative habitat mapping and monitoring in the Polar Night

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Abstract

The Polar Night has long been regarded as a period of no biological activity. As a logical consequence, environmental management has mainly neglected this period. We will use the *Northguider* accident in December 2018 as a case study for the need to prioritize operative habitat mapping and monitoring to provide a sufficiently knowledge-based environmental operative management. After the ship ran ashore in a remote location in the northern part of Svalbard, the entire crew was safely rescued and airlifted back to Longyearbyen within hours. The ship, however, remained, potentially posing a threat to wildlife - not only wildlife that is expected to return in spring, but also for the many organisms that we now know are present and active during the Polar Night. There is, however, still a strong need to provide necessary understanding of the dynamic marine biodiversity at the sea-surface, water column and seafloor during the Polar Night, focusing on the threats for ecosystem and habitats.

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10.1 Introduction

Warmer seas have already caused fishery activities to move some 300 km further north in the European part of the Arctic. In addition, new ship-based cargo transport routes, oil-gas and mineral exploration activities and cruise traffic is proceeding northwards. The cruise traffic activity in the Svalbard region has increased by a factor of four from 2010-2018. In the case of a large cruise vessel accident in the Arctic, Norwegian rescue and environmental management authorities are arguably ill-prepared and under-resourced to handle such situations. In this chapter we will go through information of importance for operational marine nature management during the Polar Night. The chapter consist of three parts: First we will describe a vessel accident, the *Northguider*, from December 2018 on Svalbard (10.2) as a case study for operational management comprising current rescue operations and knowledge-based management. Second (10.3) we will, based on the *Northguider* accident, go through what we know about marine life in the sea-surface, water column and seafloor during the Polar Night and focus on the major threats to ecosystems and habitats posed by spotential imilar vessel accidents. Third (10.4-5) we will focus on future perspectives and knowledge gaps with respect to optimizing operative marine environmental management, focusing on mapping and monitoring, during the Polar Night and to provide appropriate decisions during critical periods.

10.2 *Northguider* – fishing vessel grounded during the Polar Night December 2018

Hinlopenstredet is a well-known fishing and a breeding and feeding area for a range of Arctic marine animals such as seals, walrus and several bird species. These species are mainly seasonal visitors present mainly in spring and summer. What we present in this book, is that during the Polar Night there is high biological activity at the sea surface (birds), water column (seeding stock of phytoplankton (Chapter 4), zooplankton and larvae (Chapter 5), fish (Chapter 7) and seafloor (high activity and reproduction of benthic organisms (including macroalgae/kelp forests) (Chapters 4 and 6). The Norwegian trawler *Northguider* (47 m long) ran aground at Nordaustlandet on the 28th of December 2018 (Fig 10.1). After a dramatic operation using two rescue helicopters from the Governor on Svalbard, the 14 fishermen were ultimately brought to safety. The rescue was particularly challenging given harsh weather and fuel restrictions of the helicopters. During grounding and the rescue operation, the weather was characterized by high winds, snow (low visibility), and a temperature of around -23°C. Another concern was development of sea ice that possibly would entomb the *Northguider* in the coming days, hindering a potential fast towing of the vessel out of the strait. In fact, responders decided to only remove crew and salvage hazardous materials, waiting to extract the vessel until the following summer. A detailed timeline for the Northguider accident is presented in Box 10.1). This situation was not only a learning experience for all parties involved, but has re-opened the discussion about Norway's capacity for search and rescue (SAR) in Svalbard waters. It also raised the question of how to manage marine natural resources based on ecological knowledge in such situations. Both local and national management (including environmental protection organisations) were mainly concerned about potential effect on whales and seabirds "when they return in the spring", indicating that they do not have the overall understanding of how the Arctic ecosystem functions during winter, and in particular the Polar Night. In this book, we have provided information that clearly shows that accidents like the *Northguider* do in fact pose an imminent threat to organisms thriving throughout the Arctic year.

Fig 10.1 *Northguider* accident 28th December 2018. Photo of the grounded vessel and personnel from the coastguard and management authorities in small boat examining the ship in January 2019. The ship grounded in the northern part of Hinlopen Strait at 79°53N and 18°04E. Photo: Kystverket.

10.3 What do we now know about life in the Polar Night - What are the real threats?

The story of the *Northguider* accident provides an example of what will be required for planning and carrying out rescue operations in the Arctic as environmental change increases maritime access during winter and the Polar Night. The media coverage at the time of the accident mainly focused on large and charismatic organisms, with the primary- and secondary producers were not addressed at all despite their ecological significance. Perhaps more concerning, most of the information that is general knowledge with respect to marine life and dynamics that might go into SAR decision making, and the public perception of its environmental impact, is based on information from spring-summer-autumn. Fortunately, management authorities were able not only to remove all fuel from the vessel, they also were able to remove the trawl that was still floating in the sea behind the grounded vessel. In fact, personnel present at the site (Hjort-Larsen, *pers.com*) regarded this as an important task, as they witnessed seabirds, in particular Brunnich's guillemots being caught in the trawl as it was floating in the sea!

10.3.1 Current management of Svalbard waters

Environmental management in the Arctic is based on knowledge gathered during the well-lit part of year, i.e. the spring, summer and autumn. Quillfeldt et al. (2009) reviewed the Norwegian national plan covering the Norwegian Economic Zone and Fisheries protection zone in Svalbard waters. Areas closer than 12 nautical mile to the shoreline are managed according to the EU water management directive. Within the area of the national environment management plan, the integrated management of all human activities are constructed to ensure continued health of the whole marine ecosystem. Norway enacted this plan in 2006. At that time, three knowledge gaps were put on the agenda: 1) research (knowledge gathering), 2) mapping of resources, and 3) monitoring needs. The most important gaps with respect to monitoring were the horizontal distribution of Atlantic and Arctic water masses; the need for registration of introduced/alien species; and the establishment of time-series for stock assessment of keystone species, temporal variation in diet composition and habitat of commercial fish and benthic fauna, and long-term monitoring of pollutants in biota and water masses. The top priorities in ecological studies for the Barents Sea comprised studies of primary production (planktonic, ice-algal and ice-faunal energy transfer and ecology at all trophic levels), studies to identify environmental indicators of non-commercial fish species of key ecological importance, and studies to provide critical threshold values for biomass of herring. The Institute of Marine Research (IMR, Bergen and Tromsø) and Norwegian Polar Institute (NPI, Tromsø, Longyearbyen) do have annual resource and ecosystem cruises, including stock assessment of plankton and fish, north and south of the polarfront in the Barents Sea and Svalbard area, see details in Quillfeldt et al. (2009). Further studies of the ecology of the productive Barents Sea were taken in the large Norwegian research program "Nansen Legacy" (2018-2023), with the important addition of examining the ecosystem during winter. This is critical as the ecological questions posed above depend on biological processes that are ongoing throughout the winter, including the Polar Night.

10.3.2 Framework for filling knowledge gaps concerning ecosystem dynamics during the Polar Night

Response to future incidents like the *Northguider* will require different ecological information than is currently available for effective knowledge-based nature management. Accordingly, we identify three steps that are necessary to acquire this knowledge:

1. *Identification*: What organisms are present at different times of the year at all trophic levels?
2. *Mapping*: What are the spatial dynamics of biodiversity, production (photosynthesis, growth rates), biomass and health state of keystone organisms and/or habitats?
3. *Monitoring* (re-visit a given site, providing time-series): What are the temporal dynamics of biodiversity, production, biomass and health state of keystone organisms and/or habitats?

A major challenge in answering the above questions is that marine ecosystems in general are highly dynamic in time (sec-years) and space (mm-1000 km), with the latter including both horizontal (area) and vertical (depth) dimensions (Fig. 9.2). The Arctic marine system during the Polar Night has additional logistical constraints, being poorly accessible due to challenging conditions (dark, cold, sea ice). However, with appropriate technologies and sampling designs, researchers can overcome such time and space issues (Nilssen et al. 2015; Chapter 9). Below we describe these three elements with respect to filling knowledge gaps for ecosystem management during the Polar Night, and specifically how technology can play a role.

Identification involves identifying *objects of interest* (OOI, in this case, different organisms) in the Arctic ecosystem during the Polar Night, and how this compares to other times of the year. Since we have different size fractions, including viruses, bacteria, microalgae (phytoplankton, ice algae, benthic and epiphytic microalgae), zooplankton (holoplankton and meroplanktonic larvae), benthic macroalgae and invertebrates, fish, birds and mammals – we need methods to identify them using high-throughput, autonomous techniques to cover large spatio-temporal scales. However, such methods also require robust testing and quality control aided by taxonomic specialists to ensure that optical, acoustical and molecular methods/sensors/instruments identify organisms correctly. What is an important organism with respect to nature management? Here we need to define indicator organisms (bio-indicators) and keystone species that are important for ecosystem function between trophic levels, and species that may be particularly vulnerable to stress. Consider for example pollution that could have resulted if bunker fuel leaked from the *Northguider*. What species should we be most concerned about given the time this spill occurred? Again, coordination among disciplines will be required to answer this question on an ecosystem scale.

Mapping involves creation of habitat maps (surface, water column and seafloor), including both physical and biological components, to give information about the current state of the ecosystem when a management decision needs to be made. Since the current state is dependent on seasons and time of day (e.g. diurnal variation in presence/absence of a given group, taxon or species), we need to appreciate the ecosystem as a dynamic system. Utilizing instrument-carrying platforms to provide information across time and space is critical (Fig. 9.2; Chapter 9). The last decade has seen a revolution in using data from instrument-carrying satellites (Volent et al. 2011), airplanes (Volent et al. 2007), drones, unmanned surface vehicles (USV = autonomous surface vehicles, ASVs, Mogstad et al. 2019), autonomous underwater vehicles (AUVs, Berge et al. 2012; Johnsen et al. 2018) and remotely operated vehicles (ROVs, Mogstad and Johnsen 2017) to map Arctic ecosystems. At the surface and in the water, the use of acoustics and optics in concert has revolutionized knowledge acquisition (e.g. Ludvigsen et al. 2018). Optical approaches to mapping are particularly difficult during the Polar Night since sunlight is absent (making passive optical remote sensing impossible, see Johnsen et al. 2009; Fig 9.2), sea ice is present, and temperatures are low, all of which combined cause considerable logistical challenges with respect to equipment, transport and human interactions.

Monitoring of ecosystems, habitats and taxa involves extended, georeferenced observations over time and space. During the last decade, instrument-carrying platforms (e.g. ROVs, AUVs and ASVs) have been developed and improved significantly with respect to motion control (pitch, roll, yaw, distance to the OOI; Chapter 9). This is crucial for the generation of accurate, time-stamped information maps with metadata, which is a prerequisite for carrying out pixel-specific georeferencing of habitat maps, exemplified in a benthic habitat mapping case study below (10.4.3).

Through identification, mapping, and monitoring we can obtain appropriate knowledge for operational nature management and make sound decisions accordingly.

10.3.3 Ecosystem-based management of living resources during the Polar Night – what are reliable indicators of the ecological state of the marine environment?

During the *Northguider* accident, the first step was, obviously, to secure human life, and then obtain information about what happened with the vessel and equipment, along with identifying potential environmental pollution and how best to bring the vessel back to mainland. Shortly after the accident, it was concluded that the ship should be left until the light returns in spring-summer to secure necessary boats and equipment, but that fuel should be removed. Even though this decision was based on a fear of what would happen if the fuel leaked when seabirds and mammals returned to the area in the spring, it also prevented any potential effects on the organisms that we now know remain present and active throughout the Polar Night. During removal of fuel from the ship it was observed that seabirds got trapped and entangled in the trawl that was floating behind the vessel, and a decision to remove also this was made. However, it poses the question on what the consequences could have been had emptying of the fuel been prevented by, for example, weather or ice conditions? For sound environmental management and decision making, solid background information gained from the above framework (identification, mapping, monitoring) is essential. Are there birds, seals and polar bears close to the vessel in the winter darkness? Is there a high biomass of zooplankton, larvae, fish in the water column, and what effect will an oil spill have on the kelp forest/sea floor and its associated organisms nearby? These simple questions can be related to large transport vessels carrying oil and gas, which currently is a fast-growing activity in the Arctic. What are the effects of, for example, oil released from such a vessel? One of the main ambitions with this book have been to illustrate that the levels of biological diversity, biomass and dynamics are high during the Polar Night, and what we need to know for proper nature management and decision-making:

a) What organisms are present during the Arctic winter (Berge et al 2014, 2015a-c)?
b) How do we identify these organisms at the surface, in the water column and on the seafloor (e.g. Vader et al. 2015; Mogstad and Johnsen 2017; Johnsen et al. 2018; Ludvigsen et al. 2018; Fossum et al. 2019)?
c) Where are these organisms in time and space – which organisms during the Polar Night are typically found at the sea surface, in the water column or on the seafloor (Berge et al 2012; Johnsen et al. 2014; Cronin et al. 2015; Mogstad and Johnsen 2017)?
d) How do we identify, map and monitor these organisms in time and space (Fig. 9.2)?
e) What information is needed for nature management and sound decisions (Nilssen et al. 2015)?
f) What is the sensitivity to environmental stressors of different taxa levels (bacteria, phytoplankton, zooplankton, larvae, fish, birds and mammals)? Organismal effects to harmful substances are dependent on both exposure time and concentration. In addition, several stressors may affect an organism simultaneously with synergistic effects. What are the exposure limits with respect to time and concentration?
g) In case of accidents or catastrophic events – we need information from a-f to provide fast, knowledge-based data (on-line to near real-time data) to provide the best decisions.

In the following sections, we give a short overview, with questions (a-f) above in mind, of important organisms we have identified, mapped, and/or monitored in the Svalbard region during the Polar Night at the surface (10.3.4), in the water column (10.3.5) and on the sea floor (10.3.6).

10.3.4 Organisms at the sea surface

At the sea surface, six species of seabirds have been observed actively foraging in Svalbard waters during the Polar Night. These species comprise little auks (*Alle alle*), black guillemots (*Cepphus grylle*), Brünnich's guillemots (*Uria lomvia*), Atlantic fulmars (*Fulmarus glacialis*), black legged kittiwakes (*Rissa tridactyla*), and glaucous gulls (*Larus hyperboreus*). Most of the birds examined for stomach content revealed recent feeding on fish (e.g. polar cod), krill (*Thysanoessa* spp.) and benthic amphipods (e.g. *Anonyx nugax*) (Berge et al. 2015a,b,c; Ostaszewska et al 2017). Most stomach contents were minimally digested, indicating that the birds had found their prey locally. Moreover, the prey had not been selected randomly. Specifically, the birds appeared to have targeted key species such as bioluminescent krill (Berge et al 2012; Johnsen et al. 2014; Cronin et al. 2016; Chapter 3). These observations call for further examinations, such as: Do seabirds as visual predators dive into bioluminescent layers made of different taxa of zooplankton, krill and mesopelagic fish, making it easier for them to target prey? In the summer months, during which a large fraction of the food is fed to the chicks, the little auk prefers large copepods such as *Calanus hyperboreus* and *C. glacialis*. During the Polar Night, the stomach contents of little auks were dominated by bioluminescent krill (unpublished and Berge et al. 2015b). Some Arctic seabirds also appear to be attracted by artificial light, such as light from vessels, piers/quays, roads and settlements (Ostaszewska et al. 2017). Birds have been observed actively feeding, nearby artificial light from harbor lamps and from SCUBA diver-operated lamps. Especially the black guillemot, but to some extent also the Brünnich's guillemot utilized the light available from SCUBA divers and pier lamps to feed on large zooplankton, such as krill in the Polar Night. The Atlantic fulmars also follow ships during winter, looking for prey and fish/food waste at the surface. Both adult and juvenile birds have been observed, but the significance of these observations needs further examination. Currently, there is still little knowledge of how these birds obtain their food and what strategies they use to survive in the low-light conditions of the Arctic Polar Night, which emphasizes the need for further research.

Human-induced stressors, such as an oil spill, will destroy the plumage of seabirds, inducing loss of insulation (reducing the ability to cope with the cold and reducing the buoyancy when swimming), loss of ability to fly (defect feathers). This could also have direct toxic effects since birds will actively try the get rid of the oil by using their beaks to rinse their plumage, introducing toxic oil into the digestive system (review in Gabrielsen and Sydnes 2009). If seals and polar bears are around, similar effects will be the case. Indeed, we have documented walruses from the northern part of Svalbard during the darkest part of the Polar Night (unpublished). Birds that have avoided direct oiling of their plumage may feed on oil-exposed krill, and consequently transfer oil-related toxins into the digestive system indirectly. Some parts of the oil will stay afloat, while other components will sink or disperse into the water column and kelp forest with all its associated organisms.

There are also other organisms at the sea surface and in shallow areas that may be affected by an oil spill. In addition to birds, observations of mesopelagic fish, such as the bioluminescent silvery lightfish (*Maurolicus muelleri*), and the deep water helmet jellyfish (*Periphylla periphylla*) indicate that organisms that up until now have been regarded as deep-water organisms in fact may be at the sea surface, both during day and night during the Polar Night (Geoffroy et al. 2018; unpublished data). The observed presence of the two aforementioned species suggests that many other deep-water species could be capable of "surfacing during the Polar Night" as well, consistent with the Polar Night light climate resembling that of the deep sea (Chapter 3).

10.3.5 Organisms in the water column

Both natural and human-induced stressors may affect the biodiversity, biomass, health state and growth rates of the primary- and secondary producers to a high degree. Bacteria, phytoplankton (autotrophic, mixotrophic and heterotrophic) and zooplankton (comprising major taxa such as crustaceans, gelatinous plankton, ciliates, chaetognaths and pteropods) are highly active and represent the basic food source for marine life in the region (Chapter 4-8). The Polar Night is also the time for growth and development of primary producers – phytoplankton. At this time of year, the phytoplankton are dominated by heterotrophs (active) and seeding stocks of autotrophic species (few, but alive, often in resting states such as cysts (Kvernvik et al. 2018; Chapter 4). Note that the "seeding stock" of phytoplankton cells may lie in sediments or "hibernate" in sea-ice or water column waiting for enough light to start the initial spring bloom of phytoplankton. Natural environmental stressors and human pollution may deteriorate the health state of these key organisms, which will have domino effects on ecosystem function. One example is "elevated sea temperature causes smaller-sized primary- and secondary producers" (Leu et al. 2015; Fragoso et al. 2018). Reduced size of "phytoplankton" can subsequently change biodiversity and the growth and timing of primary consumers (herbivore zooplankton), secondary consumers (carnivore fish) and tertiary consumers (birds and mammals). A particular concern is that climate-induced sea temperature changes may alter the timing and size fractions of phytoplankton blooms, causing mismatches between producers and consumers (Leu et al. 2015).

During the Polar Night, the activity and biomass of secondary producers – zooplankton and larvae – is high in the upper 100 m of the water column (Chapter 5). Zooplankton for instance follow a persistent diel vertical migration pattern throughout this period of prolonged darkness, with ascent to the upper water masses during the night and descent to deeper waters during the day (Berge et al. 2009, 2015a-c). Furthermore, deep-water organisms, such as mesopelagic fish and gelatinous plankton, can be found at the surface during the Polar Night (the light regime at the surface during the Polar Night is comparable to that found at 2000m depth in the mid-Pacific). The organisms are highly affected by the light regime (Chapter 3), which regulates their biological clocks (Chapter 8).

10.3.6 Organisms on the seafloor

Seafloor habitats are diverse and comprise e.g. the littoral zone (0-30 m, with soft-hard substrates). Recently, reduced ice scouring has caused the upper zone of the kelp forest to move vertically from around 3-5-m depth (under the sea ice scouring zone, Chapter 4) towards the surface. Due to the absence of sea ice, we for instance now see kelp at the surface in most of the fjords and coastal areas of W-Spitsbergen (Bartsch et al. 2016, own annual observations from 1987-2018). Increased sedimentation and reduced salinity caused be glacial meltwater running off into surface waters may induce stress that lowers the growth rate of macroalgae. In addition, human-induced pollution may expose these habitats to an array of new stressors, which is especially relevant now that most kelp forests have migrated into shallower waters, closer to the surface (the source of anthropogenic pollutants). Large kelp forests (found in rocky habitats throughout all regions of Svalbard), seafloor habitats dominated by coralline red algae (3-40 m; see Chapter 4), and the variety of benthic organisms living on hard and soft substrates (0 m-deep waters; Chapter 6) are all fragile to additional stressors from humans in an area that keeps getting warmer.

Note that some species of perennial brown macroalgae are growing during the Polar Night, and they possess functional chloroplasts that can perform photosynthesis if artificial light is provided (Aamot et al. 2014; Chapter 4). There is a current need to identify, map and monitor the high biomass of macroalgae (especially species making up kelp forests), which forms important habitats for epi-growth organisms, crustaceans (e.g. amphipods and mysids), bristle worms, mussels, snails, juvenile fish and seabirds. These habitats are not only important for providing shelter and food, but also for reproduction of invertebrates and fish (including species that up until now only have been seen in deeper waters), based on summertime surveys. Mass occurrences of organisms living in kelp forests, such as ghost shrimps, have been regularly observed in January in Kongsfjorden over the last decade (Chapter 6). The holdfast of kelp and other macroalgae provides shelter and food for an array of important organisms, including smaller species of macroalgae (Chapter 4), common bivalves, such as *Hiatella arctica*, and the recently arrived blue mussel *Mytilus* spp. (Berge et al. 2005; Leopold et al. 2018). The reappearance of blue mussels on Svalbard is likely caused by increased seawater temperatures (favoring blue mussel survival and reproduction), blue mussel larval advection by ocean currents and human introduction by ship traffic. Baseline information on species distribution and their genetic composition is imperative for quantifying the impacts of climate change and other human-induced stressors on species distribution ranges, biodiversity, and genetic alterations such as hybridization between species and populations of *Mytilus* spp. (Mathiesen et al. 2016). Significant bivalve growth and annual differences in the abundance of polar cod versus Atlantic cod in kelp forests indicates differences in the flux of Atlantic versus Arctic water masses (Berge et al. 2015c). In addition, juveniles of the deep-water-dwelling beaked redfish (*Sebastes mentella*; Chapter 7) have been found in the kelp forest in January, and at the same time at 80m depth close to Kongsbreen in Kongsfjorden.

10.4 New technologies for habitat mapping and monitoring

Instead of using conventional sampling procedures (e.g. sampling by SCUBA diving), new enabling technology can be used to provide maps of habitats from the littoral zone to deep-water basins in the Arctic down to 4000 m depth. Here, we show how some of this technology can be used for management purposes by using underwater instrument-carrying platforms such as a Remotely Operated Vehicle (ROV) equipped with an Underwater Hyperspectral Imager (UHI) to automatically identify, map and monitor bio-geo-chemical objects OOI (for applications, see Johnsen et al. 2013, 2016; Mogstad and Johnsen 2017; Dumke et al. 2018a,b; Mogstad et al. 2019). This approach has been used to map seafloor habitats down to 4200-m depth (Dumke et al. 2018a,b). Currently, there are several examples of instrument-carrying platforms and sensors that can be used to obtain an overview of the current state of marine biodiversity, physiology and biomass during the Polar Night for habitat mapping and monitoring (Cohen et al. 2015; Berge et al. 2016; Johnsen et al. 2014, 2016; Mogstad and Johnsen 2017). These are detailed in Chapter 9, comprising buoy data at different depths (tethered observation systems; Berge et al. 2016), Autonomous Underwater Vehicles (AUVs; Berge et al. 2012; Johnsen et al. 2018; Fossum et al. 2019), Remotely Operated Vehicles (ROVs; Mogstad and Johnsen 2017) and Unmanned Surface Vehicles (USVs; Ludvigsen et al. 2018).

In regions that are rough-weathered in addition to being dark, cold and icy, the most used mobile platforms are large vessels and smaller boats. Large mobile platforms can serve as the base (mothership) for further surveys using ROVs, AUVs and USVs to obtain information without risking human lives. These vehicles can be equipped with sensor technology capable of "seeing in the dark", such as imaging acoustics, infrared (IR) sensors and radars (Berge et al. 2015a; Ludvigsen et al. 2018), reviewed in Chapter 9.

Biological maps represent essential baseline information that should be considered strictly necessary for assessing the environmental impacts of accidents, such as that of the *Northguider*, to a satisfactory extent. It is widely recognized that we know more about the terrestrial realm that constantly surrounds us than the marine realm hidden beneath the surface of the world's oceans. This is perhaps not surprising, considering we are a terrestrial species and that the technology required for carrying out marine mapping surveys only has been commonly available since the mid-twentieth century. To put things into perspective, a figure that frequently appears in both media and scientific literature is that only about 5% of the seafloor has been mapped (Copley 2014). However, this is not a completely accurate depiction. On the contrary, complete maps of the entire seafloor do in fact exist, but often with a spatial resolution of ~5 km (Sandwell et al. 2014). Unfortunately, this resolution does not tell us much about the biological and chemical processes that take place on the seafloor and is consequently far too coarse for most management purposes. When looking to answer questions related to biological seafloor processes, spatial resolution requirements are often particularly strict. Unless you are investigating uncommonly large biogenic structures, such as coral reefs, your mapping technique has to be able to resolve objects of interest <1 m. If you for instance wish to monitor change in abundance or areal coverage of a given species, mm-cm scale resolution may even be necessary. It is clearly not realistic to map the global – or even the Arctic – seafloor with this kind of resolution in the immediate future, but by carrying out highly detailed surveys in small, defined areas considered appropriate for the topic at hand, the knowledge needed to make sound management decision can still be generated.

There are arguably two main approaches to mapping the seafloor: by means of acoustics (sound) and by means of optics (light). Which of them is most beneficial depends on the question at hand, and the two approaches should be regarded as complementary rather than overlapping.

10.4.1 Acoustics

The acoustic approach is perhaps the most widespread way of characterizing the benthic environment and water column (Brown et al. 2011). Active acoustic sensors (e.g. multibeam echo sounders and side-scan sonars, see Chapter 9) work by emitting sound pulses into the water column and subsequently recording the corresponding sound pulses (echoes) reflected off the seafloor or organism of interest in the water column. The advantage of active techniques is that they are largely independent of environmental variables, and that they consequently are capable of “seeing” in challenging environments such as the Arctic during the Polar Night. Sound has the associated benefit that it travels exceptionally well in water, which typically gives acoustic techniques superior range as compared to e.g. optical techniques.

In terms of seafloor management, acoustic maps can provide valuable information about research and management issues of interest ranging from seafloor and indicate sediment type to coral reef distribution and marine archaeology. During the Polar Night, side-scan sonar mapping has for instance been used as a tool for wreck site identification off the coast of Svalbard (Chapter 9). Acoustic techniques can also be used for assessing processes that take place in the water column. Diel vertical migration (DVM) of zooplankton during the Polar Night has for instance been observed using moored acoustic doppler current profilers (ADCPs, see Chapter 9; Berge et al. 2015a-c). Furthermore, acoustic zooplankton fish profilers (AZFPs, see Chapter 9) have been used to demonstrate that artificial light (light pollution) repels zooplankton in dim Polar Night conditions (Ludvigsen et al. 2018).

A considerable advantage of acoustic techniques is that their range permits mapping of large areas (Table 9.3; Chapter 9). However, the detail level and spatial resolution of acoustic data is typically insufficient for assessing small (<10 cm) OOIs. In addition, certain defining object characteristics (e.g. colour) cannot be assessed by means of acoustics alone. To provide a holistic and sufficiently detailed overview of a given area of interest, other techniques should also be included for ground truthing. The following section presents the utility of optics in relation to environmental mapping and monitoring of the marine Arctic during the Polar Night.

10.4.2 Optics

The other major approach to seafloor mapping is through optics. Optical techniques are based on measurement of electromagnetic radiation, or more specifically, light. For seafloor mapping purposes, the relevant optical techniques can for simplicity’s sake be narrowed down to different forms of imaging. The rapid development and application of aerial and satellite imaging has permitted detailed mapping of most terrestrial environments. These techniques are capable of covering vast areas at frequent intervals and have consequently become indispensable tools for terrestrial monitoring and management (Fig. 9.2 in Chapter 9). Unfortunately, their applicability is severely limited in the marine realm. The reason for this is simple: light is attenuated extremely rapidly in water compared to sound. Furthermore, both aerial and satellite imaging relies on illumination provided by the sun, which makes them “passive” mapping techniques. In the clearest, sunlit waters, passive optical techniques are limited to a maximum depth of approximately 20 m at best (Armstrong 2016). This implies that air- and space-borne sensors can be used to map shallow-water habitats such as seagrass meadows and tropical coral reefs, but not much else – especially not Arctic regions during the Polar Night. To map deep, dark and/or ice-covered areas using optical techniques, other approaches have to be used.

In particular, two criteria have to be fulfilled to permit optical mapping of deep and dark seafloor environments: the imaging sensor has to be brought closer to the target area or OOI, and an artificial light source has to be deployed along with the imaging sensor to “see in the dark”. The latter converts passive imaging to active imaging that no longer relies on ambient light provided by the sun. Both requirements relate to the optical properties of seawater (Chapter 3). The properties of seawater and its constituents (phytoplankton, cDOM, TSM) prevent long-distance optical imaging, and therefore, the imaging sensor needs to be close to the seafloor (typically <10 m) to permit acquisition of satisfactory data. Unless the mapping survey is carried out in very shallow waters with strong daylight present, an artificial light source is as mentioned also a survey necessity, as the downwelling irradiance from the sun rapidly becomes insufficient for optical imaging purposes with increasing depth. This is especially relevant during the Polar Night, where ambient light is practically absent.

There are multiple methods and techniques by which optical seafloor imagery can be acquired. A traditional and simple approach is equipping a SCUBA diver with an underwater camera with flash light. This is a beneficial method for highly detailed studies of small areas of interest (Beuchel and Gulliksen 2008; Beuchel et al. 2010). The downside is, however, that this methodology is limited in terms of both spatial coverage and depth. To assess larger areas beyond diving range, other means are necessary. ROVs and AUVs represent platform types that are widely used for optical seafloor mapping. Both of them have associated pros and cons, and ultimately, the platform has to be chosen based on survey goals and the research/management question under assessment (detailed in Chapter 9).

The final decision that has to be made in relation to an optical seafloor mapping survey is which imaging sensor to use (Nilssen et al. 2015). Regular RGB (red, green, blue) digital cameras arguably represent the most simple and common alternative. An RGB digital camera captures imagery by means of a CCD or CMOS image sensor. These sensors produce images where each pixel is assigned a red, a green and a blue intensity value. The RGB wavebands (channels) largely correspond to the three wavebands the human eye is sensitive to, and when their values are interpreted together, the result is the colour we perceive. One way of using an RGB digital camera for seafloor mapping is by mounting it downward facing onto e.g. an AUV. As the AUV follows its survey path, the camera can be set to take pictures of the seafloor at fixed intervals. Provided that there is sufficient overlap between neighboring pictures (ideally ≥50%), the imagery can subsequently be mosaicked together to form a continuous RGB map of the surveyed area (Johnsen et al. 2018). Digital cameras may also be used in tandem in what is known as a stereo camera rig. In a stereo camera rig, two synchronized cameras are typically mounted in parallel with a known, fixed distance between them. Similar to how our binocular (two-eyed) vision gives us depth perception, the stereo setup permits estimation of object distance and position through point triangulation, and is thus capable of acquiring 3D imagery as well as navigation data. Possible applications of stereo camera rigs include deployment on ROVs for 3D model generation of wreck sites, vertical rock walls and coral reefs (Nornes 2018).

Although RGB digital cameras potentially can provide researchers and decision makers with highly valuable data, there is one optical aspect of their data products that can be considered under-sampled: the spectral aspect (Fig. 10.2). As mentioned, a digital camera records a value for red, green and blue light for each pixel. A typical camera can be expected to measure these colours using waveband channels with peak sensitivities at approximately 460 nm (blue), 530 nm (green) and 590 nm (red; Sigernes et al. 2009). Considering that visible light spans the entire range of 400-700 nm, this leaves a substantial portion of the visible light spectrum un-sampled. To utilize more of the available colour information, other imaging sensors have to be used.

Over the past decade, Underwater Hyperspectral Imaging (UHI) has emerged as an interesting alternative to regular digital cameras for optical seafloor mapping in deep and dark environments. In the Arctic, it has for instance, been used to assess the spectral characteristics of coralline algae during the Polar Night (Mogstad and Johnsen 2017). Instead of a simple RGB value, an underwater hyperspectral imager assigns each image pixel a contiguous light spectrum (Fig. 10.2). The spectrum typically covers the range of 380-800 nm at a spectral resolution of 0.5-4 nm (Johnsen et al. 2016), depending on the chosen settings. This implies that each hyperspectral image pixel serves as a sensor that may record as many as 600 colour values (wavelengths) within the range of 400-700 nm, providing an optical fingerprint (as opposed to just three for an RGB pixel), and consequently that practically all visible light is accounted for. Another defining characteristic of the underwater hyperspectral imager is that it is a so-called "push broom scanner". Instead of capturing a rectangular 2D image during each exposure, the underwater hyperspectral imager only captures a single hyperspectral pixel row through a thin light entrance slit. To acquire 2D imagery, the imager has to be moved across the target area with the light entrance slit oriented perpendicularly to the direction of movement. This can be achieved through e.g. ROV- or AUV-based deployment. During the "scanning" motion, the imager continuously captures hyperspectral pixel rows (slit images) at a set frame rate. When these rows are mosaicked together, the result is a 2D image transect where each pixel holds a detailed optical signature (optical fingerprint) of the seafloor object or area it represents. The benefit of this mode of operation is that it essentially givers photo-mosaics over larger areas on the fly, potentially providing important information for further actions needed. In addition, the use of a light entrance slit (as opposed to a regular camera objective) minimizes the detrimental effect scattering of light may have on captured imagery, which permits imaging in relatively turbid waters. UHI surveys are typically carried out at altitudes of 1-2 m above the seafloor, and at these altitudes, a spatial image resolution of <2 mm is achievable. For data interpretation and analysis, recorded UHI transects can be visualized as RGB images. A practical aspect of this possibility is that wavelengths representing R, G and B can be chosen from the entire available spectral range based on the survey target(s) of interest. Moreover, the detailed colour information of the optical fingerprints recorded using UHI provides an excellent foundation for colour-based (spectral) image classification, and the following section shows an example of how UHI data can be used for biological assessments of the seafloor during the Polar Night.

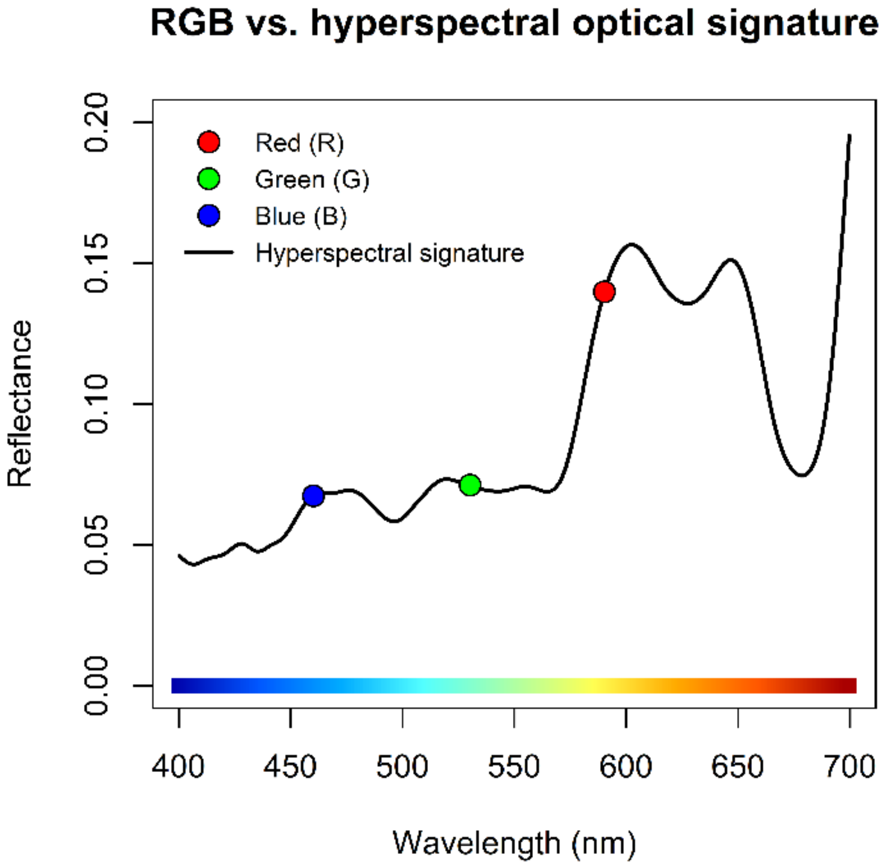

Fig. 10.2 The optical signature of a red coralline alga displayed in RGB (coloured dots; spectrally positioned according to Sigernes et al., 2009) and as a contiguous spectrum (black line). The former represents the output of a regular digital camera pixel, whereas the latter shows the equivalent output of

a pixel captured by an underwater hyperspectral imager (UHI) at 0.5-nm spectral resolution. Reduced reflectance in green (545 and 570 nm due to absorption by phycoerythrin) and red (679 nm absorption maxima of Chl a, Mogstad and Johnsen 2017).

10.4.3 Case example: supervised classification of underwater hyperspectral imagery from Kvadehuken, Kongsfjorden, Svalbard

The data presented in this section were acquired during a Polar Night cruise off the coast of Svalbard in January 2016. Hyperspectral imagery was recorded at Kvadehuken by deploying the underwater hyperspectral imager "UHI-2" (2nd generation; Ecotone AS, Trondheim, Norway) on NTNU's ROV "Minerva". Two 250-W halogen lamps mounted 35 cm aft and fore of the UHI provided illumination, and the imagery was captured at 2-nm spectral resolution. Figure 10.3a shows an RGB representation of one of the recorded UHI transects from Kvadehuken. The benthic biota at this particular location was dominated by coralline algae (Rhodophyta), sea anemones (Actinaria) and sea urchins (Echinoidea). Of the aforementioned organism groups, coralline algae can be considered particularly important, as they are known to be important ecosystem engineers in the marine Arctic (Jørgensbye and Halfar 2017; Teichert et al. 2014). The transect was recorded at a depth of ~14 m from an ROV altitude of ~1 m, and covered a seafloor area of approximately 5.90 x 1.15 m. It features a black and white polyethylene disk, which was placed at the location to serve as a colour reference (reflectance standard). Figure 10.3b shows the results of a support vector machine (SVM) classification of the UHI transect. SVM is a supervised classification algorithm that utilizes training data from hyperspectral image pixels of known identity/class to create rules based on which it classifies all pixels in the entire image. Pixels that spectrally resemble a given training data class sufficiently, will be classified as that class. The classification results in Fig. 10.3b are for instance based on 100 training pixels from each of the eight classes displayed in the figure legend. In other words, the classification is a result of SVM rules generated from a total of 800 pixels. To put that into perspective, the entire UHI transect in Fig. 10.3a consists of 13.6 million pixels. Table 10.1 shows the estimated areal coverage of each SVM class in Fig. 10.3b.

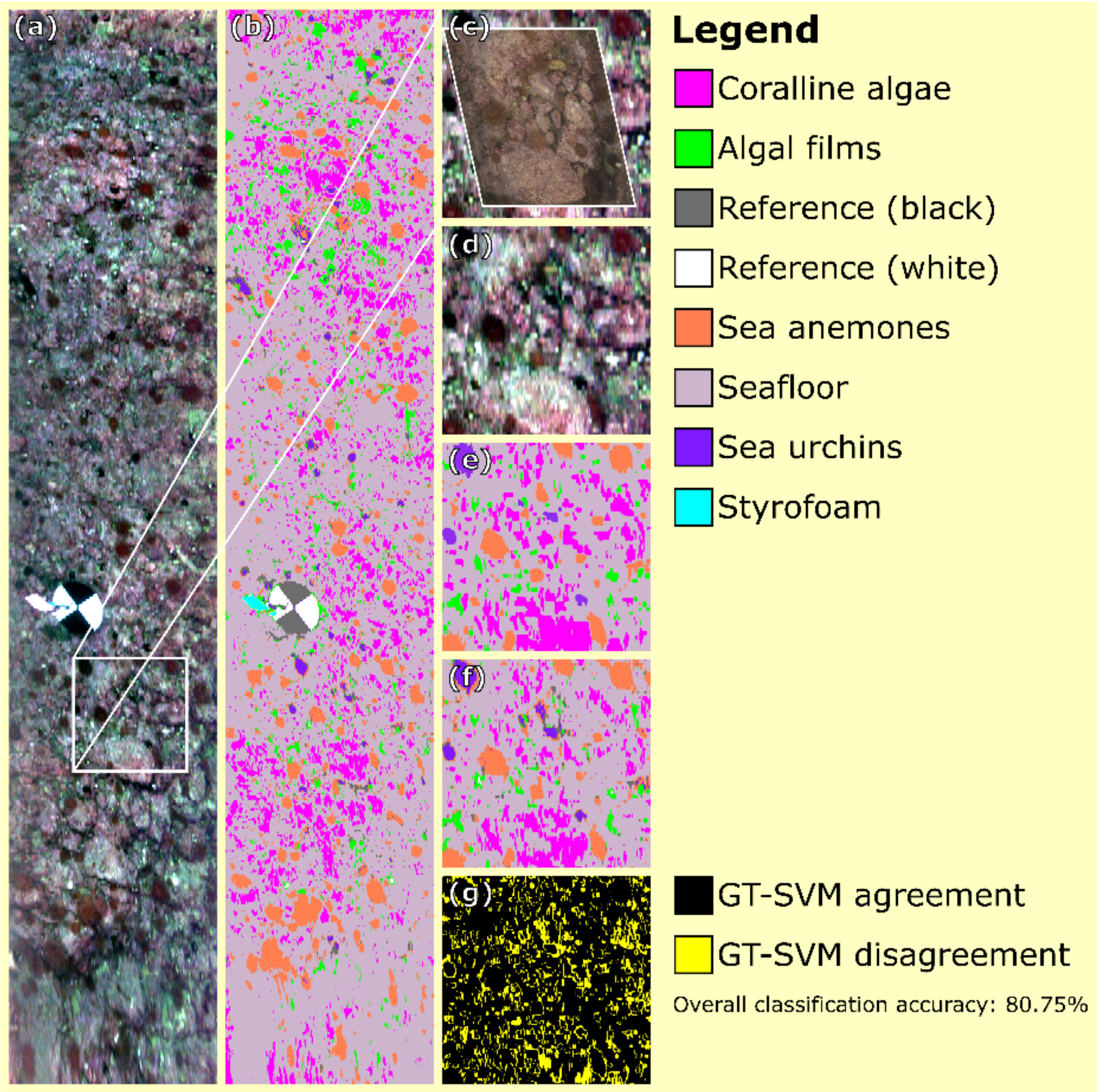

Fig. 10.3 Analysis of ROV-based Underwater Hyperspectral Imaging (UHI) data from Kvadehuken, Kongsfjorden, Svalbard during the Polar Night (January 2016). Panel (a) shows an RGB photo-mosaic representation (R: 490 nm, G: 550 nm, B: 620 nm) of one of the recorded UHI transects. The transect covered an area of approximately 5.90 x 1.15 m. Panel (b) shows the results of a support vector machine (SVM) classification of the same transect. Panels (c-g) correspond to a specific 60 x 60-cm subset area within the transect. The panels respectively show a dive-acquired photograph of the area (c; UiT The Arctic University of Norway, 2018), an RGB-visualization of UHI data from the area (d), a manually labelled ground truth (GT) image of the area (e), the SVM classification results from the area (f) and a comparison of the GT image and the SVM classification (g).

Table 10.1 Estimated areal coverage (%) of each spectral class in Fig. 10.3b.

Class [SVM, panel b]	Estimated areal coverage (%)
Coralline algae	11.41
Algal films	3.00
Reference (black)	1.40
Reference (white)	0.50
Sea anemones	8.26
Seafloor	74.63
Sea urchins	0.71
Styrofoam	0.10
Total	100

The benefit of using classification algorithms like the SVM classifier for assessment of seafloor imagery is that it is an automated approach, which reduces processing time. This can be highly useful for management purposes, presuming that the classification results are sufficiently accurate. To assess the validity of a given classifier, its classification results have to be compared to "ground truth" data, such as an image of a subset of the surveyed area, where an expert has manually assigned all pixels to their correct class (the class the pixels actually represent *in situ*). This is an extremely tedious and time-consuming job, which is what makes automated classification such an attractive image analysis tool. Panels c-g in Fig. 10.3 show various components that often are included in an assessment of classification accuracy. In the presented example, the assessment was performed on an approximately 60 x 60-cm subset of the UHI transect shown in Fig. 10.3a. The subset area corresponds to a location where UiT, the Arctic University of Norway (2018) has a photography time-series, and Fig. 10.3c displays a dive-acquired photograph taken four months prior to the UHI survey. Figure 10.3d shows a zoomed-in RGB representation of UHI data from the same subset, and based on interpretation of this in context with the photograph in Fig. 10.3c, a ground truth image was created by manual pixel labelling (Fig. 10.3e). As stated, the purpose of such an image is to serve as an "answer key" to which classification results can be compared. In this example, the results of interest were from the previously described SVM classification (Fig. 10.3b), and the specific SVM results from the subset area are shown in Fig. 10.3f. Figure 10.3g shows the final results of the accuracy assessment. Here, a pixel-by-pixel, class-specific comparison has been carried out between the ground truth image (Fig. 10.3e) and the SVM classification results (Fig. 10.3f). Correctly classified pixels, meaning pixels whose class in the SVM results *match* the class assigned in the ground truth image, are labelled in black. Incorrectly classified pixels, meaning pixels whose class in the SVM results *differ from* the class assigned in the ground truth image, are labelled in yellow. In this particular case example, the overall classification accuracy (percentage agreement between ground truth image, Fig. 10.3e, and SVM results, Fig. 10.3f) was 80.75%. This result is acceptable, albeit not perfect.

Tables 10.2-3 display the results of the Fig. 10.3 accuracy assessment in a class-specific, quantitative fashion. The tables are what is known as confusion matrices. A confusion matrix shows the accuracy estimate for each class, as opposed to the overall classification accuracy of the entire assessment combined. This is useful because it both highlights the classes that are well predicted by the given classifier (in this case the SVM classifier), and the classes that are not. Table 10.2. shows the estimated accuracy for each class in terms of percentage. Table 10.3. shows the same estimates in terms of pixel numbers. Ground truth classes (Fig. 10.3e) are represented as columns, whereas SVM classes (Fig. 10.3f) are represented as rows. The proportion of correctly classified pixels for each class can be read diagonally from the top left to the bottom right (green cells). In Table 10.2, we can for instance see that only 56% of the pixels corresponding to coralline algae in the ground truth image were classified as coralline algae by the SVM classifier. We can also see that 44% of the coralline algal pixels in the ground truth image were classified as seafloor, which suggests that the SVM seafloor class in this case appears to be too general, with a tendency to encompass some pixels that in reality belong to other classes. Although this is sub-optimal, it is arguably better that the classification algorithm underestimates rather than overestimates the areal coverage of biological seafloor classes. This especially applies to marine management, which should follow the precautionary principle. To make sound management decisions and maintain functioning ecosystems, it is safer to assume we have less than to assume we have more.

Table 10.2 Confusion matrix from comparison of Fig. 10.3e (ground truth; GT) and Fig. 10.3f (SVM classification results). Results are displayed in %.

Class [SVM, Fig. 10.3f]	**Ground truth [GT, Fig. 10.3e] (%)**							
	Coralline algae	Algal films	Reference (black)	Reference (white)	Sea anemones	Seafloor	Sea urchins	Total
Coralline algae	56.22	0.09	0	0	0	3.27	0	12.70
Algal films	0.03	52.41	0	0	0.02	1.76	0.01	2.98
Reference (black)	0	0.37	0	0	3.74	1.32	7.74	1.41
Reference (white)	0	1.93	0	0	0	0	0	0.07
Sea anemones	0	1.35	0	0	82.06	4.29	16.42	10.43
Seafloor	43.75	43.63	0	0	11.38	89.19	2.59	70.24
Sea urchins	0	0.23	0	0	2.81	0.16	73.25	2.17
Total	100	100	0	0	100	100	100	100

Table 10.3 Confusion matrix from comparison of Fig. 10.3e (ground truth; GT) and Fig. 10.3f (SVM classification results). Results are displayed in pixel numbers.

Class [SVM, Fig. 10.3f]	**Ground truth [GT, Fig. 10.3e] (%)**							
	Coralline algae	Algal films	Reference (black)	Reference (white)	Sea anemones	Seafloor	Sea urchins	Total
Coralline algae	81294	23	0	0	0	16890	0	98207
Algal films	50	13929	0	0	12	9096	2	23089
Reference (black)	0	98	0	0	2506	6836	1481	10921
Reference (white)	0	513	0	0	0	0	0	513
Sea anemones	0	358	0	0	54995	22168	3141	80662
Seafloor	63268	11594	0	0	7625	460357	495	543339
Sea urchins	0	61	0	0	1883	830	14015	16789
Total	144612	26576	0	0	67021	516177	19134	773520

The presented UHI results from Kvadehuken highlight both advantages and pitfalls associated with hyperspectral mapping of the seafloor. On the plus side, automated classification based on spectral signatures represents a convenient means of quickly providing distribution and abundance estimates of different organism groups present in a given UHI transect. By visually comparing Fig. 10.3e and f, it is also evident that automated classification estimates are capable of closely depicting the truth. However, the estimates are still just estimates, and a downside to hyperspectral seafloor mapping is that different spectral classes are not equally distinctive. Certain species or organism groups may for instance be highly variable spectrally (different colour morphs, such as the cold water coral *Lophelia pertusa*, Johnsen et al. 2013), which intrinsically makes them much more difficult to map based on colour. Another factor that complicates analysis of UHI data is seafloor three-dimensionality. As an example, objects that protrude from the seafloor may appear disproportionately bright, whereas shaded areas may seem completely dark. The latter phenomenon is apparent in Table 10.1 of Fig. 10.3, where the estimated areal coverage of black and white reference disk should have been practically equal. However, the black reference is estimated to cover an area nearly three times as large as that of the white reference, which largely is a result of shaded and underexposed pixels in other parts of the transect being classified as the former. Despite these caveats, the utility of UHI should not be downplayed. Any given mapping technique has its limitations. The take-home-message is to be aware of them, so that the acquired data can be used in a justifiable manner.

10.4.4 Human activity, habitat function, future challenges and knowledge gaps

In general, the interest from media with respect to negative environmental effects from human activity has focused on the oil industry, while fisheries on commercial species have not been under the same attention (Norse and Crowder 2005). Likewise, marine mining, tourism and new transport routes has not been a focus. However, we know that human activity is expanding fast in a mostly unknown environment – the Arctic Polar Night. We also know that human activity degrades ecosystems rapidly and the period we live in is frequently referred to as the 6th mass extinction period – the Anthropocene (Kolbert 2014). In view of this, actions need to take place to understand the function of unstressed ecosystems, providing knowledge-based data from undisturbed ecosystems and habitats, the basis for environmental management. When this is provided, we can minimize the effects of human activity (direct and indirect factors) by identifying, mapping and monitoring organisms/habitats for future environmental management

In environmental management, the focus has often been directed at commercial species, especially fish, seals and whales, while non-commercial organisms often have been overlooked. Since commercial fish, such as cod and capelin, are highly dependent on diverse food sources (from the water column to benthic habitats) surveys have also been conducted on the basic food sources in the ecosystem, i.e. the phytoplankton (primary producers) and zooplankton (primary consumers/secondary producers, including larvae), but only in the light season. However, we do not know much of plankton dynamics during the Polar Night. Likewise, we have limited knowledge about the distribution, biomass and function of different benthic habitats during winter darkness as living areas for benthic invertebrates, bottom dwelling fish and crustaceans. These habitats are important for interaction between organisms filling up all the niches that must be operative to provide a well functional ecosystem.

In Norway, the management of fish stocks is an excellent example of the importance of providing data for species, biomass, age groups (recruits) and physiological state. Also, the success with Norwegian and Russian co-operation has proven to be extremely valuable (Sakshaug et al. 2009; Jakobsen and Ozhigin 2011). Stock assessment surveys are of key importance for the recommendations subsequently discussed at the Joint Norwegian-Russian Fishery Commission. For 2018, the findings of the researchers were instrumental for the reopening of catch on capelin, the species that for years had been at a historical low. Based on stock assessments, the Norwegian-Russian Fishery Commission also set the Atlantic cod quotas for the region. Food-web analysis and functional biogeography provides important information of relationships between bio-diversity, ecosystem functioning, and environmental drivers. This knowledge is highly important when species, communities, habitats and ecosystems change due to climate warming and managers seek advice for sound decisions. In 2012, the Norwegian Directorate of Fisheries (Fiskeridirektoratet) has opened an area for shrimp trawling, including Hinlopenrenna and the Hinlopen strait, as well as deep-water areas north and south of them that had previously been off limits for fishing vessels (Fig.10.4). This is also in the region where *Northguider* grounded 28th December 2018.

There are several unknowns that need to be addressed during the Arctic winter, especially how light affects behaviour of organisms at all trophic levels. For stock assessment of fish and commercial species such as krill and shrimp at night or during the Polar Night, new findings indicate that artificial light from research vessels (or light pollution from humans in general) may affect these stock estimations due to phototactic (directed swimming away or towards a light source) responses that will affect biodiversity and biomass estimates (Ludvigsen et al. 2018; Chapter 3).

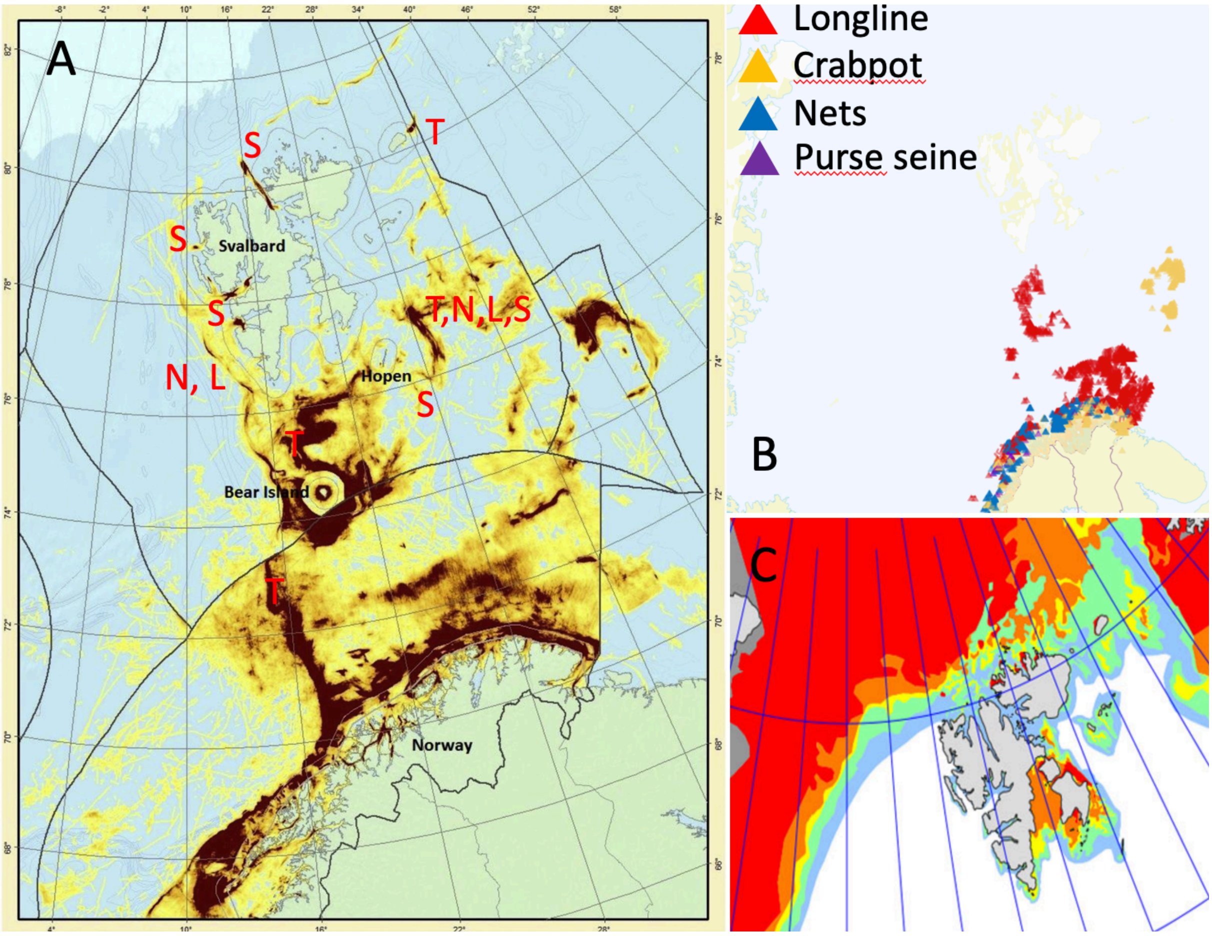

Fig.10.4 (**a**) Annual fishing activities in the Svalbard area and during the Polar Night. A. Modified from Misund et al. (2016)/Kystverket. Annual activity of fishing vessels longer than 15 m at 1-5 knots speed, indicating fishing activity; S (shrimp trawling, dominated by *Pandalus borealis*), T (trawling for large fish, e.g. Atlantic cod), N (net) and L (longline). (**b**). Fishing activity in January 2019 in the Barents Sea and Svalbard region (trawling activity not included) Source: BarentsWatch. (**c**). Sea-ice distribution in Svalbard January 2019 (red: very close drift ice, orange: close drift ice, yellow: open drift ice, green: very open drift ice and blue: open water. Source: Norwegian Meteorological Institute.

The *Northguider* accident exemplifies a best-case scenario with no humans hurt and with no environmental pollution. The only part left is to rescue the fishing vessel and bring it back to the mainland of Norway (still not done in June 2019). However, when reviewing the incident, the outcome could easily have been different with loss of human life and with 300 000 metric tons of diesel leaking into the ocean. How would this diesel have affected the active organisms at the surface, water column and seafloor? There are not any good procedures available (vessels, robots, methods, equipment, sensors, trained people, companies) that are available to perform a clean-up mission and perform corresponding monitoring during the Polar Night. How do you see in the dark with sea ice and low temperatures that may affect the functionality of equipment and people during a clean-up survey?

Scale is also an important factor to address – how many vessels, rigs and humans will be involved in the new and growing Arctic activities, including fisheries, oil and gas, marine mining, new transport routes and tourism? Until now, the focus has been on human security, infrastructure and logistics for further activity in the Arctic. There has not been an **evaluation of ecosystem vulnerability during the Polar Night** since most decision makers still think that dark and cold waters will comprise a situation with low biomass, biodiversity and activity. The findings reviewed in this book show that the opposite is the case.

Box 10.1 Timelines for rescue operations and corresponding environmental management during the Polar Night

Reduced sea ice coverage has expanded fishery activities, resource exploitation and ship traffic in the marine Arctic. These activities are dependent on a functional search and rescue (SAR) plan which currently is prioritized as follows: (1) Rescue, (2) Clean-up of environmental hazards and (3) Return of infrastructure (e.g. a stranded vessel) to owner. All this is to ensure that the environment will not be affected by oil, chemicals and other human-made substances capable of influencing microbes, phytoplankton, zooplankton, larvae, benthic organisms, fish, seabirds and mammals.

In short, the timeline for a **rescue operation** can be summarized by the following steps:

1. Rescue of humans (time window: hours)
2. Clean-up of environmental hazards (in this case diesel, oil, batteries and plastics) related to the vessel (time window: days-weeks)
3. Return of the vessel to mainland (time window: days to months)

The timeline for corresponding **environmental management** and decision-making differs from that of the rescue operation:

1. Detection of anthropogenic substances harmful to the environment (e.g. eco-toxins and oil; time window: days-months)
2. Responses of organisms to these harmful substances (time window: days-years)
3. Environmental monitoring (time-series; time window: days-years)
4. Action plan to reduce stress to ecosystem.

The following paragraphs describe the Northguider rescue and clean-up operation, step by step:

28 December 2018*: *Northguider* grounded around 13:00 on Friday 28 December 2018, and the main rescue central for North Norway got the first emergency call at 13:22. There were no other vessels in the area available to help. One and a half hour later, the first helicopter provided the first of two rescue operations. The whole vessel crew of 14 was rescued by two helicopters and arrived in Longyearbyen at 17:00 with no serious injuries. The stranded vessel was tilted, and water was penetrating the hull. There were difficulties with darkness, cold temperatures, geo-positioning of *Northguider* and communications. Furthermore, the continued absence of other vessels was an important issue. The rescue operation was entirely dependent on helicopters. The next step was for Kystverket (The Norwegian Coastal Administration) to map available resources and possibilities for clean-up and rescue of the vessel. By requirement of the Norwegian Coastal Administration, the ship owner is responsible for recovery of the capsized vessel. The Norwegian Coastal Administration requested access to the Coastguard vessel KV *Svalbard* (currently at Sortland, mid-Norway), which would be available to empty fuel tanks (incl. other chemicals) and to salvage the vessel by the following week.

30 December 2018*: *Northguider* was still floating at the same position. Sea ice was closing in around the vessel. A hole in the hull beside the machine room was identified. The KV Svalbard left Norway Sunday evening, with an estimated four-day transit time to reach the site of Northguider to:

1. Check for vessel damages
2. Empty diesel tanks if possible
3. Try to tow the vessel out of the area (provided that the vessel was still afloat)

The ship owner was worried about sea ice developing in the area. There was possibly a calm weather window in "the middle of next week", i.e. the time that KV Svalbard would arrive. There was a race against time with respect to the developing ice edge and the rescue operation of Northguider. There was uncertainty surrounding the vessel's ability to stay afloat if towed from the shallow accident site, and additionally, a fear of diesel leakage. It was established that the ship owner had to pay the vessel rescue bill.

31 December 2018*: Environmental institutions (e.g. Bellona) and the Svalbard Governing Authority (SGA) feared pollution of wildlife in the area (with a focus on seabirds and marine mammals). The institutions also stated that Norwegian authorities have no capacity to start an oil rescue operation in the area. There was a fear that diesel leakage would be frozen into sea ice, providing a new oil spill during spring and the associated ice melt and rising biological activity in the area. Bellona was concerned about birds, walrus and polar bears since these are “most threatened by oil spills”. The ship owner was in meetings in Longyearbyen with The Norwegian Coastal Administration and the Coastguard to ensure that details regarding the vessel were communicated to optimize the ship rescue operation. No concerns were raised about primary- and secondary producers.

2 January 2019*: The ship stranded when sea ice cover was low, but emerging ice was approaching the vessel. Meanwhile, politicians in Oslo started to ask questions since shrimp trawling is permitted in waters adjacent to the Northguider accident site year-round. In addition to being remote, some of these waters are also situated in Svalbard’s nature reserves. Questions about the safety of fishing in these areas, far away from harbours and SAR facilities, have received new attention after this incident.

6-10 January 2019*: Coastguard vessel KV *Svalbard* had left the Northguider site, steaming towards Longyearbyen after finalizing the mission with the Dutch rescue company Ardent Global (hired by the ship owner) to map the state of the vessel and to gather data to plan for the removal of the vessel from the area. KV Svalbard came to Longyearbyen Sunday night 6 January 2019 for further planning. Items from Northguider that could have polluted the area, such as paint, chemicals, ropes, fishing gear (nets), batteries etc., had been successfully removed. Outlet points for recovery of diesel had been cleared and made ready for pumping. A new geo-positioning sensor had been placed on Northguider. There were concerns that KV *Svalbard* did not have the capacity to pump up all available diesel from Northguider. KV *Svalbard* returned to the Northguider site Thursday 10 January, waiting for better weather to board the stranded ship.

13 January 2019*: *Northguider* was successfully emptied for 332 metric tonnes of diesel. No pollution into the environment was detected. For the operation, KV Svalbard was equipped with smaller boats, extra oil tanks, hoses, pumps and special equipment for transferring the diesel. The recovery was carried out using manual pumping of diesel into 1000-L plastic tanks followed by subsequent use of small boats to load the diesel onto KV Svalbard. KV Svalbard had the capacity to load 600 000 liters (600 plastic tanks) onboard. During the oil rescue, 65-70 persons were involved, and the operation was performed in calm weather. Sea ice and slush was developing around Northguider during the operation. After diesel extraction had been successfully conducted, the next step was to extract engine oil and plastics. The final step was removal of the vessel – a step that at the time of writing still has not been performed.

15 January 2019*: Ship owner tells the media that they will proceed with shrimp trawling in the Svalbard area, including Hinlopen , which gives rise to several questions:

1. Can these fishing activities in these area be considered safe?
2. What is the associated cost for society?
3. Do we have the necessary infrastructure to carry out rescue and monitoring operations?
4. Svalbard is a highly productive area for marine life – should fisheries and other industry have the right to operate in protected areas such as nature reserves?

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*Media publication date and sources

28, 30 and 31 December 2018: Norwegian Broadcasting Corporation (NRK, Nyheter), Troms
2 January 2019: Spitsbergen-Svalbard.com
6-10 January 2019: Newspaper “Vesterålen”
13 January 2019: NRK Troms
15 January 2019: Teknisk Ukeblad

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Chapter 11

Life and light at the dead of night

Jørgen Berge and Geir Johnsen

Abstract

The Polar Night has a unique beauty. The aurora borealis, the moonlight, the faint glow of the sun behind white mountains, and, not the least, the mysteries of the living creatures that we have found in the Polar Night. This, in addition to the many scientific discoveries that have radically changed our perception of what the Polar Night is, inspired us to make an exhibition aimed at the general public. It opened at *Polarmuseet* in Tromsø in January 2015 with the title "Life and light in the dead of night", and was our attempt to communicate not only the surprising discoveries we had made regarding organisms and processes that govern the high Arctic Polar Night, but in essence also how important light is as a cue for all life, even in the dead of the Polar Night. Since its opening in Tromsø, the exhibition has been at display (Fig. 11.l) at several museums and cities in the US (Washington, Anchorage, Boston and Delaware), Canada (Ottawa, St. Johns), Russia (Russian translated version in Moscow and St. Petersburg) and Norway (Tromsø, Longyearbyen and Trondheim). Here we present the 27 original posters that is the backbone of the exhibition. The text accompanied each figure is not updated and may in some cases not fully describe current status of knowledge. Yet, the texts and figures still represent key aspects, important discoveries and the breadth of marine life in the dark Polar Night.

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11.1 Introduction

The famous Norwegian explorer and scientist Fridtjof Nansen had ample opportunities to familiarize himself with the Polar Night during his famous ski-trip with Hjalmar Johansen from the MS *Fram* trying to reach the North Pole, but was forced by bad ice condition to overwinter at Franz Josef Land in 1895-6. He was obviously taken by the grandeur, hardship and beauty, and compared the Polar Night with a "marvelously lovely woman" (Figure 11.9). We were taken by the same beauty during our expeditions into the Polar Night, although the hardship and basic conditions endured by Nansen can hardly be compared with the luxury offered to researchers onboard modern research vessels and comfortable research stations. But the Polar Night is not only a lovely woman, she is also most mysterious and full of secrets. The Polar Night exhibition had as its main objective to present some of these mysteries – through recent scientific discoveries that have changed the way we look upon seasonality and the role of the Polar Night in high Arctic marine ecosystems. Arguably, these discoveries were phenomenological, rather than process oriented. This, however, is what make the presented material still relevant, even though we now know much more about how e.g. moonlight a regulating factor for diel vertical migration of zooplankton.

Fig 11.1 Rector Anne Husebekk (UiT) and HM Kong Harald of Norway opens the Polar

The Polar Night of the high arctic is most commonly conceived as a period when marine organisms reduce their activity levels commensurate with a primary production close to zero. Food web interactions and metabolic rates are thought to be at a minimum pending the return of the sun. This exhibition presented new and compelling evidence of a system that is rather characterized by high activity and strong interactions, from the sea-surface, to the water-column and at the seafloor. In contrast to a system that has entered a state of rest, we documented a system in which there is an end-to-end high production and turnover. Ultimately, this new understanding of life in the Arctic oceans during the Polar Night will have strong implications both for our perception of high latitude ecosystems and for development of management- and decision strategies for an area of the world receiving increasing economic and political attention. The complex interactions between the biosphere, hydrosphere and cryosphere are central, yet poorly understood, features of the Arctic Ocean. Variability or change in one or more of these systems may lead to disproportionally large changes in the ecosystem. The rapid warming of the Arctic and loss of sea ice are two well-known examples of such a phenomenon, with the potential to affect most living organisms in the region, and, in fact, in ecosystems throughout the world. Spatial and temporal changes in critical ecosystem processes, such as primary productivity, can alter pelagic community structure and function, with potential consequences for such ecosystem services as fisheries harvests and sequestration of atmospheric carbon in the deep-sea. However, such ecosystem effects resulting from climate change have been considered primarily from the perspective of the polar summer, while the polar winter has essentially remained a black box – a box that is rarely considered and less frequently opened. These posters will, hopefully, still make the reader curious and stop a little and wonder about things we do not know.

11.2 Overview of posters

Figure 11.2. Front cover of exhibition
Figure 11.3. The Polar Night project
Figure 11.4. "Somewhere, something incredible is waiting to be known"
Figure 11.5. Polar Night
Figure 11.6. The Polar Night in Svalbard
Figure 11.7. Light in the dark
Figure 11.8. Are you scared of the dark, lad?
Figure 11.9. Fridtjof Nansen in the Polar Night
Figure 11.10. Planktonic algae – everywhere, always
Figure 11.11. Krill – the marine potato
Figure 11.12. *Calanus* – the happy pill of the sea
Figure 11.13. Arctic kelp – the energy savers
Figure 11.14. Polar cod – the Barbie of the sea
Figure 11.15. Common whelk – the master of the packed lunch
Figure 11.16. Skeleton shrimp – picking up partners in the night
Figure 11.17. When the nights are long (and lust is great)
Figure 11.18. Milky seas effect
Figure 11.19. Upside down sea
Figure 11.20. Trickster light
Figure 11.21. Svalbard rock ptarmigan – the stayer
Figure 11.22. Black and Brünnich's guillemots – the food seekers
Figure 11.23. The little auk – the chatterbox
Figure 11.24. Ups and downs all year round
Figure 11.25. Moonlight
Figure 11.26. Climate change in the Arctic
Figure 11.27. Sea ice and light
Figure 11.28. Disaster in the darkness
Figure 11.29. The robots of the sea

Night exhibition in Anchorage, Alaska in May 2015. Photo: J. Berge

THE POLAR MUSEUM, TROMSØ, ARCTIC NORWAY

POLAR NIGHT

Life and light in the dead of night

ПОЛЯРНАЯ НОЧЬ жизнь и свет в темноте ночи


POLHAVET
NORSKEBANKEN
Hinlopenrenna
Kvitøya
Kræmerpynten
Kvitøyjøkulen
Hornodden
Andréeneset
80°N
79°N
78°N
77°N
76°N
Vesle Tavleøya
Phippsøya
Sjuøyane
Martensøya
Parryøya
Waldenøya
Karl XII-øya
Foynøya
Repøyane
Kapp Platen
Nordkapp
Castrénøyane
Kapp Wrede
Nordenskiöld-bukta
Platenhalvøya
PRINS OSCARS LAND
Glenhalvøya
Bergströmodden
Kapp Bruun
Kapp Leigh Smith
Storøya
Kapp Laura
Sørodden
Purchasneset
Lågøya
Franklinsundet
Langgrunnodden
Duvefjorden
ORVIN LAND
GUSTAV V LAND
Vestfonna
NORDAUSTLANDET
AUSTFONNA
Italiaodden
Isispynten
Helvetesflya
Oxfordhalvøya
Etonbreen
Wahlenbergfjorden
Hartogbukta
GUSTAV ADOLF LAND
Vegafonna
Svartknausflya
Vibebukta
Bråsvellbreen
Kapp Mohn
Murchisonfjorden
Verlegenhuken
Mosselhalvøya
Sparreneset
Velkomstpynten
Bangenhuk
Nordvestøyane
Fuglesongen
Amsterdamøya
Smeerenburg
Danskøya
Biscayarhuken
Reinsdyrflya
Grähuken
Andøyane
Woodfjorden
Wijdefjorden
NY FRIESLAND
Åsgardfonna
Valhallfonna
HINLOPENSTRETET
Lomfjorden
Lomfjordhalvøya
Hoelhalvøya
ALBERT I LAND
HAAKON VII LAND
ANDRÉE LAND
SJUBREBANKEN
Mitrahalvøya
Kapp Mitra
Kapp Guissez
Kongsfjordrenna
Kvadehuken
Fuglehuken
Barentsjellet
Ny-Ålesund
Brøggerhalvøya
Kongsfjorden
Kronebreen
JAMES I LAND
OSCAR II LAND
DICKSON LAND
Pyramiden
BUNSOWS LAND
PRINS KARLS FORLAND
Forlandsundet
Dawespynten
St. Jonsfjorden
Kaldneset
Haukebukta
Forlandsøyane
Salpynten
ISFJORDRENNA
ISFJORDEN
Daudmannsodden
Kapp Linné
Nordfjorden
Kapp Thordsen
Bohemanneset
Diabasodden
Sassenfjorden
Hiorthhamn
Longyearbyen
Hotellneset
Flytangen
Grumantbyen
Heerodden
Barentsburg
Grønfjorden
NORDENSKIÖLD LAND
SABINE LAND
Nordmannsfonna
Dunérbukta
Hellefonna
Storfjorden
Wilhelmøya
Langeøya
Bastianøyane
Kiepertøya
Rønnbeckøyane
Kapp Payer
OLAV V LAND
Vaigattbogen
Vaigattøyane
Von Otterøya
Sørporten
Negribreen
Edlundfjellet
Ginevrabotnen
Kapp Antinori
Mistakodden
Bakanbukta
Heleysundet
Freemansundet
BARENTSØYA
Barentsjøkulen
Kapp Heuglin
Kapp Pechuel-Lösche
Blåbukta
Kapp Lee
Barkhamodden
Blankodden
Kapp Dufferin
Revnosa
Diskobukta
Raddeletta
EDGEØYA
Stonebreen
St. Jakobsbukta
Ryke Yseøyane
Russebukta
Kvalpynten
Tjuvfjorden
Tjuvfjordlaguna
Stones Forland
Dianabukta
Halvmåneøya
Kong Ludvigøyane
Bölscheøya
Negerpynten
Menkeøyane
Meinickeøyane
Tusenøyane
Brækmoholmane
Tiholmane
Kuststadholmane
Høya
ERIK ERIKSENSTRETET
KONG KARLS LAND
Abeløya
Kongsøya
Nordneset
Nordaustpynten
Bünsowbukta
Breibukta
Tømmerneset
Kennedyneset
Helgolandøya
Kapp Altmann
Tirpitzøya
Arnesenodden
Rivalensundet
Svenskøya
Kapp Weissenfels
Kapp Hammerfest
OLGASTRETET
BARENTS-HAVET
ISFJORDBANKEN
Nordenskiöldkysten
Lågneset
Kapp Martin
Bellsund
Kapp Lyell
Van Mijenfjorden
Akseløya
Midterhuken
NATHORST LAND
HEER LAND
Van Keulenfjorden
Dunderbukta
WEDEL JARLSBERG LAND
TORELL LAND
Storvika
BELLSUNDBANKEN
Kapp Borthen
Isøyane
Dunøyane
Hornsund
Hornsundneset
HORNSUNDBANKEN
Hambergbukta
SØRKAPP LAND
Isbukta
Stormbukta
Sørkappfonna
Øyrlandet
Øyrlandsodden
Sørneset
Sørkappøya
Sørkapp
SØRKAPPBANKEN
STORFJORDRENNA
STORFJORDBANKEN
Hopen
Beisaren
Kapp Thor
HOPENBANKEN
STORFJORDEN

The Polar Night Project

The fieldwork for the Polarnight project is taking place in three different locations at Svalbard: Lonyearbyen, Ny Ålesund and Rijpfjorden.
Polar Night was produced by The Polar Museum – Tromsø University Museum in collaboration with the Department of Arctic and Marine Biology, UNIS, NTNU and Akvaplan-niva.
The exhibition is based on the research project
Mare incognitum – ecological processes during the polar night.

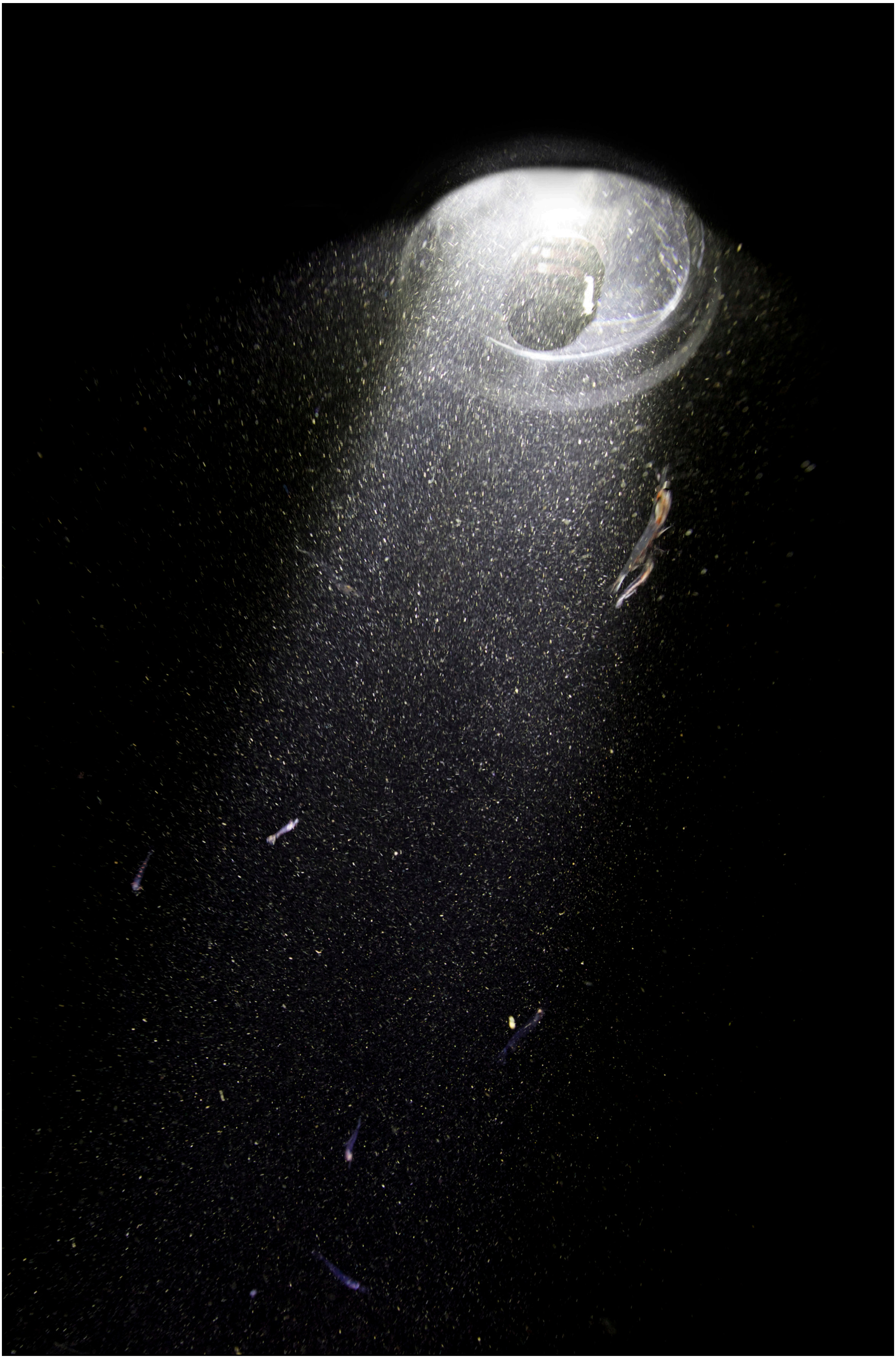
PROJECT MANAGER: Jørgen Berge, UiT The Arctic University of Norway (Department of Arctic and Marine Biology) and the University Centre in Svalbard (UNIS).
SUBJECT COORDINATOR AND PHOTOS: Geir Johnsen, Norwegian University of Science and Technology (Department of Biology) and the University Centre in Svalbard, and Anne Helene Tandberg, University Centre in Svalbard
PRODUCER: Lena Aarekol, The Polar Museum – Tromsø University Museum
TEXT: Jørgen Berge, Geir Johnsen, Anne Helene Tandberg, Lena Aarekol, Marit Anne Hauan and Eva Therese Jenssen
PRODUCTION ASSISTANT: Therese Marienborg Lindseth – The Polar Museum – Tromsø University Museum
DESIGN: Reibo
CARPENTER: Willy K. Sørensen, The Polar Museum – Tromsø University Museum
PRINT: Ernst Høgtun, Tromsø University Museum
ENGLISH TRANSLATION: Gavin Tanguay
FILM: Original Film – talking heads; Robert Staven – Swimming Brünnich's guillemots and underwater film; Reibo – time-lapse films
PREPARATION OF BIRD SKINS: Håkon Dahl & Tino Schott, Tromsø University Museum
TECHNICAL ASSISTANCE: Nina Kronstad & Sebastian Arumainayagam
OTHER PHOTOS: Joan Costa, Jonas Thormar, Peter Leopold, Norwegian Army Press Office
THANKS TO: Akvaplan Niva, NTNU, UNIS, Tromsø Museum - Universitetsmuseet
THE EXHIBITION IS FINANCED BY: The Polar Museum, Tromsø University Museum, the project ”*Mare incognitum – ecological processes during the polar night*” by UiT, UNIS NTNU & Akvaplan Niva

This is the fourth exhibition in a series by the Polar Museum that conveys new research in the north performed by UiT - The Arctic University of Norway.

Проект Полярная ночь

Полевые исследования по проекту Полярная ночь выполняются в трех районах архипелага Шпицбергена: Лонгиербюен, Ню-Олесунн и Рийпфьорд
Выставка ПОЛЯРНАЯ НОЧЬ подготовлена Полярным музеем Университета Тромсе – Арктического университета Норвегии (UIT) в сотрудничестве с кафедрой морской и арктической биологии факультета биологических наук, рыболовства и экономики университета, Университетским центром на Свальбарде (UNIS), Норвежеским университетом науки и технологии (NTNU) и АО Акваплан-нива по результатам научного проекта
«**Mare incognitum – экологические процессы в период полярной ночи**»

Руководитель проекта: Йорген Берге, профессор факультета биологических наук, рыболовства и экономики Университета Тромсе – Арктического университета Норвегии и Университетского Центра на Свальбарде
Координаторы проекта и авторы фотографий: Гейр Йонсен, профессор факультета биологии Норвежского университета науки и технологии и Университетского центра на Свальбарде; Анне Хелене Тандберг, Университетский центр на Свальбарде
Продюсер: Лена Орекол, Полярный музей Университета Тромсе – Арктического университета Норвегии
Текст: Йорген Берге, Гейр Йонсен, Анне Хелене Тандберг, Лена Орекол, Марит Анне Хауан и Эва Терезе Йенссен
Помощник постановщика: Терезе Мариенборг Линсет, Полярный музей Университета Тромсе – Арктического университета Норвегии
Дизайн: Рейбо
Фильм: оригинальный фильм «Говорящие головы» фильм «Ошибка времени» Рейбо
Роберт Ставен - подводные съемки и плавающая толстоклювая кайра
Фотографии: Джоан Коста, Йонас Турмар, Петер Леопольд, Пресс-офис норвежской армии
Благодарность: Норвежскому университету науки и технологии, АО Акваплан-нива, Университетскому центру на Свальбарде и Тромсе - музею Университета Тромсе – Арктического университета Норвегии
Финансирование: Университет Тромсе - Арктический Университет Норвегии, проект
«Mare incognitum – экологические процессы в период полярной ночи»



“Somewhere, something incredible is waiting to be known”

- Carl Sagan

Research likes to border on what we know and test the unknown.
Who knows what we’ll find?

The ocean and darkness bear secrets and can seem intimidating to humans. What and who is hiding in the wet, cold, dark and deep ocean that has long been almost inaccessible? Even now, it remains hard to carry out research at great depths or in the dark. In the polar night, the ocean is a complex but important sphere in which to perform research! We can use the knowledge from the waters around Svalbard to understand more about life in the Arctic in the bright parts of the year, and to understand processes in the eternal darkness of the deep ocean. We already know that we need to understand the secrets that lie deep in the sea. Research in the polar night requires the use of new enabling technology. We can now send autonomous robots and sensors down into the unknown darkness of the ocean.

In many ways they resemble small spaceships. Back on land, we can sit in the control room and download images and data of unknown organisms and how they are affected by the environment.

We still don’t know what we will find in the polar night, but we are starting to learn. Join us on a journey down into the dark depths of the ocean and see what we have learned so far!

«Что-то, совершенно невероятное ждет своего открытия»

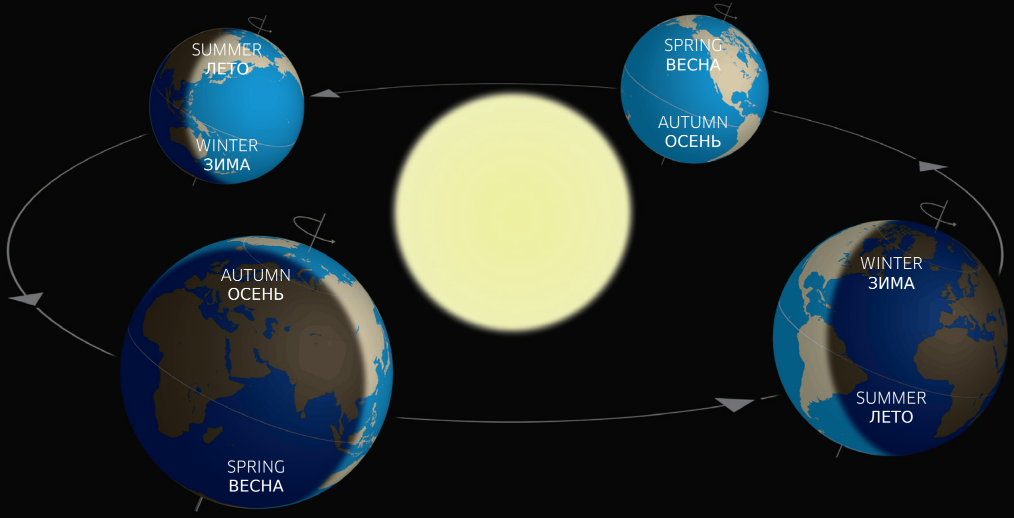
- Карл Саган

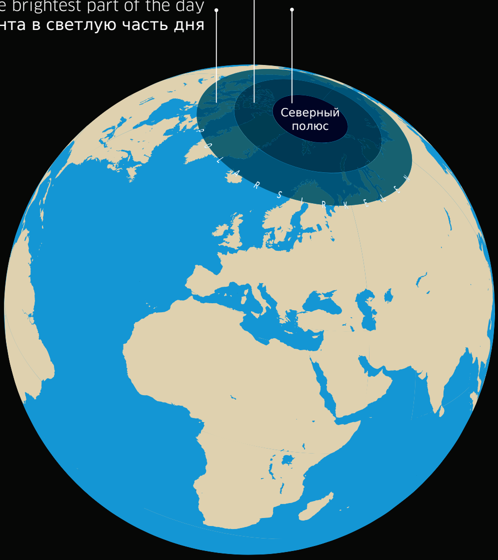
Наука исследует границы познания и неопознанное.
Кто знает, какие еще открытия нас ждут?

Океан и темнота таят в себе множество тайн, зачастую пугающих нас. Кто и что спрятано в холодных и темых океанских глубинах, которые долгое время были недосягаемы? Даже сейчас здесь сложно проводить исследования и, особенно, в темное время года. Океан во время полярной ночи - это очень сложная, но важная область для исследований. Мы можем использовать знания о жизни в водах Шпицбергена для понимания жизни в Арктике в светлое время года и процессов, происходящих в темных и глубинных водах океана. Очевидно, что мы должны открыть секреты, спрятанные в глубине океана.

Исследования полярной ночи требуют использования новых технологий. Сейчас мы можем использовать автономных робот и сенсоров для работ в неизведанных темных глубинах океана. Во многом это оборудование напоминает миниатюрные космические аппараты. Ученые, находясь в своих лабораториях, могут получать информацию из глубин и, разгадывая полученные изображения неизвестных организмов, оценивать влияние среды.

Мы по-прежнему не знаем, что мы найдем в полярной ночи, но мы начали изучение. Будь с нами в этом путешествии в темные глубины океана и узнай то, что нам удалось выяснить к настоящему времени!





POLAR NIGHT / **ПОЛЯРНАЯ НОЧЬ:**

Sun more than 6 ° below the horizon brightest part of the day
СОЛНЦЕ БОЛЕЕ, ЧЕМ НА 6° НИЖЕ ГОРИЗОНТА В СВЕТЛУЮ ЧАСТЬ ДНЯ

The sun more than 12 ° below horizon brightest part of the day
Солнце более, чем на 12° ниже горизонта в светлую часть дня

WINTER DARKNESS / **ЗИМНЯЯ ТЬМА:**
The sun below the horizon at the brightest part of the day
Солнце ниже горизонта в светлую часть дня

Ill: Reibo

Polar night

The polar night is the period of year when the sun is below the horizon all day. The earth completes one revolution around the sun per year. Simultaneously, the earth spins around its own axis once every 24 hours, which gives us night and day. If the earth's waxis had been at the same angle as the sun, days and nights would all be the same length throughout the year and everywhere on earth. We wouldn't have seasons either. But the earth's axis tilts slightly to the side. During the revolution of the sun, the earth's axis points in the same direction throughout the year. In this way, the North Pole points towards the sun in summer and away from the sun in winter. Consequently, north of the Arctic Circle, we get the polar night in winter and the midnight sun with its bright nights in summer.

The further north you go, the longer and darker the polar night is.

Полярная ночь

Полярная ночь – это период года, когда солнце находится за горизонтом весь день. Земля совершает полный оборот вокруг Солнца за год. Одновременно она вращается вокруг своей оси, совершая полный оборот за 24 часа. Из-за этого вращения происходит смена дня и ночи. Если бы земная ось была перпендикулярна плоскости вращения Земли вокруг Солнца, то дни и ночи были бы одинаковой длины в течение всего года, не было бы и смены сезонов. Но, на протяжении всего времени движения Земли вокруг Солнца, ось её вращения постоянно сохраняет одно и то же положение по отношению к плоскости земной орбиты — она наклонена к ней под некоторым углом.

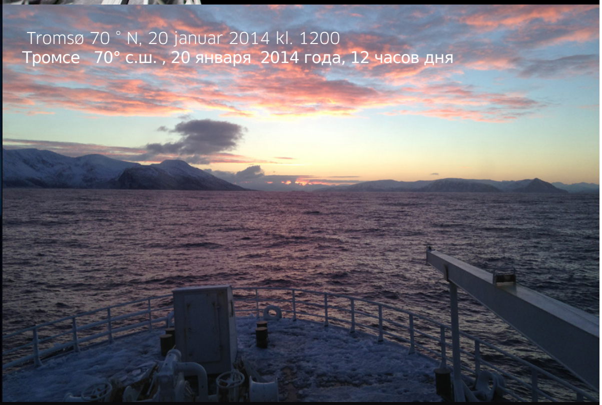
Когда на северное полушарие приходит больше тепла и света, дни здесь более продолжительны, наступает лето, в то время как в южное полушарие приходит зима. Когда же у нас наступает зима, в южном полушарии начинается лето. Так происходит смена времён года. Зимой, к северу от полярного круга наступает полярная ночь, а летом - полярный день, с незаходящим солнцем.

Чем дальше на север, тем длиннее полярная ночь.

Rijpfjorden 81 ° N, 13 januar 2014 kl. 1200
Рийпфьорд 81° с.ш. , 13 января 2014 года , 12 часов дня

Ny Ålesund 79 ° N, 15 januar 2014 kl. 1200
Ню -Олесунн 79° с.ш. , 15 января 2014 года, 12 часов дня

Bjørnøya 76 ° N, 19 januar 2014 kl. 1200
Остров Медвежий 76° с.ш. , 19 января 2014 года, 12 часов дня



Tromsø 70 ° N, 20 januar 2014 kl. 1200
Тромсе 70° с.ш. , 20 января 2014 года, 12 часов дня

Light levels as seen by the human eye during the polar night at 81° North. All pictures were taken onboard the RV Helmer Hanssen at local sun noon within one week in January 2014

Восприятие человеческим глазом света в период полной полярной ночи на 80 ° с.ш. Все фотографии сделаны с борта научно-исследовательского судна «Helmer Hanssen» в самое светлое время дня в течение одной недели в январе 2014 года.

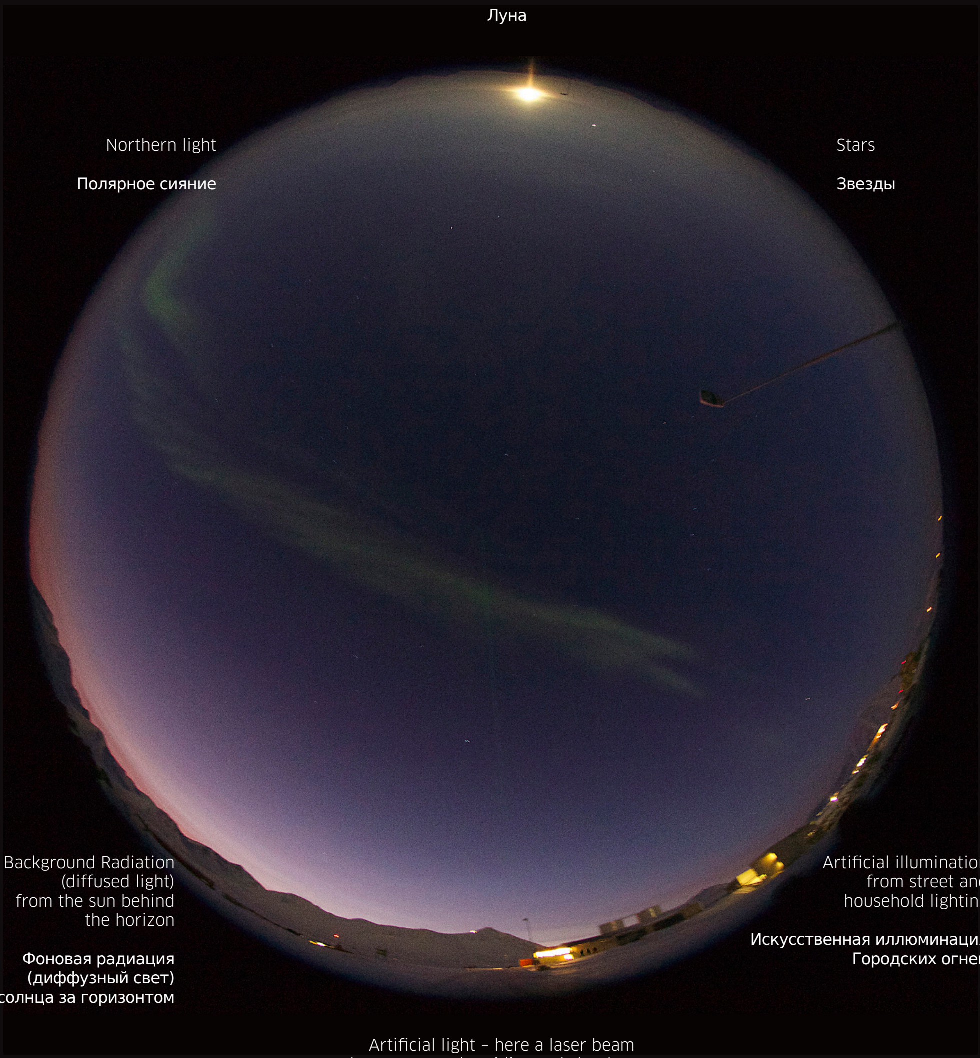
Photo: Geir Johnsen, NTNU

The Polar night in Svalbard

In Tromsø, the polar night only lasts from 21 November to 20 January. In the middle of the day the sun is just below the horizon and the sky is still light despite the fact that the city lies in the shadow of the sun. This is known as polar twilight. Further north, in Longyearbyen on Svalbard, the sun is below the horizon for four months from 26 October to 20 February. The first rays of the sun don't hit Longyearbyen until 8 March. Here, the polar twilight becomes a true polar night. However, even in Longyearbyen, it's possible to catch a glimpse of light in the middle of the day. Even further north, at approx. 80 ° N (in Rijpfjorden), the sun is more than 12 ° below the horizon and there is continual darkness in the polar night.

Полярная ночь на Свальбарде

В Тромсе полярная ночь длится только с 21 ноября до 20 января. В середине дня, когда солнце ниже горизонта, небо светлеет несмотря на то, что прямой солнечный свет не достигает города. Это явление называется полярные сумерки. Севернее, в городе Лонгиербюен на Свальбарде, солнце находится ниже горизонта в течение четырех месяцев – с 26 октября до 20 февраля, и только 8 марта в городе можно наблюдать первые лучи солнца. Здесь и полярные сумерки превращаются в настоящую полярную ночь. Однако, даже в Лонгиербюен можно увидеть иногда проблески света в середине дня. Далее на север, приблизительно на 80° с.ш. (Риийпфьорд), солнце находится ниже 12° за горизонтом; здесь настоящая нескончаемая полярная ночь.



Moonshine

Луна

Northern light

Полярное сияние

Stars

Звезды

Background Radiation
(diffused light)
from the sun behind
the horizon

Фоновая радиация
(диффузный свет)
От солнца за горизонтом

Artificial illumination
from street and
household lighting

Искусственная иллюминация
Городских огней

Artificial light – here a laser beam
that measures humidity and cloud cover

Искусственный свет – лазерный луч для
Измерения влажности и облачности

Photo: Geir Johnsen, NTNU

Light in the dark

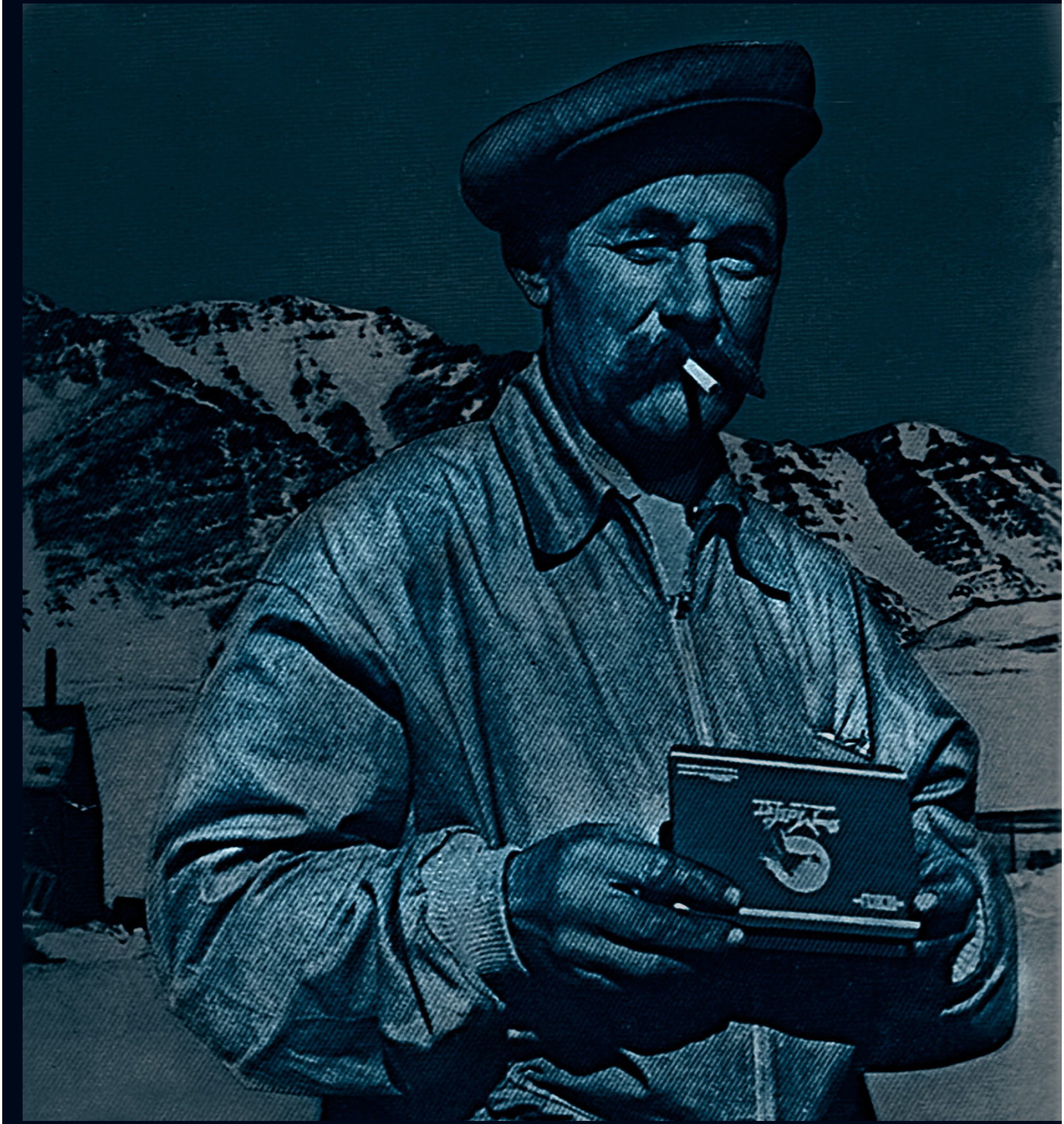
In areas not affected by artificial light from human activity, the polar night is so dark that even the smallest light sources are very visible. The twilight in the middle of the day seems bright, and the moon can shine so brightly that everything casts a shadow! In addition, the northern lights (*aurora borealis*) are not only beautiful, but also a source of light for marine organisms.

The research stations in Ny-Ålesund on Svalbard constitute a small village, and the light from there is visible from a long distance in the polar night. Near the houses you can see how the light from the lamps reaches far into the darkness. While in Rijpfjorden, where no one lives, the moon and the northern light are the only sources of light in the middle of winter. This makes Rijpfjorden an ideal place to measure the activity of marine animals and algae in the polar night.

нoтe

В районах, куда не достигает искусственный свет от человеческой деятельности, полярная ночь настолько темна, что виден даже небольшой источник света. Полуденные сумерки кажутся светлее, лунный свет настолько ярок, что все предметы отбрасывают тени. В дополнение ко всему, полярное сияние не только красиво, но оно еще является источником света для морских организмов.

Научные станции в Ню-Олессунне представляют собой небольшие поселения, свет от которых в полярную ночь виден на большом расстоянии. Вблизи домов можно видеть, как свет от ламп проникает далеко в темноту. В то время как в необитаемом Рийпфьорде единственный источник света зимой – это Луна и полярное сияние. Это делает его идеальным местом для исследования активности морских организмов во время полярной ночи.



From the book "*Henry Rudi. Isbjørnkongen*" by Lars Normann Sørensen

Are you scared of the dark, lad?

This was the first question expedition leader August Olafsson asked Henry Rudi when he applied to be part of the team of trappers that was going to Hopen. Henry Rudi was alone at a trapper's station in winter 1958. He described the darkness as follows:
"And then the day is put out for good. The black sky covers a sun drowning in blood and blue and green. The polar night plays down over me with cold breath, the cold breath of death. And the silence whispers in my ears."
(Henry Rudi, Isbjørnkongen, 1958, p. 40)

When the polar night ended, he wrote: *"Finally the night was gone, the day was complete and the land glowed."*

During overwintering expeditions to Svalbard, the trappers have really felt the polar night. Descriptions of the darkness are a recurring theme in many of the accounts of these expeditions.

On Wednesday 26 December 1934 Wanny Woldstad wrote the following entry in her diary: *"A little wind from the east and minus 3. We have been at home because it is the weekend. The rain has washed the snow away and we now have an icy surface. Heavy storm clouds. Extremely dark."*

Ты боишься темноты, парень?

Это был первый вопрос, который руководитель экспедиции Август Улафсон задал Генри Руди, который хотел участвовать в группе охотников, отправляющихся к Хопету. Генри Руди остался один на охотничьем зимовье зимой 1958 года. Он описывал темноту следующими словами: *«когда заканчивался день, чернота укрывала солнце, тонущее в багряных, голубых и синих небесах. Полярная ночь была вокруг меня с ее холодным дыханием, смертельно холодным дыханием. И тишина шептала мне в уши,»*
(Генри Руди. Король белых медведей.1958. С.40).

Когда закончилась полярная ночь, он написал : *«наконец-то отступила темнота и наступил полный день, все светилось вокруг.»*

Во время зимовок охотники ощущали всю полноту полярной ночи и возвращались к этой теме в своих дневниковых записях. В среду, 24 декабря 1934 года первая женщина-охотник, зимовавшая на Свальбарде, Ванни Вольстад писала: *«небольшой ветерок с востока, -3 ˚ С. Дождь смыл снег и вокруг голый лед. Тяжелые штормовые облака и полная темнота.»*

“In the winter night”, drawing by Fritjof Nansen

Fridtjof Nansen in the polar night

Frozen into the ice on board Fram, Fridtjof Nansen described the polar night as such:

"… But, O Arctic night, thou art like a woman, a marvellously lovely woman. Thine are the noble, pure outlines of antique beauty, with its marble coldness. On thy high, smooth brow, clear with the clearness of ether, is no trace of compassion for the little sufferings of despised humanity; on thy pale, beautiful cheek no blush of feeling. Among thy raven locks, waving out into space, the hoar-frost has sprinkled its glittering crystals. The proud lines of thy throat, thy shoulders' curves, are so noble, but, oh! unbendingly cold; thy bosom's white chastity is feelingless as the snowy ice. Chaste, beautiful, and proud, thou floatest through ether over the frozen sea, thy glittering garment, woven of aurora beams, covering the vault of heaven. But sometimes I divine a twitch of pain on thy lips, and endless sadness dreams in thy dark eye. Oh, how tired I am of thy cold beauty! I long to return to life. Let me get home again, as conqueror or as beggar; what does that matter? Bet let me get home again to begin life anew."

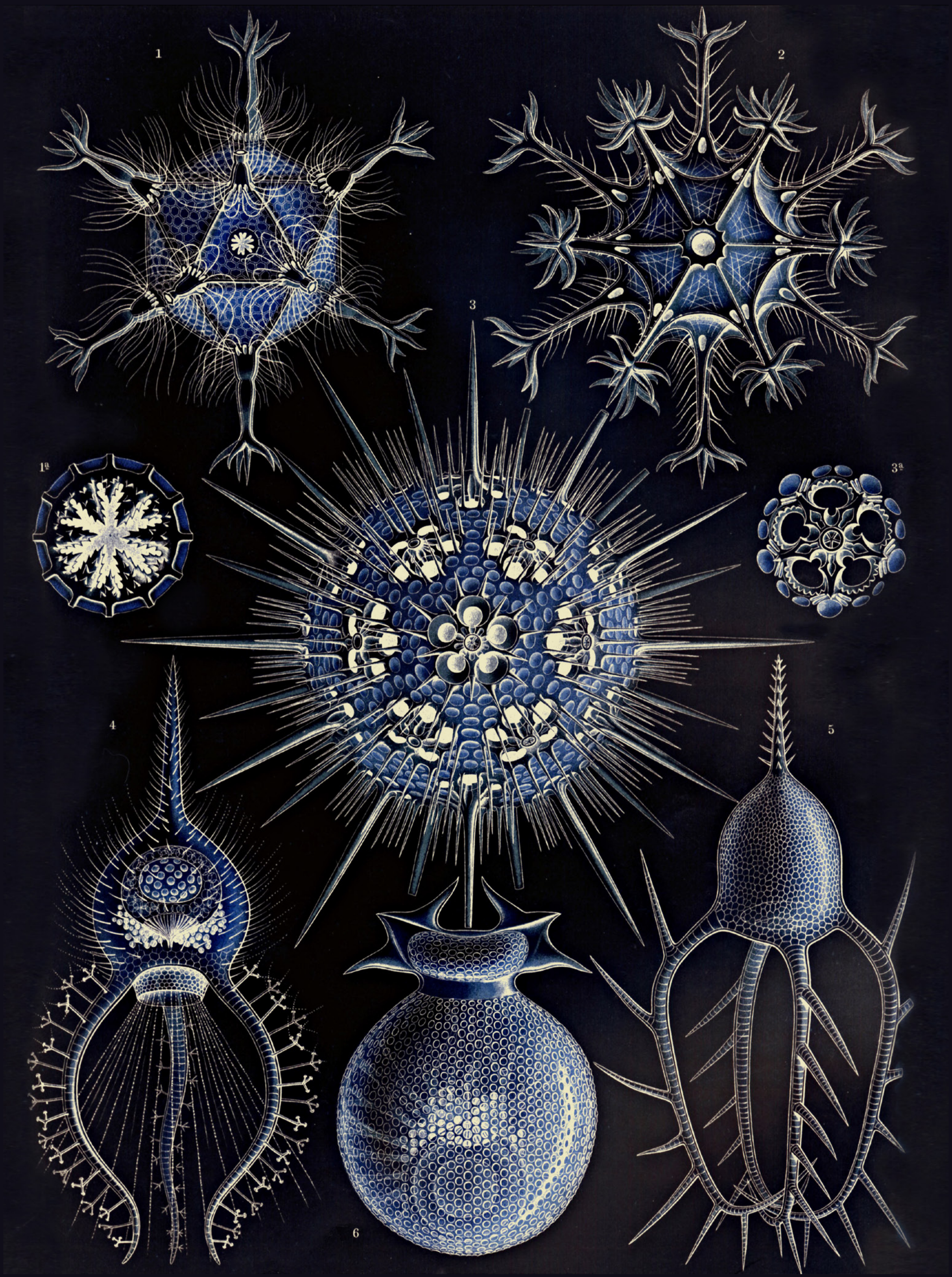
Fridtjof Nansen, Farthest north: being the record of a voyage of exploration of the ship Fram 1893-96 and of a fifteen months' sleigh journey, 1904, London, Archibald Constable and co. ltd., p 183-184

ьоф Нансен и полярная ночь

Находясь на борту «фрама», вмерзшего во льды, фритьоф нансен так описывал полярную ночь:

«…Полярная ночь, ты похожа на женщину, пленительно прекрасную женщину с благородными чертами античной статуи, но и с ее мраморной холодностью. На твоем высоком челе, ясном и чистом, как небесный эфир, ни тени сострадания к мелким горестям человечества, на твоих бледных прелестных щеках не зардеет румянец чувств. В твои черные, как смоль, волосы, развевающиеся в пространстве по ветру, вплел свои сверкающие кристаллы иней. Строгие линии твоей горделивой шеи, твоих округлых плеч так благородны, но, увы, какой в них непреклонный холод. В целомудрии твоей белоснежной груди – бесчувственность льда, покрытого снегом. Непорочная, прекрасная, как мрамор, гордая, паришь ты над замерзшим морем; сверкающее серебром покрывало на твоих плечах, сотканное из лучей северного сияния, развевается по темному небосводу. И все же порою чудится скорбная складка у твоих уст и бесконечная печаль в глубине твоих темных глаз. Быть может, и тебе тоже знакома жизнь, жаркая любовь южного солнца? Или это отражение моего собственного томления? Да, я устал от твоей холодной красоты, я стосковался по жизни, горячей, кипучей! Позволь мне вернуться либо победителем, либо нищим, для меня все равно!
Но позволь мне вернуться и снова начать жить,»

(Фритьоф нансен. Фрам в полярном море. Глава 7.)



Ernst Haeckel (Plate 1 from Kunstformen der Natur (1904)

Plankton algae – everywhere, always

Most zooplankton species and many fish species feed on plankton algae and, as such, it forms the foundation for all life we observe in the winter darkness. For a long time, scientists thought there were no plankton algae in the water column for the duration of the polar night. We thought that a few plankton algae rested on the ocean floor or that they did not exist at all in the coldest bodies of waters when there was no sunlight, which they need for photosynthesis.

This research project has demonstrated that there are plankton algae in the water columns throughout the polar night, although there are a lot fewer of them than at other times of the year. Some of these plankton algae are in “hibernation”, but others are mixotrophs (they acquire energy in the same way as both animals and plants) and don’t depend on photosynthesis through the winter in order to survive.

Фитопланктон - всегда и везде

Многие виды зоопланктона и рыб питаются фитопланктоном, таким образом, эти микроводоросли формируют основу жизни, которую мы можем наблюдать в полярной тьме. Долгое время ученые считали, что в период полярной ночи в толще вод нет фитопланктона. Мы думали, что некоторые его виды зимой покоятся на дне и не могут быть в толще холодных вод, куда не проникает свет, необходимый для фотосинтеза.

Результаты исследований показали, что в толще вод во время полярной ночи есть фитопланктон, хотя и в меньшем количестве, чем в другое время года. Одни виды находятся как бы в «зимней спячке», но другие, миксотрофы, в зимний период способны получать энергию для жизни другими путями, и не зависеть от фотосинтеза.

Photo: Geir Johnsen, NTNU

Krill – the marine potato

Krill (*Euphausiacea*) is an ancient group of crustaceans that has existed for 130 million years. It can be found in all the world's oceans. Antarctic krill are mainly algae eaters and feed on the algae blooms in the upper water column. However, in the Arctic, krill feed on everything from small single-celled algae to "larger" crustaceans. Krill are an important food source in the ocean for larger animals – from birds and fish to whales. In Japan, krill – okiami – is also consumed by humans and is fished commercially. Most krill species live near the ocean surface at night and hide in the dark depths by day. This movement is known as vertical migration. We know little about how the Arctic krill lives in the winter. But our measurements show there are many of them some years and virtually none at all other years.

Криль - хлеб океана

Криль (*Euphausiacea*) - группа мелких морских ракообразных, существует 130 миллионов лет и обитает во всех районах Мирового океана. Антарктический криль, главным образом, питается микроводорослями во время их цветения в верхних слоях водной толщи. Однако в Арктике, криль питается всем – от маленьких одноклеточных водорослей до «больших» ракообразных. Криль является важным пищевым объектом для многих морских животных: от птиц и рыб, до китов. В Японии криль – окиами используется в качестве продукта питания и добывается в промышленных масштабах. Криль большинства видов ночью скапливается у поверхности, а днем прячется в темных глубинах океана. Эти передвижения называются вертикальными миграциями. Мы мало знаем о жизни криля в зимний период. Но наши исследования показывают колебания численности криля: в некоторые годы его много, а в другие – практически нет.

Photo: Joan Costa

Calanus – the happy pill of the sea

Calanus glacialis is one of three common species of copepods found in the waters around Svalbard. They are especially acclimatized to be able to exploit the abundance of plankton algae (plankton means “floating” in the water) that is available during the spring bloom. It gorges on this abundance and rapidly builds up large fat reserves stored in a lipid sac extending almost throughout its entire body. Although they measure only 5 mm, this lipid sac makes them a popular food source for birds, fish and whales. They are a bit like a fat happy pill full of Omega-3 fatty acid, which swims around all year ready to be eaten.

The classical understanding of polar night biology indicates that Calanus lives deeper in the ocean than at other times of the year, but recent research indicates that it contributes a lot to the vertical migration patterns we see with acoustic instruments.

Калянус – океанские «таблетки счастья»

Calanus glacialis - один из трех видов веслоногих ракообразных или копепод, которые распространены в районе Свальбарда. Они хорошо приспособлены к питанию фитопланктоном. Во время интенсивного питания, в период весеннего цветения фитопланктона, калянус быстро запасает значительные количества питательных веществ в жировых мешках. Хотя длина рачков около 5 мм, запасы липидов делают калянус важным источником питания птиц, рыб и китов.

Они напоминают «таблетку счастья», заполненную омега-3 жирными кислотами, которая плавает круглый год и доступна для поедания другими обитателями океана. Классическое понимание биологии полярной ночи указывает, что калянус живет в глубоких слоях океана, но недавние исследования показали, что они тоже совершают в вертикальные миграции, которые мы можем исследовать акустическими инструментами.

The brown kelp Saccharina latissima provides a nice place to sit for the shrimp

Бурые водоросли ламинария - прекрасное убежище для креветок

Photo: Geir Johnsen, NTNU

Arctic kelp – the energy savers

Seaweed and kelp are marine algae that need sunlight for photosynthesis, the process by which solar energy is converted into chemical energy. All the kelp species found on Svalbard can grow without light in winter. The Arctic kelp *Laminaria solidungula* is particularly frugal, and can survive on as little as one week's sunlight for a whole year! The kelp species on Svalbard (*Saccorhiza dermatodea, Laminaria digitata, Saccharina latissima* and *Laminaria solidungula*) have their growing season from October to June.

They use the energy they store during the period with sunlight to grow new blades, or lamina, also during the darkest time of the year. When the light returns in spring, it has new blades that can take part in the photosynthesis and obtain even more energy for the next year. This is an extreme adaptation to the polar night that can't be found in terrestrial plants in the Arctic. This special adaptation has contributed to *Laminaria solidungula* having a circumpolar distribution, including areas covered by ice for much of the year. We still need to find out whether the other kelp species have the same characteristics as *Laminaria solidungula*.

Арктические бурые водоросли – накопители энергии

Морским водорослям необходим солнечный свет для фотосинтеза – процесса, при котором солнечная энергия преобразуется в химическую. Однако, арктические бурые водоросли могут расти зимой без света. Арктическому виду ламинарии Laminaria solidungula достаточно для жизни одной недели солнечного света в году. Для бурых водорослей Свальбарда (*Saccorhiza dermatodea, Laminaria digitata, Saccharina latissima* и *Laminaria solidungula*) сезон роста длится с октября до июня.

Они используют запасы энергии, накопленные в период светового дня, для роста новых листовых пластин даже в период темного времени года. Когда свет возвращается весной, они готовы запасать энергию для следующего года. Эта особенность характерна для морских водорослей в экстремальных условиях полярной ночи и ей нет аналогов в наземной арктической флоре. Именно это способствует циркумполярному распределению *Laminaria solidungula*, включая области, покрытые льдами значительную часть года. Необходимо исследовать есть ли такая же адаптация и у других видов арктических бурых водорослей.

Photo: Geir Johnsen, NTNU

Polar cod – the Barbie of the sea

Polar cod (*Boreogadus saida*) is a key species in the Arctic ecosystem. It's possibly the most important food source for seals in winter and also forms part of the diet of many polar seabird species. It's a distant relative of the common cod given its slender body measuring around 30 cm and the lack of the characteristic cod beard. The polar cod is one of few fish species with an antifreeze fluid in its blood. This enables it to thrive in water temperatures down to -1.8 ºC, close to the freezing point of the sea in the Arctic.

The polar cod produces roe and milt throughout the entire polar night so it's well prepared when February comes and the sun slowly rises toward the horizon. At the start of the spawning season, the egg sacs or testicles can account for half the body weight of the fish. This bizarre growth of reproductive organs is due to the large amount of egg and sperm it produces and the fact that muscles and other reserves are reduced to a minimum to conserve energy. If the polar cod was a doll, it would probably look like Barbie. However, instead of big breasts, it would have the world's largest ovaries...

Сайка – Барби океана

Сайка или полярная тресочка (*Boreogadus saida*) – ключевой вид арктической экосистемы. Этот вид, возможно, самый важный источник пищи для тюленей в зимний период, а также значительная часть диеты многих видов морских птиц. Сайка сильно отличается от атлантической трески своим стройным телом, длиной около 30 см, и отсутствием характерного для трески мясистого усика. Сайка – один из немногих видов морских рыб имеющих в своей крови природный антифриз, препятствующий ее замерзанию при падении температуры воды ниже - 1,8˚ , близкой к точке замерзания.

Половые продукты созревают в течение полярной ночи, и, с возвращением солнца, начинается сезон нереста. Половые продукты могут составлять половину веса тела рыбы, в то время как другие органы и мышцы уменьшаются до минимума, для снижения энергетических затрат. Если бы сайка была куклой, то она была бы, наверное, похожа на стройную Барби.

Photo: Geir Johnsen, NTNU

Common Whelk – the master of the packed lunch

Whelks move slowly by gliding along the ocean floor instead of swimming. Consequently, we often find whelks in the same area all year round. The common whelk (*Buccinum undatum*) is a predator that feeds on other bottom-dwelling organisms, both dead and alive. The meat of the common whelk is tasty and it's very popular in several European countries. The female lays up to 2000 eggs in semi-transparent capsules on the ocean floor or on the stem of kelp. These capsules are clustered in large groups and look like a handful of white peas stuck together. In each capsule, around 30 eggs hatch, while the rest are small nutritious packed lunches for the young whelks. The "packed eggs" are also tasty meals for other bottom-dwelling animals such as nudibranchs and amphipods.

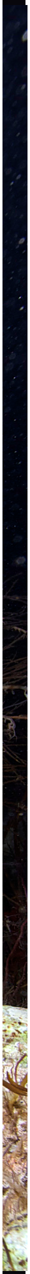
In January we find an abundance of whelks in the kelp forest because that is the time its lays its eggs. After the eggs have hatched, the egg capsules on the kelp stems are often washed ashore. You have probably seen many of them on the seashore.

Обыкновенный букцинум – мастер упаковки ланча

Букцинум не плывет, а медленно скользит по морскому дну. Вследствие этого, мы часто находим этих моллюсков на том же самом месте в течение всего года. Обыкновенный букцинум, или волнистый рожок (*Buccinum undatum*) – это хищный моллюск, который питается другими донными животными, как живыми, так и мертвыми. Сам моллюск является популярной едой во многих европейских странах. Самка откладывает около 2000 яиц в полупрозрачных капсулах на дно или на слоевище бурых водорослей. Эти капсулы собираются в большие группы и выглядят как горстки белого горошка склеенного вместе. Из каждой капсулы вылупятся около 30 моллюсков, в то время как остальные яйца будут служить им источником питания, как хорошо упакованные ланчи. Эти яйца - вкусная еда и для других донных животных, таких как голожаберные моллюски и амфиподы.

В январе мы часто находили множество букцинов в ламинариевом лесу, где они откладывали яйца. Пустые оболочки яиц выносит на берег, где вы, наверное, их видели.

Photo: Geir Johnsen, NTNU



Skeleton shrimp - picking up partners in the night

Caprellidae, which are commonly known as skeleton shrimps (*Caprella sp*), are long, thin amphipods that look like threads or thin sticks with front and hind legs. They can't swim very far and remain near seaweed and kelp, which they climb on and use as a "rack". They cling on to the kelp with their abdomen while lifting their pereon to catch prey that swims past. During the polar night, we see much greater densities of skeleton shrimps in shallow water than we do during the rest of the year. However, we still don't know the reason for this with certainty. In all likelihood, they use the darkest months of the year to catch food under cover of darkness and as a place to "pick up" a partner.

Морские козочки – охота в ночи

Caprellidae, которые известны как морские козочки – это узкоспециализированная группа амфипод с удлиненным телом, не умеющих плавать, а приспособленных к лазающему образу жизни на водорослях и различных животных (губках, мшанках и гидроидах).

Большую часть своей непродолжительной жизни (она, как правило, не превышает одного года) "морские козочки" сидят на водорослях, веточках гидроидов или других животных, прочно закрепившись задними парами ножек. При этом передняя часть их тела поднята вверх и совершает движения из стороны в сторону в поисках пищи.

В период полярной ночи мы наблюдали на мелководье намного большие морских козочек, чем в другое время года. Однако, мы не знаем, с чем это связано. В любом случае, морские козочки используют темные месяцы для поиска пищи под покровом ночи.

An Atlantic cod sleeps under the brown kelp Saccharina latissima

Атлантическая треска спит в зарослях бурых водорослей Saccharina latissima

Photo: Geir Johnsen, NTNU

When the nights are long (and lust is great)

When the light returns after the polar night and the ice melts, the plankton algae experience an intense and short-lived growth period. This is the main food source for all other life in the Arctic. For many animals, reproduction must be timed so that the offspring are just the right size to eat the plankton algae when its blooms. Approximately two-thirds of all fish species use the polar night to prepare to spawn when ice melts, while other animals lay eggs that hatch when the algae bloom. Consequently, the polar night is not a time of rest for the animal life in the Arctic. This is the time when all the preparations are made to continue the race when spring arrives. In particular, the production of energy-rich eggs in a season during which it can be difficult to find food is a costly affair, and for many species can constitute an important limitation for how far north they manage to survive.

Ночь длинна

Когда свет возвращается после полярной ночи и лед тает, у фитопланктона наступает период интенсивного роста. Фитопланктон - это главный источник пищи для жизни в Арктике. У многих морских животных период репродукции приурочен к цветению фитопланктона, чтобы молодь могла питаться планктонными водорослями. Приблизительно две трети всех видов рыб используют полярную ночь для подготовки к нересту, который происходит в период таяния льда, в то время как другие животные откладывают яйца заранее, чтобы личинки вылупились к началу весеннего цветения микроводорослей. Таким образом, в полярную ночь жизнь в Арктике не замирает, напротив, это время, когда проводятся все приготовления, чтобы продолжить гонку жизни с приходом весны. В частности, созревание богатых энергией яиц в сезон, когда сложно найти пищу, может быть затруднено, и для многих видов это служит препятствием для их распространения на север.

Bioluminescent algae in the seaice in the Adventfjord by Longyearbyen

Светящиеся водоросли в Адвентфьорде возле города Лонгиербюен

Photo: UNIS

Milky seas effect

Many people have seen the light phenomenon known as milky seas. This is usually plankton that produce light when there is movement in the water. Other marine species can produce light too. This effect results from a controlled chemical reaction in the algae or animal. The light can come suddenly and shine brightly or have a more glowing effect and be weak. The colours vary and include red, blue, green, yellow or white.

This process is called bioluminescence and appears as radiation of light from living organisms. Although this is an energy-intensive process, many species use energy on this in the polar night because bioluminescence provides several benefits. These include sending signals to potential partners, tricking enemies and providing camouflage. Outside the Arctic, this process is most common among animals that swim in the dark, deep sea.

Эффект «молочного моря»

Многие люди наблюдали световой феномен, известный как эффект «молочного моря», который создается движущимся в воде светящимся планктоном. Другие виды морских животных тоже могут светиться. Этот эффект связан с контролируемой химической реакцией в организме водорослей или морских животных. Свет может менять свою интенсивность; цвет свечения может быть красным, голубым, зеленым, желтым или белым.

Свечение морских организмов называется биолюминисценцией. Хотя это энергозатратный процесс, многие виды используют на это энергию во время полярной ночи, поскольку биолюминисценция дает им целый ряд преимуществ, включая, например, сигнал потенциальному партнеру, маскировку и отпугивание врагов. Вне Арктики этот процесс присущ животным, обитающим в темноте глубинных вод.

The ctenophore *Beröe cucumis* produces its own light and reflects the light others make

Гребневик *Beroe cucumis* светится сам, а также отражает свет других светящихся организмов

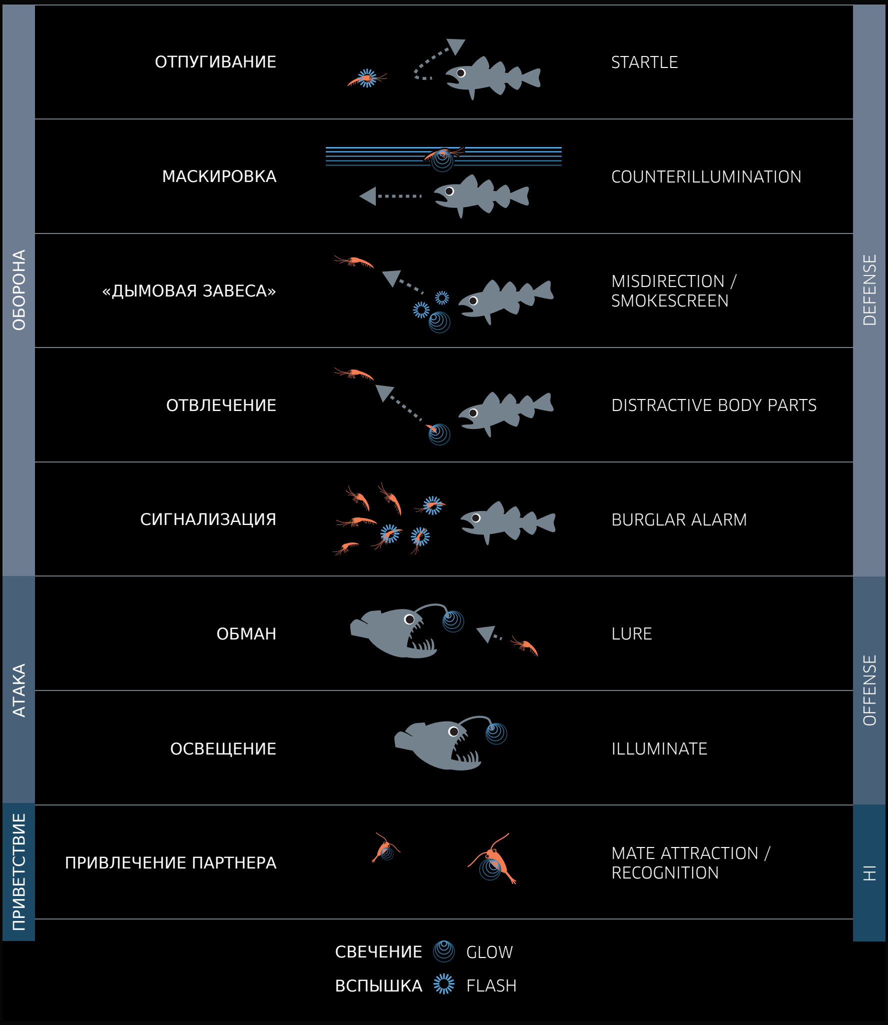
Photo: Geir Johnsen, NTNU

Upside down sea

Along with the Arctic polar night, the deep sea is the least known part of the earth. Mapping the biology here is a demanding and expensive exercise. Despite the differences, it's possible that the polar night can provide us important insights into the deep sea. The dominant darkness is a common characteristic, while the milky seas effect is a characteristic in the deep sea. In the Arctic, there are an astonishing number of animals that produce light in the polar night. They can do this in shallow water too. This gives us a unique opportunity to study processes that we would otherwise only find in the deep sea. Animals that produce light is one of the processes we still know little about, and it's a subject that is difficult to study. By researching in shallower Arctic waters in the polar night, we can acquire new knowledge that can help us to understand the deep sea better.

Море вверх ногами

Наряду с Арктикой в период полярной ночи, глубины моря - это наименее исследованная часть Мирового океана. Картирование биоразнообразия в таких районах – очень сложное и дорогостоящее занятие. Несмотря на различия, возможно, что изучение процессов во время полярной ночи, может помочь нам понять процессы происходяшие в глубинах океана. Доминирующая темнота - общая характеристика для этих районов, в то время как эффект «молочного моря» присущ глубинным районам. В Арктике обитает удивительно много животных, светящихся во время полярной ночи, даже и на мелководье. Это дает нам уникальную возможность изучить процесс свечения организмов в мелководных арктических районах во время полярной ночи и получить новые знания.



Ill: Reibo, basert på Haddock 2010

Trickster light

There are several reasons why animals produce light. The main ones are protection, food and sex. They normally produce the light to attract prey or to find a partner. Light is also practical for animals who use their eyes to find their bearings. It's also important for defence so the animals can frighten or confuse their enemies. Some species produce a weak light on the underside of their body so they don't make any shadows from below. The method that warships or military aircraft use to emit heat signals to avoid missiles or torpedoes is a carbon copy of what occurs in nature. An animal can excrete bioluminescence in the water and create the milky seas effect at same time as it moves away. In this way, it can escape from a predator that focuses on the point where the light is shining. But often the prey is no longer there.

In the polar night even the slightest flash of light is clearly visible and extremely revealing! Consequently, it can also be dangerous because it makes the luminous animal easy prey for others. But the predators wanting to eat the luminous animals are not the only ones who can see this light. Their enemies can also see it, which provides extra protection for the luminous animals. The saying about your enemy's enemy being your friend also applies in the polar night – and this may be the reason why so many small animals such as krill, copepods and jellyfish produce light.

Свет-обманщик

Морские организмы используют способность к свечению в различных жизненных ситуациях. Главное - для защиты, поиска пищи и продолжения рода. Они зачастую производят свечение для привлечения жертвы или для поиска партнера. Свечение также необходимо тем животным, которые используют зрение для ориентации, для защиты и отпугивания врагов. У некоторых видов нижняя часть тела светится слабо для того, чтобы не отбрасывать тень. Военные суда и самолеты, использующие тепловую защиту и ложные тепловые цели, позаимствовали эту идею у природы. Некоторые животные могут вызывать биолюминисценцию в воде, создавая эффект «молочного моря», например, убегая от преследования.

Во время полярной ночи даже слабый свет хорошо виден и может быть опасен, так как делает светящееся животное легкой добычей для других. В то же время, свет видят не только хищники, которые охотятся на светящиеся организмы, но и их враги, что создает дополнительную защиту для светящихся животных. Выражение «враг моего врага – мой друг» вполне применимо к жизни во время полярной ночи. Может быть, по этой причине многие мелкие животные, такие как криль, копеподы и медузы, светятся.

Svalbard ptarmigan in winter plumage by the marine lab in Ny Ålesund

Шпицбергенская тундровая куропатка в зимнем наряде возле морской лаборатории в Ню - Олесунне.

Photo: Geir Johnsen, NTNU

Svalbard rock ptarmigan – the stayer

The Svalbard rock ptarmigan (*Lagopus mutus hyperboreus*) used to be known as the only bird that does not migrate away from Svalbard in the winter. It remains here throughout the polar night, but in other places than the usual summer grazing and breeding sites. The rock ptarmigan is a herbivore and in the winter feeds on most plants including saxifraga. Consequently, we believe that the rock ptarmigan stays in areas with less snow in the winter, such as under the bird cliffs and near the coast.

Our research project confirms that the rock ptarmigan is not alone in Svalbard in the dark. It has the company of several species of seabirds that remain here through the winter. This is particularly interesting since seabirds mostly use their eyes to look for food. But how do they manage that when it's dark?

Шпицбергенская тундровая куропатка – выносливое животное

Шпицбергенская тундровая куропатка (*Lagopus mutus hyperboreus*) считалась единственной птицей, которая не улетает зимой со Шпицбергена. Она остается на время полярной ночи, но обитает в других местах, отличных от летних мест гнездования и питания. Будучи растительноядной, шпицбергенская тундровая куропатка, зимует в районах, где мало снега и есть возможность найти пищу, например, камнеломку, на скалах или на побережье.

Наши исследования показали, что не только шпицбергенская тундровая куропатка зимует на Шпицбергене, но и некоторые другие виды птиц. Это особенно интересно, поскольку птицы используют зрение в поисках пищи, но как они могут видеть в темноте?

Brünnichs guillemot in winter plumage

Толстоклювая кайра в зимнем наряде

Photo: Geir Johnsen, NTNU

Black and Brünnich's guillemots – the food seekers

The Brünnich's guillemot (*Uria lomvia*) and black guillemot (*Cepphus grylle*) are among the most common seabirds in Svalbard. Even though most Brünnich's guillemots migrate southwest in the winter, both species have been observed overwintering along the west coast of Spitsbergen. While the black guillemot often stays near buildings and light, the Brünnich's guillemot seems to stay in dark areas. It appears that they thrive in the darkness. As long as the sea is ice-free, there is good access to food sources such as krill, polar cod and hyperiid amphipods. Another advantage is that they don't have to use energy on long flights to search for food. Even though most guillemots migrate southwards, many choose to remain in Svalbard.

Обыкновенный чистик и толстоклювая кайра – искатели пищи

Толстоклювая кайра (*Uria lomvia*) и обыкновенный чистик (*Cepphus grylle*) - одни из наиболее распространненных птиц на Шпицбергене. Хотя большинство толстоклювых кайр мигрируют зимой на юг, некоторые особи этого вида зимуют в районе западного побережья Шпицбергена. В то время как чистик часто обитает вблизи поселений и света, толстоклювая кайра, похоже, селится в темных районах. До тех пор пока море свободно ото льда, кайры находят здесь пищу. Это криль, сайка и амфиподы. Другое их преимущество – они не используют много энергии для перелетов в поисках пищи. Хотя большинство толстоклювых кайр мигрируют на юг, многие остаются на зимовку на Шпицбергене.

Photo: Geir Johnsen, NTNU

The little auk – the chatterbox

The little auk (*Alle alle*) is the smallest auk, but also the most abundant seabird species in Svalbard. Some colonies along the west coast of Svalbard consist of several hundred thousand birds. While most little auks migrate southwards in the North Atlantic for the winter, small flocks have been observed in Svalbard's fjords throughout the winter. The little auk has a big appetite for the copepod Calanus glacialis, but also feeds on other zooplankton and small fish.

Unlike most other winter birds, the little auk shuns the light. When it returns to the surface after diving for food in the dark, the little auks talk to each other so that the flock can gather again. In Svalbard the little auks are referred to as Tromsø residents because they make so much noise in the summer! Perhaps the little auks that remain here in the winter should be called Bergen residents since they chatter so much. We think they are Svalbard's most social birds in winter, but we still don't know what they chat about...

Болтливый люрик

Люрик (*Alle alle*) – самая маленькая птица семейства чистиковых и самая многочисленная птица на Шпицбергене. Некоторые колонии на западной побережье Шпицбергена насчитывают несколько сотен тысяч птиц. В то время как большинство люриков мигрируют зимой на юг, в районы Северной Атлантики, небольшие скопления люриков наблюдали во фьордах Шпицбергена на протяжениивсей зимы. Люрики питаются, в основном, калянусом (Calanus glacialis), но также едят и другие виды зоопланктона и мелкую рыбу.

В отличие от других видов зимних птиц, люрик сторонится освещенных мест. Когда люрики возвращаются на поверхность после ныряния в поисках пищи в темноте, они «разговаривают» друг с другом, собираясь в стаю. На Шпицбергене люриков сравнивают с жителями северного города Тромсе, потому что они очень шумные летом. Возможно, люриков, которые остаются на зимовку на Шпицбергене, следовало бы называть бергенцами, потому что они много болтают как жители города Берген. Нам кажется, что шпицбергеновские люрики – самые общительные птицы, но мы не знаем о чем они болтают…

Krill, Calanus and other plankton fills the water column

Криль, калянус и другой планктон, парящий в толще воды

Photo: Geir Johnsen, NTNU

Ups and downs all year round

The largest synchronised movement of organisms on earth is generally referred to as diel vertical migration of zooplankton. This phenomenon is based on the principle that animals swim up to the surface at night to feed under cover of darkness then swim back down into the darkness to hide during the day. This process is controlled by light and is common in all the oceans on earth. Research performed in Svalbard demonstrates that this also happens when it is completely dark in the polar night. What encourages them to behave like this?

Even though the sun is below the horizon all day, it comes further up in the middle of the day. This is called diffuse light. Nonetheless, this small amount of light is still enough for zooplankton to prefer to hide during the day and feed at night. When the moon is up, we observe that this has a stronger effect on migration patterns of the life in the Arctic Ocean.

Взлеты и падения круглый год

Вертикальные миграции зоопланктона часто называют самыми большими синхронизированными движениями организмов на Земле. Это феномен основан на том принципе, что животные всплывают ночью в верхние слои водной толщи, для питания на поверхности под покровом темноты, а днем мигрируют вниз, и прячутся в темных глубинах. Это процесс контролируется освещением и является общим для всех морей на Земле. Исследования, выполненные на Шпицбергене, показали, что это происходит даже в темный период полярной ночи. Что же толкает зооплантон на эти миграции?

Хотя солнце и находится за горизонтом весь день, в середине дня оно поднимается выше. Это называется рассеянным светом. Даже такого небольшого количества света достаточно для зоопланктона, чтобы спрятаться от него во тьме глубин. Мы также заметили, что лунный свет оказывает большой эффект на миграции организмов в Арктике.

Full moon over Ny Ålesund

Луна над Ню-Олесунном

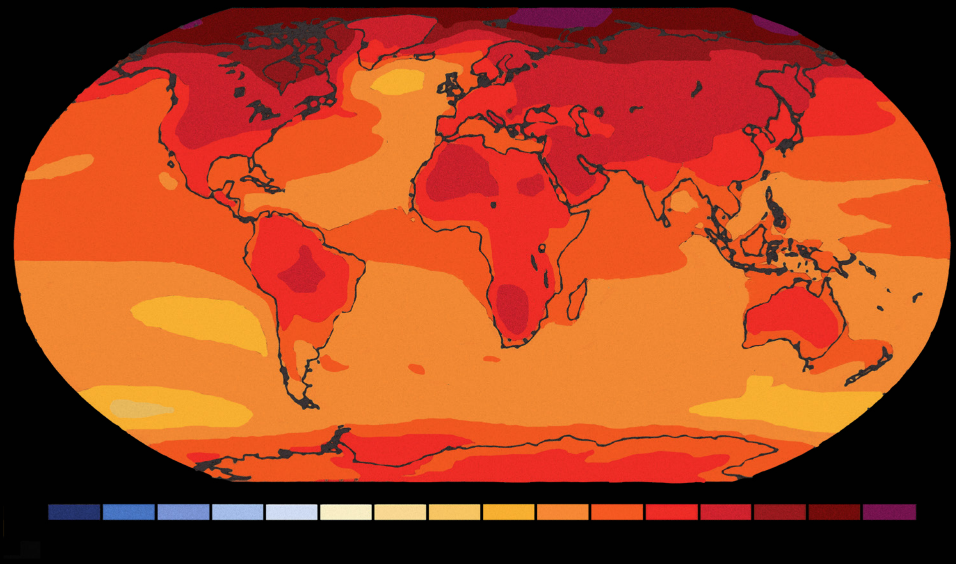
Photo: Geir Johnsen, NTNU

Moonlight

The moon reflects light from the sun and is not a source of light in itself. But the Arctic moonlight is perceived differently than at lower latitudes. In the summer the moon is virtually invisible. The sun is above the horizon all day and overshadows the moon completely. However, in the winter, the moon is the strongest source of light. But that's not the case all the time. The moon's orbit around the earth combined with the earth's tilt relative to the sun results in a "lunar day" and "lunar night" at high latitudes. The full moon remains above the horizon for several days in a row (a lunar day), while the new moon remains below the horizon (a lunar night). The length of lunar days and nights vary from year to year and between months, but the phenomenon is always related to the phases of the moon. When this occurs in addition at a time of year when the sun is not visible, it creates a special and unique light climate that can only be experienced in polar regions!

Лунный свет

Луна отражает свет Солнца, а сама не является источником света. Но арктический лунный свет воспринимается иначе, чем в низких широтах. Летом солнце находится над горизонтом весь день, поэтому лунный свет практически невидим. Однако зимой лунный свет – это значительный источник света, но не все время. Лунная орбита, в сочетании с наклоном Земли относительно Солнца, приводит к так называемому «лунному дню» и «лунной ночи» в высоких широтах. Полная луна остается над горизонтом несколько дней к ряду («лунный день»), в то время как новая луна остается ниже горизонта («лунная ночь»). Длина «лунных дней и ночей» варьирует от года к году, существуют различия и между месяцами, но феномен всегда связан с фазами луны. Когда он проявляется в то время, когда солнца не видно, то возникает уникальный световой режим, который можно наблюдать только в полярных районах.



Expected change in average surface temperature the coming 85 years

Ожидаемые изменения средней температуры поверхности Земли в следующие 85 лет

Ill: Reibo, basert på IPCC20114 WGI AR5 Fig SPM 8a

Climate change in the Arctic

The climate has never been stable. It undergoes constant change. However, these changes are now taking place faster than previously due to greenhouse gas emissions. In order to understand how algae and marine animals react to these changes, it's also important to understand how they have adapted and live all year round, not just during the months when it's light. We need to try to find out if the same species that live here in the winter darkness are also here in the summer light. Are the species that dominate the ecosystem in the winter the same ones that dominate it in the summer? Do marine animals and algae look different in the winter darkness when they are preparing for reproduction? Do they have the same behaviour patterns? That's why research projects that map the sea life in the polar night are so important!

Изменение климата в Арктике

Луна дает самый сильный свет во время полярной ночи. Некоторые виды зоопланктона, такие как Calanus glacialis и криль, могут замечать лунный свет на глубинах до 170 метров. Это частично определяет, где именно в водной толще эти виды живут. Наши исследования показали, что когда луна ниже горизонта, наибольшая активность зоопланктона наблюдается в поверхностных слоях водной толщи.Но когда луна поднимается выше горизонта и начинается «лунный день», животные мигрируют в глубины моря. В противоположность оборотням, которых привлекает лунный свет, зоопланктон убегает от него. Эта активность полностью контролируется фазами луны.

Foto: NASA

Sea ice and light

When the sea temperature drops to -1.8 °C, the water freezes and forms sea ice. The ice acts like a cover and prevents the light from entering the water column. This cover becomes more opaque when snow settles on the ice, and most of the light that hits the ice or snow is reflected back instead of penetrating down into the water. This is called albedo.

The water under the sea ice will always be darker than seawater that is not covered by ice. However, in the polar night it will be extra dark because there is so little light in the first place.

The vicious circle: As the sea temperature rises, it's harder for the ice to form. This leads to more light entering the water column, which in turn leads to further rises in the sea temperature, particularly in closed fjord systems. Since 1980 the polar ice cap has reduced by almost 15% per decade, and Svalbard now experiences considerably more snow and rain than was common 10-20 years ago. Admittedly, most of the reduction in the polar ice cap is related to increased transport of heat into the Arctic Ocean via ocean currents. However, regardless of the mechanism, this has major implications for the life in the Arctic, not least for the organisms that live in and on the sea ice.

Морской лед и свет

Когда температура морской воды снижается до -1.8 °, она замерзает и образуется лед. Лед препятствует проникновению света в водную толщу. Этот покров становится более непроницаемый, когда лед покрывается снегом и свет отражается ото льда и не проникает в воду. Это явление называется альбедо.

В морской воде, покрытой льдом всегда будет темнее, чем в воде свободной ото льда. Во время полярной ночи будет еще темнее, поскольку изначально мало света.

Замкнутый круг: по мере того как температура моря повышается, сложнее сформировать лед, что приводит к большему количеству света, попадающему в толщу воды, что, в свою очередь, приводит к дальнейшему повышению температуры моря, особенно в закрытых фьордовых системах. С начала 80х годов, полярная ледяная шапка сокращалась почти на 15% каждое десятилетие, и на Шпицбергене сейчас выпадает снега и дождя больше, чем 10-20 лет назад. По общему признанию, таяние льдов связано с увеличением переноса тепла в Северно-Ледовитый океан с океанскими течениями. В любом случае, независимо от механизма, это явление имеет очень серьезные последствия для организмов, жизнь которых связана со льдами.

Rescue rehearsal at Svalbard November 2014

Тренировка спасателей на Шпицбергене. Ноябрь 2014 г.

Foto: Torbjørn Kjosvold / Forsvarets mediesenter

Disaster in the darkness

As the ice gradually retreats in the central Arctic Ocean and the surrounding shelf seas, new possibilities open up. The Arctic is opening up for new regular shipping routes via the North Pole and routes between the east and west. At the same time, an increasing number of new exploration areas for oil and gas are being planned further north in the Barents Sea and in the waters that were previously frozen. As the level of activity increases, so does the risk of accidents.

Through this research project, we have discovered that the life in the Arctic does not go into hibernation during the polar night. The zooplankton does not migrate into the depths of the sea in anticipation of spring, sun and heat. Rather the contrary. Fish and birds seem to thrive on hunting for food in the dark. This implies that the life in the Arctic Ocean in the polar night is at least as vulnerable and exposed to contamination as during the light time of the year. Maybe it's even more vulnerable, since the polar night is an important time for reproduction. Consequently, it's highly uncertain what effects an oil spill from a shipwreck will have. In addition, as it's so dark in the polar night, it would be extremely difficult to see what may have gone wrong. In the places where there is ice, it's harder for boats to travel at full speed. This means that in the event of an accident, it would be harder for others to come to the rescue.

Бедствие в темноте

Поскольку лед постепенно отступает в центральных районах Северного Ледовитого океана и окружающих шельфовых морях, открываются новые возможности. Арктика открывает новые регулярные маршруты доставки через Северный морской путь. В то же время возрастает количество новых месторождений нефти и газа, планируемых для разработки на шельфе севера Баренцева моря - в районах, ранее недоступных из-за льдов. Поскольку увеличивается уровень активности, то возрастает и вероятность несчастных случаев и аварий.

В рамках этих исследований мы обнаружили, что жизнь в Арктике не замирает во время полярной ночи, скорее наоборот. Зоопланктон не мигрирует в глубины моря в ожидании весны, солнца и тепла. Рыбы и птицы вполне успешно находят пищу во время полярной ночи. Это означает, что жизнь в океане очень уязвима к возможному загрязнению, особенно во время полярной ночи – важному периоду для подготовки к размножению. Может произойти утечка нефти при аварии во время полярной ночи, и в темноте сложно увидеть и понять, что пошло не так, оценить масштабы аварии. В сложной ледовой обстановке спасателям трудно прийти на помощь при авариях.

Ill: Bjarne Stenberg (NTNU AMOS)

The robots of the sea

Our knowledge of the life in the polar night has been limited by the enormous challenges that working in cold, dark, deep and often icy waters entail. The same challenges would apply in the event of an environmental disaster in the polar night. Over the past 10-15 years, there have been significant advances in the development of environmentally-friendly autonomous underwater vehicles (UAVs). These robot-like vehicles can help us to map and monitor the Arctic Ocean and the life that exists here. They are equipped with sensors, which can help reveal more about the life in the sea. As these robots of the sea are battery powered, they don't cause any form of pollution. By using the knowledge these autonomous vehicles can help us to acquire, we will be in a better position to make good decisions about how the ocean in the Arctic should be managed – in both the polar night and during the summer.

Бедствие в темноте

Наши знания о жизни в полярную ночь были ограниченными из-за сложностей работы в темных, глубоких и зачастую покрытых льдом районах. Эти же сложности могут возникнуть в случае экологической катастрофы в полярную ночь. За последние 10-15 лет были достигнуты значительные успехи в развитии экологичных автономных подводных аппаратов. Эти роботоподобные транспортные средства смогут помочь нам отобразить и контролировать жизнь в полярных широтах. Аппараты оснащены датчиками, которые помогут нам узнать больше о жизни в океане. Поскольку эти аппараты снабжены батареями, они не будут загрязнять океан. Использование этих автономных аппаратов поможет нам приобрести новые знания для принятия решений о том, как нам управлять ресурсами в Арктике – как в полярную ночь, так и в течение лета.