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In the dark: A review of ecosystem processes during the Arctic polar night

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ABSTRACT

Several recent lines of evidence indicate that the polar night is key to understanding Arctic marine ecosystems. First, the polar night is not a period void of biological activity even though primary production is close to zero, but is rather characterized by a number of processes and interactions yet to be fully understood, including unanticipated high levels of feeding and reproduction in a wide range of taxa and habitats. Second, as more knowledge emerges, it is evident that a coupled physical and biological perspective of the ecosystem will redefine seasonality beyond the "calendar perspective". Third, it appears that many organisms may exhibit endogenous rhythms that trigger fitness-maximizing activities in the absence of light-based cues. Indeed a common adaptation appears to be the ability to utilize the dark season for reproduction. This and other processes are most likely adaptations to current environmental conditions and community and trophic structures of the ecosystem, and may have implications for how Arctic ecosystems can change under continued climatic warming.

1. Introduction

Early studies in the Arctic suggested that ice-covered areas were generally unproductive (Nansen, 1902). Evidence of human settlements in the high Arctic over several thousand years, however, conflicted with these early observations and constituted a paradox as to how human populations could subsist in regions considered to be biological deserts. Further investigations revealed significant productivity under ice-covered seas (Wheeler et al., 1996), and the existence of productivity hot spots (e.g. Falk-Petersen et al., 2014), demonstrating the significance of the complex links between ice, ocean, and land in Arctic ecosystems. During the last 20 years, national and international research efforts in the Arctic have increased significantly, leading to the 4th

International Polar Year (IPY, 2007–2009, see http://www.ipy.org/). Highlights of the IPY work include cataloguing marine biodiversity from bacteria to top predators, documenting the importance of sea ice cover for a variety of ecosystem processes, studying the relationships between physical, chemical, and biotic processes on small spatial scales, describing the oceanography of previously poorly known areas, and investigating atmosphere–ice–ocean feedback relationships (e.g. Bauerfeind et al., 2009; Barber et al., 2010; Forest et al., 2011). In addition, there have been significant developments in research infrastructure, including novel remote sensing and in situ monitoring technologies and the algorithms for interpreting their output (Pabi et al., 2008; Schofield et al., 2010; Johnsen et al., 2011), enhanced oceanographic mooring networks (Kahru and Brown, 1997), development of international databases, and long-term monitoring facilities (Johnsen et al., 1997, 2011; Meyer et al., 2014). Nevertheless, observations of the properties and processes occurring during the winter have been sparse and to a large degree opportunistic. With

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some exceptions, data have generally been restricted to fixed observatories, which lack important spatial resolution, or from freely drifting autonomous platforms, which compromises the repeatability necessary to quantify interannual variability.

A classical paradigm in Arctic marine ecology holds that most biological processes at high latitudes are reduced to a minimum during the polar night due to low food availability and the reduction in light (Smetacek and Nicol, 2005; Piepenburg, 2005); in effect a period of winter dormancy. Recent discoveries under the extreme conditions of the Arctic winter challenge our understanding of Arctic marine organisms and ecosystem processes. For example, there is a long-held presumption that the polar night at high latitudes represents total darkness, yet new data indicate that Arctic organisms respond to light levels undetectable by the human eye (Båtnes et al., 2013). Further, recent research reporting active vertical migration of zooplankton (Berge et al., 2009) and bioluminescence levels indicative of functional activity in several zooplankton taxa (Berge et al., 2012a, 2014; Johnsen et al., 2014) has challenged the assumption of winter dormancy. Also, changes in the Arctic ocean–sea ice–atmosphere interface are leading to rapid shifts in the structure, resilience and function of Arctic ecosystems (Kortsch et al., 2012; Barber et al., 2015). Rapid decline in sea ice extent and thickness, increased air and ocean temperatures, increased water-column stratification, and multiple dynamic physical and chemical changes significantly alter the patterns of productivity at the base of marine food webs (Walsh, 2008). Such changes are also anticipated to affect ecosystem structure and productivity higher in the food web. Ultimately, Arctic marine ecosystem structure and productivity within the next decades should be substantially different from what we observe today. Predictions as to how Arctic marine ecosystems may change are hindered by our inability to understand the year-round response of the Arctic system. Therefore, challenging the prevailing view of the polar night as devoid of biological activity is necessary for developing a holistic pan-Arctic view of ecosystem structure and function.

In addition, the current reduction of Arctic sea ice cover and thickness (Comiso and Steffen, 2008; Barber et al., 2015) is likely to have both direct and indirect impacts on marine organisms,

their interactions and ultimately ecosystem processes (e.g. Krause-Jensen et al., 2012; Ji et al., 2013). However, without a more complete perception of Arctic ecosystem function, such impacts will remain largely impossible to understand and predict. *Research into the polar-night biology of the Arctic has the potential for radically altering our perception of the Arctic marine ecosystem, mechanisms governing ecosystems processes, and how a continued warming of the Arctic will affect ecosystem structure and function.*

Here, we present a review of our current understanding of polar-night biology and known coupling processes between physics and the biological components of Arctic marine ecosystems. We include an overview of the physical characteristics of the polar night (Sections 2 and 3), a historical review of scientific campaigns during this time (Sections 4 and 5), and a description of those ecosystem processes that have been studied during the polar night (Sections 6–9).

2. A heterogeneous polar night

The light climate of a region is described by its intensity, spectral composition and day-length (Kirk, 2011; Sakshaug et al., 2009; Cohen et al., 2015). At latitudes above the polar circle, the sun will stay above the horizon a minimum of one 24-h cycle during summer (polar day), and below the horizon for at least 24 h during winter (polar night). As latitude increases these periods of polar day or polar night get longer – at the two poles this reaches a maximum, with only one sunrise and one sunset over the entire year. The polar night is, therefore, a highly heterogeneous light regime depending upon the angle of the sun and the latitude in question (Fig. 1). Moving from south to north, irradiance during the polar night gradually declines necessitating a terminology to differentiate between varying levels of darkness (see Figs. 1 and 2). Accordingly, the *nautical polar night* (when the sun is more than 12° below the horizon) covers the entire Arctic Ocean defined here as excluding the marginal shelf seas, whereas the surrounding shelf seas fall within either the *civil polar night* (when the sun is between 6° and 12° below the horizon) or the *civil twilight* (when the sun is less than 6° below the horizon) zones, depending on time of the year. Consequently, it is vital to consider latitude when interpreting data

81°N, 13th January 2013　　78°N, 15th January 2013

76°N, 19th January 2013　　70°N, 20th January 2013
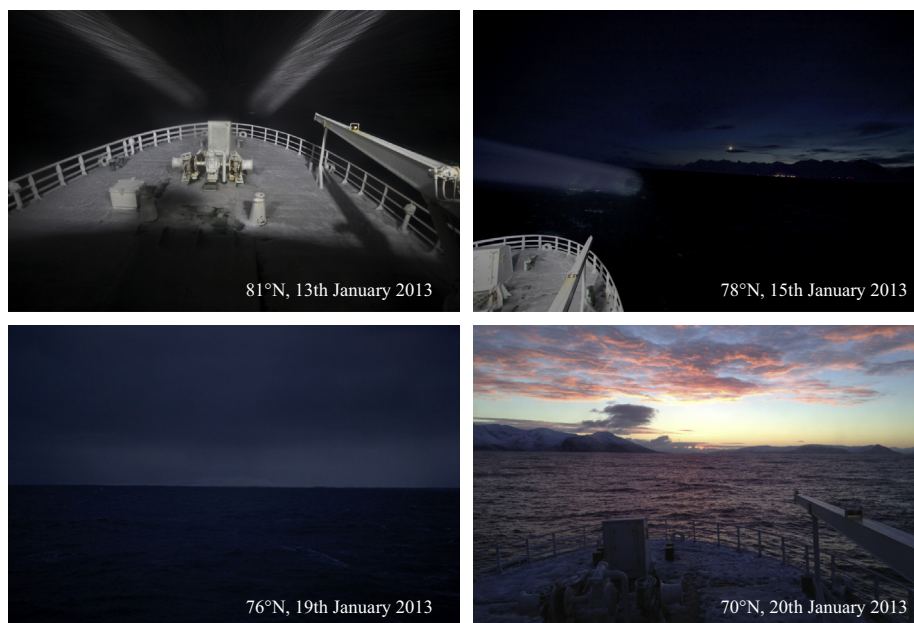
Fig. 1. Light levels as seen by the human eye during the polar night at 81° (upper left, Rijpfjorden), 78° (upper right, Longyearbyen), 76° (lower left, Bear Island), and 70° (lower right, Tromsø) North. All pictures were taken onboard the RV *Helmer Hanssen* at local sun noon within one week in January 2013. Photo: G Johnsen.
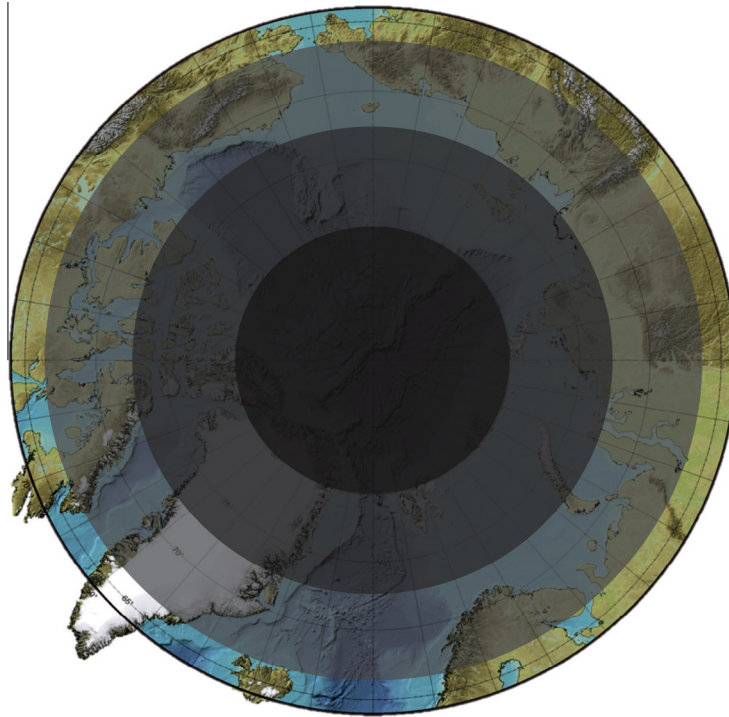
Fig. 2. Differences in light regimes according to the angle of the sun; Civil twilight at latitudes between the polar circle and 72°N, civil polar night at latitudes between 72° and 78°N, nautical polar night at latitudes above 78°N. Moving from south to north, both the duration of the polar night as well as the level of solar radiation change.

from the Arctic polar night as the light climate, and hence potential external cues for marine organisms, will be grossly different in various regions of the Arctic, even during the darkest part of the polar night. In particular, the physical characteristics of the polar night in the Arctic Ocean are very different from the surrounding shelf seas such that it is not adequate to simply presume that processes and responses observed under the different light regimes further south can be simply translated to the Arctic Ocean.
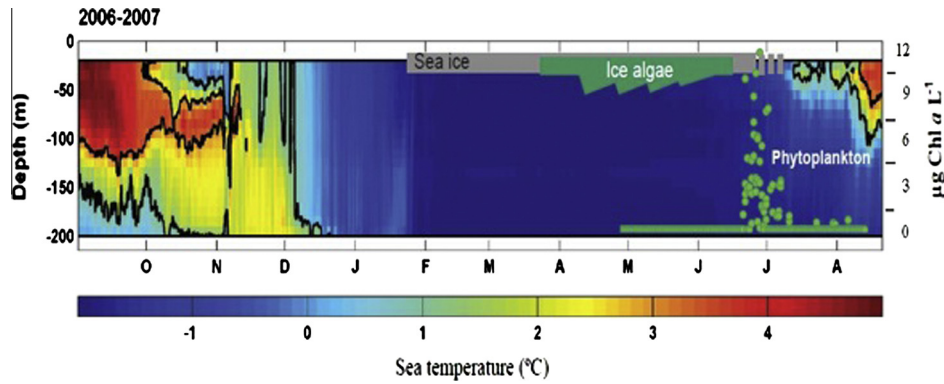
3. Polar night vs winter

We can also distinguish between the terms "winter" and "polar night". Arguably, "winter" is often used in relation to temperature, whereas "polar night" is defined by the light regime and the angle of the sun (see above). In this review, we concern ourselves primarily to the latter term, although it is impossible not also to consider the former in many cases. Rijpfjorden on the northern coast of Svalbard (Norway) provides an excellent example on the importance of distinguishing between "winter" and "polar night" (Fig. 3); the fjord freezes in early 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 freezing point (Fig. 3). Further, pelagic algae blooms often occur while temperatures are at a minimum (see also Hodal et al., 2012) and close to the freezing point, hence demonstrating the relative importance of light rather than temperature as a regulating factor for primary production.

Limiting our review 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 snow, clouds, ice cover, and by the water itself and its constituents such as phytoplankton, colored dissolved organic matter (cDOM) and total suspended matter (e.g. Sakshaug et al., 2009; Barber et al., 2015). 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 sensitivity of ambient irradiance and extreme low thresholds for detecting light intensity by key Arctic zooplankton (Båtnes et al., 2013), irradiance levels when the sun emerges above the horizon but beneath a thick ice and snow cover, may still be sufficient to resemble an early spring (rather than a polar night) situation. Since the winter–spring transition is the main subject of a detailed review by Leu et al. (2015), we will not focus on work carried out later in the winter when there is a distinct diurnal pattern in irradiance (e.g. Kosobokova, 1978, 2003; Sazhin et al., 2004; Legeżyńska et al., 2012).

4. The early history of winter exploration in the Arctic

The Arctic Ocean has long held a fascination for explorers and geographers. Early expeditions were mostly focused on physical studies such as mapping the depth of the ocean, its hydrography. The first major scientific expedition was Nansen's *Fram* expedition of 1893–1896. Nansen allowed his ship to freeze into the sea ice north of eastern Siberia, from where it drifted across a previously uncharted Arctic area before finally escaping the ice into the Fram Strait three years later. A great deal of significant information was gathered during this expedition, although relatively little concerning the polar night. Later, several explorers attempted various expeditions into the Arctic, including Admiral Peary in 1909, Stefansson in 1914, Storkerson in 1918, and Amundsen in the early 1920s. Then, in 1937, the former Soviet Union established their first Severnyi Poljus (SP, =North Pole) drift ice stations, and

Fig. 3. Modified from Leu et al. (2011). Case study from Rijpfjorden on Svalbard, Norway at 80°N. The winter, defined by an ice cover and water temperatures at −1.8 °C, does not coincide with the polar night. At this latitude, the polar night lasts from medio November to medio February, while water temperatures reached −1.8 °C throughout the water column only the last days of January.

between 1937 and 1991, no fewer than 31 ice drift stations were established. During the first 20–25 years, Russian scientists described the topography of the polar basin, the main patterns of the oceanographic current system, meteorology, and how the air pressure system influenced the dynamics of the Transpolar ice drift. Regular marine biological investigations only started in mid 70s (Melnikov, 1997; Proshutinsky et al., 1999; Ugryumov and Korovin, 2005). Biological studies from the Russian drift stations summarized by Melnikov (1997) show that concentrations of ATP (adenosine triphosphate) were generally two orders of magnitude lower under winter sea ice compared to summer values. Ice-associated diatoms were found to form resting spores in ice, assumed to be an adaptation against sinking to the bottom. Living microplankton cells with functional chloroplasts were found to survive in darkness and under low temperatures, however most of microplankters were able to switch to heterotrophy during polar night indicating that these cells are mixotrophic. A total of 21 diatom species were collected with plankton nets just below the ice. Large strands of the Arctic diatom *Melosira arctica*, with a length of more than two meters were detected primarily under the multiyear ice (see picture on page 73 in Melnikov, 1997). During the drift of *Fram* (Nansen, 1902), Nansen and his colleagues established that zooplankton of Atlantic origin was present in the central Arctic Ocean. Russian scientists confirmed these findings and identified 18 species during winter, compared to 22 species in summer. It was also noted that ice fauna (amphipods) were abundant in both winter and summer under the ice cover, the most abundant being *Gammarus wilkitzkii*, *Apherusa glacialis*, *Onisimus nanseni* and *O. glacialis*.

In 1950, the U.S. initiated their programme of observations in the Arctic Ocean with seismic studies on the pack ice of the Beaufort Sea just north of Barter Island, Alaska. During this program three "ice islands" were discovered, and in 1952, the Fletcher Ice Island T-3 was established. From 1957 it was used as a year-round scientific base. The Fletcher Ice Island T-3 was in many ways the western equivalent to the Russian SP program, but the T-3 was last visited in 1979. Echosounders installed on T-3, first a 12 kHz system in 1963, followed in 1967 by a 100 kHz system (Hunkins et al., 1971), provided a new and valuable opportunity to gain insight into the biology of the Arctic Ocean. For the first time, deep scattering layers were documented in the Arctic Ocean. Such deep scattering layers are a common feature of the world's oceans, and are commonly seen at depths ranging between 200 and 600 m, often exhibiting a diel pattern of migration (Ringelberg, 2010). In the Arctic, however, this scattering layer appeared shallower in the water column at depths between 25 and 200 m and only during the summer months. Interestingly, as it was a well-established "fact" at this time that the polar night did not host any biological processes, neither echograms nor any information regarding the presence of acoustic scatterers in the water column during the polar night were mentioned (Hunkins et al., 1971).

Starting from the late 1970s, overwintering expeditions were carried out annually at the Hornsund station at 77°N on Svalbard, Norway (Table 1). Szaniawska and Wolowicz (1986) demonstrated that the caloric value of coastal amphipods from Hornsund varied little from winter to summer, supporting the concept of active metabolism and foraging in winter. Later, Weslawski et al. (1991)

Table 1
Large Arctic research programs involving biological studies during the polar night.

Leading country	Region	Period	Program	Sampling platform	References
Russia	Central Arctic	Mid 70s-present	SP	Drift ice	Melnikov (1997)
United States	Central Arctic	1957–1979	T-3	Drift ice	Hunkins et al. (1971) and Dawson (1978)
Poland	Hornsund, Svalbard	Late 70s-present	Polish Polar Station	Vessel	Szaniawska and Wolowicz (1986) and Weslawski et al. (1991)
Canada/US	Canada Basin	October 1997–October 1998	SHEBA/JOIS	Drift ice	Perovich et al. (1999) and Melnikov and Kolosova (2001)
Canada	Beaufort Sea	September 2003–August 2004	CASES	Fast ice, ice breaker	Fortier and Cochran (2008)
Canada	Beaufort Sea	October 2007–August 2008	CFL	Drift ice, ice breaker	Barber et al. (2010)
Norway	Svalbard fjords	March 2007–August 2008	ARCTOS-IPY	Fast ice, vessel	Søreide et al. (2010) and Leu et al. (2011)
Norway	Svalbard and Greenland Sea	2012–2013	CircA, Cleopatra II, ARCTOS	Vessel	Lønne et al. (2015)
Norway	Kongsfjorden (Svalbard)	2013–2015	Marine Night	Vessel, land based	Berge et al. (in press)

showed a decrease in zooplankton biomass of 90% between summer and winter, reflecting a seasonal vertical migration of zooplankton down to depths during winter. A number of seabirds were also observed at sea in Hornsund during the winter months, including black guillemots, fulmars and glaucous gulls (Weslawski et al., 1991).

5. Recent campaigns including the IPY

With the dramatic impact of climate warming on the Arctic sea ice cover (ACIA, 2005; Stroeve et al., 2011), a more comprehensive understanding of how the Arctic marine ecosystems function as a whole became crucial to predict their response to the fast disappearance of summer sea ice and changes in oceanic and atmospheric forcing (Barber et al., 2010, 2015). Toward that goal, new national and international research networks were established that could integrate their observations within single large projects. These projects set out to investigate various compartments of a given ecosystem, from bacteria to apex predators, and from short-term atmospheric forcing to paleoceanographic records within Arctic sediments. Three of these projects involved overwintering expeditions focused in the western Arctic at the margin of the Canada Basin: (1) the Surface Heat Budget of the Arctic Ocean/Joint Ocean Ice Study (SHEBA/JOIS), (2) the Canadian Arctic Shelf Exchange Study (CASES), and (3) the Circumpolar Flaw Lead System Study (CFL) (Table 1).

The SHEBA/JOIS project froze an icebreaker into the pack ice between October 1997 and October 1998 to study the permanently ice-covered waters above the Canada Basin and adjacent areas from 75°N, 142°W to 80°N, 162°W (Perovich et al., 1999). The SHEBA project focused on issues of climate and heat budgets, particularly the feedback processes that govern the thermodynamics of the ice pack (Macdonald et al., 1999; Perovich et al., 1999, 2002, 2003; Shimada et al., 2001; Stern and Moritz, 2002; Holland, 2003; Lindsay, 2003; Kadko and Swart, 2004); and the JOIS studies were centered on biological and geochemical aspects of the sea-ice/upper ocean system (Melnikov and Kolosova, 2001; Melnikov et al., 2002; Macdonald et al., 2002; Ashjian et al., 2003; Sherr et al., 2003; Sherr and Sherr, 2003; Stern and Macdonald, 2005). The Beaufort Gyre entrained the ice station over several oceanographic and ecological regimes across the Canada basin, Northwind Ridge, Chukchi shelf and slope, and finally the Mendeleev abyssal plains (Table 1). Sampling during the polar night period was carried out in the Beaufort Sea across the deep Canada Basin (Perovich et al., 1999; Ashjian et al., 2003), a region that has experienced dramatic sea-ice decrease, enhanced water column stratification and acidification during the past years (Shimada et al., 2006; McLaughlin et al., 2009; Yamamoto-Kawai et al., 2011).

The CASES and CFL programs used the research icebreaker CCGS *Amundsen* as a platform to conduct field programs in the southeastern Beaufort Sea from September 2003 to early August 2004 and from October 2007 to early August 2008, respectively. The study region comprising the Mackenzie shelf, the more oceanic Mackenzie slope, Amundsen Gulf and McClure Strait, and shallower embayments such as Franklin Bay (Table 1) is complex, influenced both by the Beaufort Gyre and the large Mackenzie River freshwater and sediment discharge (Carmack and Macdonald, 2002). The CASES 2003–2004 sampling during the period of the polar night took place at an overwintering station (70.05°N, 126.30°W) in the landfast ice of Franklin Bay (Benoit et al., 2010), whereas fieldwork at the same period during the CFL 2007–2008 was carried out when the ship remained mobile in the unconsolidated ice cover of Amundsen Gulf further offshore (70.47–71.18°N, 121.46–124.38°W) (Geoffroy et al., 2011).

In addition, and in parallel with the Canadian IPY projects, Norwegian ARCTOS IPY projects carried out on Svalbard were to a large extent aimed at understanding the ecology of key Arctic organisms, both from an evolutionary (life-history and behavioral adaptations) and physiological (short term acclimation) perspective. These endeavors encompassed the polar night (December–January) and were among the very first to achieve a full seasonal perspective on high-Arctic ecology (Nygård et al., 2010; Wallace et al., 2010; Grigor et al., 2014). However, none of these campaigns included subprojects that were specifically aimed at the polar night. The Russian Arctic and Antarctic Research Institute today carries out the most consistent year-around investigations, with their drifting SP stations in the Arctic Ocean. Unfortunately, little information on biological or oceanographic data during the polar night has been made public from these endeavors.

Studies stemming from the IPY programs provided a wealth of new information on the connections and seasonal dynamics of key compartments of the marine ecosystems of the western Arctic Ocean. For instance, some results from these overwintering programs challenge the longstanding paradigm that the pelagic marine food webs remain dormant for the largest portion of the long winter season beneath the sea-ice cover (Darnis et al., 2012; Lønne et al., 2015; Berge et al., in press). In fact they reveal relatively high winter activity at several trophic levels, observations that will be detailed in the following sections. In short, despite the lack of primary production in winter, bacterioplankton and heterotrophic alveolates keep a baseline level of production sufficient to compensate for mortality (Sherr et al., 2003; Garneau et al., 2008; Sala et al., 2008; Terrado et al., 2009; Forest et al., 2011). Such an active winter microbial food web had also been reported in Svalbard (Rokkan Iversen and Seuthe, 2011). At a higher trophic level, Benoit et al. (2010) and Geoffroy et al. (2011) described the initiation of a small, albeit clear, diel vertical migration (DVM) by polar cod (*Boreogadus saida*) as early as December in the depths of the south eastern Beaufort Sea, a pattern that strengthens over the winter season as the day-night contrast increases. Geoffroy et al. (2011) also reported a vertical movement of a large number of polar cod at the end of January, presumably following their zooplankton prey that had likely been transported upward by an anticyclonic eddy affecting the Amundsen Gulf. This observation suggests that polar cod is actively feeding during the polar night.

In recent years, several larger projects have carried out surveys in the fjords of Svalbard during the polar night. These projects have both been ship based (Lønne et al., 2015) and more restricted to the fjords on the western coast of Svalbard (Cohen et al., 2015; Berge et al., in press). In particular, Kongsfjorden at 79°N has been thoroughly examined, and remains the only location at which a larger co-ordinated ecosystem-scale survey has been conducted during the polar night (Berge et al., in press).

6. Microbial plankton communities

Microbial planktonic communities play a fundamental role in mediating fluxes of nutrients and carbon in marine ecosystems (Azam et al., 1983; Arrigo, 2005; Sakshaug et al., 2009), and these processes received considerable attention, particularly during the recently completed CASES and CFL projects, and the *Pro Mare* programme in the Barents Sea 1984–1989 (Sakshaug et al., 1991). While protozoa, such as flagellates and ciliates, consume large fractions of photosynthetically produced particulate organic matter (Calbet and Landry, 2004), heterotrophic bacteria convert the dissolved fraction of primary production into particulate biomass. Consequently, the biomass of phytoplankton and heterotrophic plankton is positively correlated in the world's ocean

(Gasol et al., 1997). This relationship disappears, however, (linear regression; $n = 29$; $p = 0.417$) in the limited data available from the polar night (summarized in Table 2). This demonstrates that during the polar night all heterotrophic activity must ultimately be based on biogenic carbon produced during the previous light season.

Despite the lack of photosynthetic activity during the darkest period of the year, virtually all taxonomic groups of Arctic microbes are sustained (e.g. Weslawski et al., 1999; Sherr et al., 2003; Terrado et al., 2009; Niemi et al., 2011; Rokkan Iversen and Seuthe, 2011), including chloroplast-bearing protists, such as diatoms and various flagellates. The low abundance of chloroplast-bearing plankton ($20–630$ cells l^{-1}; Table 2) is reflected in the very low concentrations of chlorophyll *a* reported from the upper water column during the Arctic winter ($0.01–0.06$ µg l^{-1}; Table 2). Many Arctic phototrophic plankters are able to persist during unfavorable conditions as resting stages such as spores or cysts (Garrison, 1984; Smetacek, 1985; Kremp and Anderson, 2000), and diatoms are known for their potential to survive long periods of darkness (Antia and Cheng, 1970; Smayda and Mitchell-Innes, 1974; Palmisano and Sullivan, 1982; Sakshaug et al., 2009; Quillfeldt et al., 2009). The survival strategies of the various plastidic flagellates of Arctic waters throughout the dark period, however, are largely unknown.

The chloroplast-bearing flagellates *Micromonas pusilla* and *Phaeocystis pouchetii* may dominate the photosynthetic community during the Arctic spring and summer (Throndsen and Kristiansen, 1991; Booth and Horner, 1997; Not et al., 2005; Schoemann et al., 2005; Pettersen et al., 2011; Hegseth and Tverberg, 2013), and both are known to persist in Arctic waters throughout winter (Terrado et al., 2011; Lovejoy et al., 2007; Sherr et al., 2003; Rokkan Iversen and Seuthe, 2011). Both species have been identified from RNA extracted from sea water samples in Svalbard waters during the polar night (Vader et al., 2014), demonstrating the presence of active cells, not only dormant stages, during the polar night. This notion is further supported by the observation of exponential growth in a *Micromonas* population from winter to early spring in Franklin Bay (Lovejoy et al., 2007). As photosynthetic growth is unlikely during the polar night, a change to heterotrophy seems likely, and bacterivory has been suggested for *Micromonas* (Unrein et al., 2007; Sanders and Gast, 2012).

Small (<5 µm) heterotrophic flagellates are believed to cover their daily carbon demand exclusively by bacterivory, with grazing rates of $0.23–0.37 \times 10^8$ bacteria l^{-1} d^{-1} in December and January (Vaqué et al., 2008). These bacterial losses seem to be balanced by low but persistent bacterial activity and growth during winter (Sherr et al., 2003; Alonso-Saez et al., 2008; Belzile et al., 2008;

Garneau et al., 2008; Vaqué et al., 2008; Forest et al., 2011). At the same time, Nikrad et al. (2012) have found the proportion of highly active bacteria to decrease substantially from summer to winter, which suggests an overall decrease in bacterial growth in Arctic waters during winter. Indeed, growth rates as low as 0.004 ± 0.003 d^{-1} have been reported for the bacterial community in the central Arctic Ocean during winter (Sherr and Sherr, 2003). Consequently, bacterial production in Arctic surface waters during the polar night are 10–80 fold lower than those from the productive season (e.g. Sherr and Sherr, 2003; Garneau et al., 2008; Rokkan Iversen and Seuthe, 2011), ranging on average from 16 to 166 ng C l^{-1} d^{-1} (Table 2).

The polar-night production must be based on carbon remaining in the system from the previous growing season, or allochthonous carbon sources from river and land run-off. Either way, the growth substrate for bacteria is likely to be refractory and less bioavailable during the winter than during the light season of the year, suggesting that bacterial growth is likely to be substrate-limited in the Arctic during the darkest period of the winter (Garneau et al., 2008; Thingstad, 2009). This notion is supported by the reanalysis of published bacterial biomass and production values from Franklin Bay and the central Arctic Ocean (Fig. 4). The log-transformed data show a significant relationship between bacterial biomass and production with slopes of <0.4 (Sherr and Sherr, 2003; Sherr et al., 2003; Garneau et al., 2008), indicating an existing albeit weak substrate limitation of bacterial communities during winter (Billen et al., 1990; Ducklow, 1992).

Arctic prokaryotic communities seem to adapt to the low concentration and complex composition of the dissolved organic carbon pool during winter by diversification. For example, Archaea increase in abundance in Arctic surface waters during winter (Alonso-Saez et al., 2008), most likely because they are better adapted to utilizing more refractory carbon sources than bacteria (Wells and Deming, 2003; Alonso-Saez et al., 2008). The number of polymeric substrates used by Arctic prokaryotes is hence higher during winter than during summer (Sala et al., 2008). Recent work further demonstrates that Arctic prokaryotic communities expand their metabolic pathways to exploit the carbon sources available in the absence of photosynthetic production. For example, *Thaumarchaeota* were found to degrade urea and to use its carbon to grow throughout the Arctic winter (Alonso-Saez et al., 2012), while psychrophilic strains of bacteria seem to directly assimilate CO_2 under dark winter conditions (Alonso-Saez et al., 2010). The relative importance of these metabolic pathways for total prokaryotic production during winter is not yet known. However, the observed diversity and constancy in Arctic microbial plankton communities

Table 2

Stock sizes of different microbial plankton groups in the Arctic during the polar night (November–January), given as mean ± standard error of plastidic and heterotrophic protists (abundance: cells $* 10^3 l^{-1}$; biomass: µg C l^{-1}), prokaryotes. (abundance: cells $* 10^8 l^{-1}$; biomass: ng C l^{-1}), concentration of chlorophyll *a* (Chl *a*; µg l^{-1}), as well as bacterial production (BP; ng C l^{-1} d^{-1}). The contribution of pico-sized plastidic protists is given as percentage of the total plastidic protist stock.

Area	Chl *a*	Plastidic protists	% Pico	Heterotrophic protists	Prokaryotes	BP	References
Abundance							
Franklin Bay	0.06 ± 0.02				2.3 ± 0.3	32 ± 4	Garneau et al. (2008)
	0.05 ± 0.01	103 ± 17		398 ± 94	2.5 ± 0.3	52 ± 18	Vaqué et al. (2008)
Beaufort Sea	0.04 ± 0.003				5.2 ± 0.3		Nikrad et al. (2012)
Arctic Ocean		631 ± 134	46	275 ± 21	1.7 ± 0.1	16 ± 2	Sherr and Sherr (2003) and Sherr et al. (2003)
Kongsfjorden	0.01 ± 0.004	20 ± 3	17	96 ± 12	1.8 ± 0.6	166 ± 40	Rokkan Iversen and Seuthe (2011) and Seuthe et al. (2011)
Biomass							
Franklin Bay	0.05 ± 0.01	0.7 ± 0.4		2.2 ± 0.8	1.4 ± 0.1	52 ± 18	Vaqué et al. (2008)
Arctic Ocean		0.5 ± 0.1	26	2.1 ± 0.2	3.4 ± 0.2	16 ± 2	Sherr and Sherr (2003) and Sherr et al. (2003)
Kongsfjorden	0.01 ± 0.004	1.1 ± 0.4	0.1	3.2 ± 0.4	3.4 ± 0.1	166 ± 40	Rokkan Iversen and Seuthe (2011) and Seuthe et al. (2011)
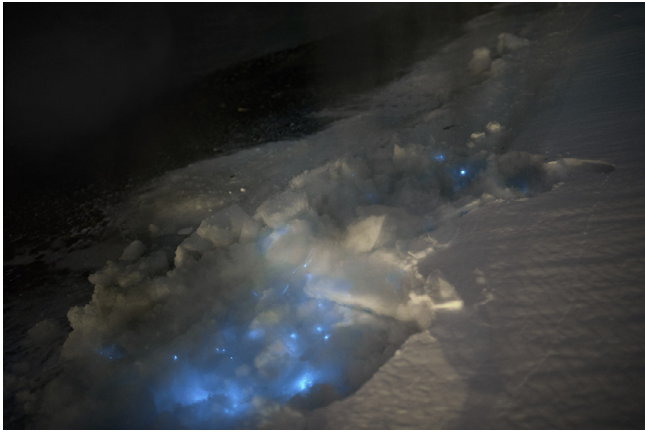
Fig. 4. Photo of bioluminescent organisms in sea ice along the shoreline in Adventfjorden February 2010. Photo: unknown.

throughout the polar night demonstrates that marine systems can sustain a baseline level of heterotrophy despite the absence of photosynthesis for a relatively long time span, such as the polar night.

7. Ice associated communities

Sea ice algae are primary producers and are therefore neither particularly active nor abundant during the polar night. However, for their vernal bloom to occur there must be a seeding population that is assumed to be trapped in the ice during its formation and survives in a state that allows viability as soon as growth conditions are favorable in late winter/early spring (for details see Leu et al., 2015; Quillfeldt et al., 2009). However, very little is known about the taxonomic composition of winter microbial communities in sea ice, and even less about their physiological activity. Near Barrow, Alaska, substantial amounts of dissolved and particulate organic matter were recorded prior to the algal spring bloom, and also in depth strata that presumably were not affected by algal activity (Juhl et al., 2011). These pools may serve as a basis for heterotrophic microbial communities. The general process of algal colonization of sea ice has previously been described by Syvertsen (1991). During the CASES study, Rozanska et al. (2008) followed the gradual development of a sea ice protist community during the autumn ice formation period. In CFL, Niemi et al. (2011) described for the very first time the taxonomic composition of a protist community in Arctic sea ice during the dark winter period. The community was characterized by very low chl *a* concentrations (max. $0.27 \, \mu g \, l^{-1}$), and low protist abundances (max. 4×10^3 cells l^{-1}), but was similar to spring ice assemblages with respect to species richness. Potential survival strategies of Arctic sea ice algae during the dark winter period were tested experimentally by Zhang et al. (1998). Only very few species formed resting spores, while heterotrophy (including mixotrophy) and energy storage seemed to be more important strategies to survive the dark winter months.

Prior to the US T-3 campaign in the 1950s, the collective scientific knowledge centered around ice associated communities are best summarized by the late Dr. J.L. Barnard in his 1959 monograph of the Amphipoda collected during the T-3 drift campaign: "The sampling area consists of a deep body of water covered with ice, far from a land mass, essentially a pelagic environment covered with a solid umbrella, offering a restricted amount of "inhospitable" living surface" (Barnard, 1959). Interestingly, all of the macrozooplankton species that have later been considered as obligate ice associated taxa (Arndt and Swadling, 2006; Macnaughton et al., 2007) were found and identified during the T-3 expedition

(Barnard, 1959), but all were considered as being strictly pelagic. It was not until the pioneering work of Melnikov (see Melnikov, 1997) and Gulliksen (e.g. Lønne and Gulliksen, 1991) that their association with sea ice became established. Since then, it has been well-known that the Arctic sea ice is host to a high number of marine invertebrates, with more than 1000 different species recorded (Bluhm et al., 2011). The sympagic macrofauna is commonly divided into two groups, the autochtonous and allochthonous species (Lønne and Gulliksen, 1991; Arndt and Swadling, 2006). The former consists of the species that are believed to live their entire life connected to the sea ice, whereas the latter consists of species that are connected to the sea ice only during parts of their life cycle. Although classified as autochthonous, there is evidence that at least several of the species in this group are in fact not totally dependent on multiyear sea ice in order to fulfill their lifecycle (Berge et al., 2012b).

Since there are few direct observations or records of ice associated organisms taken from the Arctic sea ice during the nautical polar night, their association with sea ice throughout the year has remained an assumption, rather than a fact. Recently, a new hypothesis regarding the adaptations and evolution of *Apherusa glacialis* has been proposed (Berge et al., 2012b), suggesting deep vertical migrations of at least one ice-obligate amphipod species during the polar night. Berge et al. (2012a,b) suggested that these migrations may have fitness benefits because of northward water mass movement at depth. Currently, the T-3 (Barnard, 1959), Russian drift stations (Melnikov, 1997) and Berge et al. (2012b) are the only available reports of ice associated fauna during the high Arctic polar night.

8. Zooplankton

In polar seas, zooplankton have evolved several special adaptations to survive long periods of continuous darkness with insufficient food supply (Hagen and Auel, 2001; Conover and Huntley, 1991). Diapause, a state of reduced metabolism, combined with build-up of large lipid reserves, are major features of polar life cycles (Hagen, 1999; Varpe et al., 2009). Our knowledge about the physiological state and behavior of zooplankton during the overwintering period is, however, very restricted (but see Conover and Huntley, 1991; Conover and Siferd, 1993). There is a need for studies of polar-night physiology and energy use combined with knowledge of behavior and life cycle stages. This will improve our understanding of the trade-offs inherent in the annual routines of polar zooplankton (Varpe, 2012) as well as the role of the polar night in shaping the schedule of activities at other times of the year. How strongly zooplankton reduce their metabolism during winter is poorly known even for the well- studied genus *Calanus* spp. (Darnis and Fortier, 2012), which comprise most (50–90%) of the mesozooplankton biomass in Arctic seas (Blachowiak-Samolyk et al., 2008; Kosobokova et al., 2011). For overwintering zooplankton, very few "*in situ*" measurements of metabolism are available. One recent study (Berge et al., in press) from Svalbard, reports on metabolism levels above those measured during spring and summer. Other existing studies on "winter" zooplankton metabolism are mainly from the winter–spring transition or fall (Hirche, 1989; Auel et al., 2003; Seuthe et al., 2007). Each year, the large herbivorous copepod *Calanus* spp. performs seasonal vertical migrations of several hundred meters, overwintering at depth in diapause for up to 10 months (Dawson, 1978; Hirche, 1997; Kosobokova, 1999; Ashjian et al., 2003; Darnis and Fortier, 2012). Active carbon transport by these large and lipid-rich zooplankton migrants is significant and may equal the gravitational particulate organic carbon (POC) fluxes in winter (Darnis and Fortier, 2012). The omnivorous copepod *Metridia longa* and the

smaller omnivores/detritivores copepods *Oithona similis*, *Triconia borealis*, *Pseudocalanus* spp., and *Microcalanus pygmaeus* are believed to remain active year-round and not perform extensive vertical migrations (Lischka and Hagen, 2005; Darnis and Fortier, 2012; Ashjian et al., 2003). These small omnivorous/detritivorous copepods, that numerically dominate Arctic zooplankton, contribute substantially to recycling organic carbon in the surface layer and to the attenuation of the vertical POC flux (Hopcroft et al., 2005). Predominance of small fecal pellets in the vertical POC flux in fall and winter (Forest et al., 2008; Lalande et al., 2009) suggests that these small copepods also are active and important carbon recyclers during the dark season.

Recent polar-night research has demonstrated that marine zooplankton species are not necessarily quiescent during the polar night. Some populations are found to undergo diel vertical migration (DVM) during the darkest months (Berge et al., 2009, 2012a, in press). A great deal of scientific attention has focused on DVM and the environmental signals responsible for its synchronization (for overview see e.g. Ringelberg, 2010). It is generally accepted that the ultimate reason for DVM is to avoid predation during the daytime, though the majority of experimental evidence comes from freshwater zooplankton species (Ringelberg and Van Gool, 2003). Zooplankton will move away from sunlight at dawn and follow isolumes during their downward migrations with peak photobehavioral responses demonstrated experimentally at wavelengths corresponding to those available during twilight in coastal water (Cohen and Forward, 2002). In nearly all animals and plants a light sensitive molecular machine exists called the circadian clock that provides a "time-sense" or an ability to anticipate future events. To date the only demonstration that a circadian clock exists in zooplankton is that of the krill *Euphausia superba* (Teschke et al., 2011). However, observations in the Arctic of upward migrations often pre-empting dusk (Berge et al., 2014), also provide evidence that at least part of this otherwise light-driven process include endogenous factors.

Marine organisms live in an environment influenced by not just the day/night solar cycle but also the lunar cycle which can influence both illumination and tidal movements. Under the extreme low-light conditions of the nautical polar night, the moon will for long periods of time be the dominating source of ambient light. It is well known that many marine species are able to synchronize their swimming patterns or spawning activities to the semi-lunar cycle (~15 days), which is coincident with full or new moon phases and maximum amplitude tides i.e. the spring/neap cycle (overview in Naylor (2006)). It is therefore not inconceivable to propose that any putative zooplankton clock will probably be able to entrain to lunar-day cycles at a time when the light of the moon masks the near absent solar signal.

The most extensive observations of DVM in the polar night have come from moored instrumentation, particularly the backscatter measured by Acoustic Doppler Current Profilers (ADCP). The strong seasonal variation in DVM in the Arctic was demonstrated using ADCP data by Wallace et al. (2010). Berge et al. (2009) demonstrated clearly that parts of the Arctic zooplankton community retain a diel vertical migration even during the darkest part of the polar night. Falk-Petersen and Hopkins (1981) demonstrated a distinct DVM in two krill species *Thysanoessa inermis* and *T. raschii*, but it should be noted that this study was carried out inside the civil twilight zone at 70°N. ADCPs have been deployed at several locations throughout the Arctic over a number of years such that patterns of zooplankton behavior (e.g. DVM) may in the future be compared and contrasted between the European and American sides of the Arctic Ocean. The next challenge in Arctic DVM studies is to provide a pan-Arctic view on this important process and how is modulated by the structure of zooplankton communities and physical drivers (Berge et al., 2014).

Another indirect measure of DVM has come from observations of bioluminescence during the polar night. Bioluminescence is a characteristic feature of all the world's oceans, but has been documented to be of special importance in the abyssal zone (Haddock et al., 2010). As such, it is a phenomenon likely to be dominant and persistent in dark environments such as the polar night. Documented bioluminescent taxa found in the Arctic include dinoflagellates, the copepod *Metridia longa*, the ctenophores *Mertensia ovum* and *Beröe cucumis*, and the krill species *Meganyctiphanes norvegica* (Berge et al., 2012a; Johnsen et al., 2014). Observations of a distinct and diurnal pattern of depth-varying bioluminescence in the upper 50 m of the water column during the darkest part of the polar night at 79°N have been interpreted as further evidence of DVM (Berge et al., 2012a; Johnsen et al., 2014). Bioluminescence has been observed in connection with sea ice (Fig. 4), often along edges of floes or in the intertidal where mechanical disturbance triggers a bioluminescent response in organisms (J. Berge, *pers obs*), but detailed studies of this phenomenon have not been performed.

9. Benthic communities

Benthic communities have rarely been studied during the polar night, with the lack of adequate data highlighted as one of the main gaps in knowledge in a review of Arctic marine benthos (Piepenburg, 2005). Nevertheless, the studies that do exist indicate that the polar night period is important for many elements of the Arctic benthos, including being a key period for invertebrate activity and reproductive processes, kelp growth, and elemental cycling processes in Arctic sediments (Berge et al., in press). Continuous growth throughout the year has been documented for both the bivalve *Chlamys islandica* (Berge et al., in press) and the amphipod *Onisimus litoralis* (Nygård et al., 2010), the latter without any seasonal change in total energy content, thus suggesting year-round feeding at significant levels. This species is part of a guild of scavenging amphipods active throughout the year and common in Arctic shelf waters, although different taxa appear to specialize on different prey items (Nygård et al., 2012). Such high levels of activity imply high levels of nutrient regeneration during the polar night at a time when benthic nutrients are easily mixed to surface waters due to lack of water-column stratification. Description and quantification of the activities of these and other hyperbenthic organisms, e.g. krill, which are associated with near-bottom waters during winter, could be revealing as their roles in benthic-pelagic transfer and elemental cycling during this period are virtually unknown.

Environmental conditions during the polar night can have significant consequences for recruitment success of intertidal and subtidal benthic invertebrates. Temperatures during the previous winter affect recruitment success in the barnacle, *Balanus crenatus* (Yakovis et al., 2013), as well as explaining 37% of the survival of infaunal bivalve spat during their first winter (Gerasimova and Maximovich, 2013). Furthermore, freezing of sediments, and occasional removal of the top several cm of sediment and associated fauna strongly impact infaunal community structure in the White Sea intertidal zone (Naumov, 2013). Whereas these studies conducted during winter in the White Sea investigate the benthos during a period of polar twilight due to the location of the study area just above the Arctic Circle, they do provide insight into processes that are most likely also important further north under conditions of polar night.

Primary producers require both light and inorganic nutrients (including traces of iron), but in the Arctic there is often a temporal mismatch in the availability of these two resources. Phytoplankton generally take advantage of the narrow time window in spring

when both are present, resulting in the characteristic intense spring bloom. Some macroalgae, belonging mainly to the kelp genera *Laminaria*, *Saccharina* and *Alaria*, however, are able to store the chemically bonded light energy as carbohydrates and sugar-alcohols derived from summer/autumn photosynthetic periods, but delay linear growth (lamina elongation) until winter periods (Chapman and Lindley, 1980). In fact, as much as 90% of annual linear growth in kelp, and in *Laminaria solidungula* in particular, occurs under ice cover during winter months (Dunton et al., 1982). Winter kelp growth, thus, provides an enhanced food resource and settlement substrate for benthic grazers and epifauna. The expected future 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 growth (Krause-Jensen et al., 2012; Clark et al., 2013). It is unclear, however, whether the availability of inorganic nitrogen will be sufficient to support this expected increase in winter growth, indicating a need for further studies of seasonal patterns in seawater chemistry, and its consequences for kelp growth.

In contrast to kelp, growth of many benthic fauna slows/stops during winter due to low temperatures and low food availability. This is recognizable as annual growth checks in e.g. bivalve shells (e.g. Ambrose et al., 2012). Many benthic organisms, particularly in deeper water, are long-lived and survive winter conditions, leading to little change in community structure, at least in soft-sediment communities (e.g. Pawłowska et al., 2011). Community activity (oxygen consumption), however, is at its annual minimum during winter (Welch et al., 1997; Rysgaard et al., 1998; Renaud et al., 2007), presumably due to reduced availability of sedimentary food supplies (phytopigments). 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 show that deposition of fresh organic matter even in the middle of winter leads to an almost immediate response in oxygen consumption by sediment communities (Morata et al., 2013). Studies of both oxic and suboxic mineralization (e.g. denitrification) rates in Arctic sediments, especially during winter, have led to the conclusion that biogeochemical processes are limited more by labile carbon than by low temperatures (e.g. Devol et al., 1997; Rysgaard et al., 1998). Taken together, these results indicate that the low level of activity displayed by Arctic sedimentary communities is not caused by some type of dormancy or temperature limitation, but instead by winter-feeding on sedimentary material of low quality. Thus, the paradigm of tight pelagic-benthic coupling in the Arctic is a good predictor of spatial and temporal patterns in benthic community structure and function. Changes in quality, quantity, and seasonality of food input to the benthos due to climate change (e.g. ACIA, 2005) may significantly change the nature of elemental cycling by Arctic benthos, affecting nutrient regeneration and carbon burial levels.

10. A reproductive high season

The polar night is important for various stages in the reproduction of many species of Arctic benthos. Ontogenesis of barnacle larvae (Marfenin et al., 2013) and brooding of amphipod eggs (Nygård et al., 2009) are continuous throughout winter until the release of larvae/juveniles in spring. In an examination of the life history characteristics of 63 amphipod species from Hornsund and Kongsfjorden, Weslawski and Legezynska (2002) found that most species incubated their juveniles during the polar night and/or winter months, whereas only three species incubated their offspring in spring and summer (see Weslawski and Legezynska, 2002).

Planktonic larvae (meroplankton) of benthic species (cirripeds, polychaetes) have been found to be present in the water column from mid-winter in Kongsfjorden, Svalbard (Willis et al., 2006; Walkusz et al., 2009). And in the first published year-round study of larval settlement in a location above the Arctic Circle, Kuklinski et al. (2013) documented recruitment of hard-bottom benthos throughout the year, including the polar night. Recently, the first documented records of egg-carrying females of the ice-associated *Apherusa glacialis* were made in the middle of the polar night in the Arctic Ocean (Berge et al., 2012b). Finally, the common amphipod *Pontoporeia femorata* is only known from females and immature males, with as-yet undescribed mature males believed to occur during winter months (Brandt and Berge, 2007). This indicates that the paradigm of synchronizing reproductive phases to the spring phytoplankton bloom is not consistent across Arctic benthic taxa (Berge et al., in press). Different stages in the reproductive cycle *may* be timed to coincide with the peak in pelagic food abundance in some organisms but may be completely decoupled in others. These findings suggest that alternative food sources are exploited by many meroplankton taxa and recent recruits. Clearly, further studies of reproductive dynamics of Arctic taxa, and nutrition of their early life-stages are needed, but processes taking place during the polar night are likely very important for many taxa.

Zooplankton have evolved different reproductive strategies (Fig. 5) which are closely related to their feeding strategy and ability to store and save energy (Hagen and Auel, 2001; Conover and Siferd, 1993). Small omnivorous copepods tend to be active year round in the Arctic, and *Oithona similis* and *Tricona borealis* are found to reproduce throughout the year, including the polar night, although their reproduction peaks in summer (Lischka and Hagen, 2005; Darnis et al., 2012). The opportunistic feeder *Pseudocanalus* spp., which switches between herbivory during the productive season to omnivory/carnivory in winter (Lischka and Hagen, 2007), may also spawn in winter but at very low rates (Hirche and Kosobokova, 2011; Darnis et al., 2012). The predominantly herbivorous copepods of the genus *Calanus* spp. are key zooplankters of high-latitude marine systems. They remove substantial amounts of organic matter from surface to depth by their yearly seasonal ontogenetic migration. The three co-occurring *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* are all capable of building up large lipid storages by converting low-energy carbohydrates and proteins in algae into high-energy
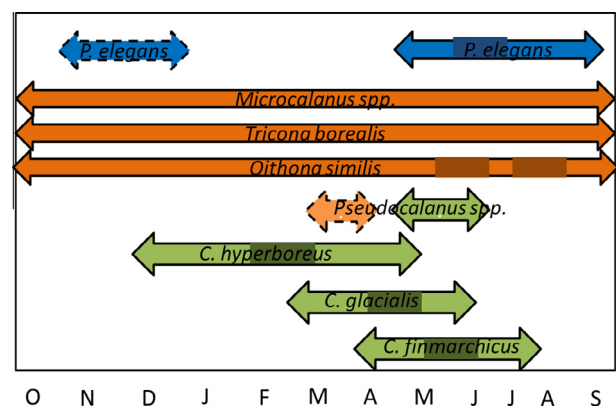

Fig. 5. Time windows of reproduction for common high-latitude zooplankton species. Darker colors within reproductive time windows indicate likely peaks in reproduction, while dashed arrows are uncertain due to few observations. Green arrows predominantly herbivorous copepods, orange omnivorous copepods and blue carnivorous zooplankton. See text for references.

wax ester lipids (Lee et al., 2006). However, only the largest of the three, the Arctic *C. hyperboreus*, is capable of reproducing during winter based on stored energy only (capital breeding) and, thus, 100% decoupled from the spring bloom (Hirche, 1997; Falk-Petersen et al., 2009). Nevertheless, males of all three species are present only during a short time-window and mainly during the polar night, underlining that important reproductive processes occur for all three species in winter (Niehoff et al., 2002; pers. obs.). The intermediate of the three *Calanus* spp.–*C. glacialis* – may start to reproduce in early February but reproduction peaks first when algal food, either in form of ice algae or phytoplankton, starts to appear (Hirche and Kattner, 1993; Søreide et al., 2010; Darnis et al., 2012). Another large Arctic copepod, the omnivore *Metridia longa*, can prey intensively on the nutritious *C. hyperboreus* eggs (Darnis et al., 2012), resulting in early reproductive start in this species also. Other carnivorous zooplankton such as *Paraeuchaeta* spp. have also been observed with eggs in winter and the abundant chaetognath *Parasagitta elegans*, a hermaphrodite, has been observed with gonads and sperm during the polar night (Darnis et al., 2012; Grigor et al., 2014).

In a recent review of the fish species occurring in the Barents Sea and Svalbard region (Wienerroither et al., 2011) it has been reported that 20% of the species reproduce during the months of December, January and February (Berge and Nahrgang, 2013). Perhaps the most well-known and best example of this is the polar cod, a species known to develop large gonads (>40% of the body weight) in preparation for spawning in January–February (Rass, 1968; Hop et al., 1995; Nahrgang et al., 2014). The reproductive strategy (including the extent of iteroparity vs semelparity) of polar cod has long been a matter of discussions (Nikolskii, 1950; Cohen, 1990; Sakurai et al., 1998; Hop et al., 1995), and is in general based upon studies of polar cod from captivity (Hop et al., 1995). Recent evidence suggests gender-specific reproductive strategies with iteroparous females and a male strategy closer to semelparity. However, these findings seem only true for polar cod from waters influenced by Arctic water masses, and did not hold true in regions of Atlantic influence (Nahrgang et al., 2014). Males enter gonadal maturation in the early autumn and reach maximum gonad size two months before females (Hop et al., 1995). The timing of reproduction is suggested to be adapted to match the period with maximum prey availability for the first feeding larvae (Fortier et al., 2006). Eggs of polar cod have only seldom been observed in the field (Rass, 1968) and have been mostly studied experimentally after natural spawning or *in vitro* fertilization (Aronovich et al., 1975; Graham and Hop, 1995; Sakurai et al., 1998). Polar cod eggs are large (1.6–1.9 mm) and buoyant (Andriashev, 1954; Aronovich et al., 1975; Andersen et al., 1994; Graham and Hop, 1995), and show normal embryonic development at between −1.5 and 3 °C and 12 and 50 psu (Doroshev and Aronovich, 1974; Aronovich et al., 1975; Sakurai et al., 1998). Extensive work has been carried out on the life history traits of polar cod larvae in particular in relation to hatching time and survival of first feeding larvae (Sekerak, 1982; Craig et al., 1982; Cannon et al., 1991; Ponton and Fortier, 1992; Gilbert et al., 1992; Ponton et al., 1993; Fortier et al., 1996, 2006; Michaud et al., 1996). Fortier and co-workers hypothesized two possible strategies: an early production of polar cod larvae (spring cohort) to match the first feeding with the potential early production of small cyclopoid nauplii, rather than the phytoplankton bloom and calanoid nauplii following ice break up. This cohort would suffer a high initial mortality but benefit from a substantially longer pre-winter growth to maximize size and body reserves for winter. A summer cohort on the contrary would have better initial conditions but a reduced growth and, thus, decreased overwintering chances (Fortier et al., 2006).

Kaartvedt (2008) hypothesized that the absence of large mesopelagic fish in the high Arctic is due to the polar-night light regime that strongly reduces encounters with prey. Recent observations on gut content of Atlantic and Arctic fishes from Svalbard (Berge et al., in press) showed that gadoids (Atlantic cod, haddock and polar cod) are able to capture prey during the polar night (also pelagic prey). Hence, it may be the ability to reproduce, rather than inability to feed during the polar night that is a key adaptation allowing only a few fish species to colonize the Arctic Ocean and adjacent shelf seas (Berge and Nahrgang, 2013). Accordingly, one would also expect that there is a higher percentage of capital vs income breeders (Varpe et al., 2009) among high Arctic fish species. Furthermore, an improved understanding of the visual capacity of Arctic fishes is needed to better understand their potential for prey encounter under low-light conditions. Initial studies of optical plasticity suggest that Arctic species, such as polar cod, may indeed differ from their sub-Arctic counterparts (Jönsson et al., in revision).

11. Outlook and important gaps in knowledge

The Arctic winter and polar night are emerging as key periods during which many reproductive and other ecological important processes occur (Berge et al., in press). Recent studies have demonstrated unexpected levels of activity in the pelagic zone during the polar night. These include diel vertical migration of zooplankton (Berge et al., 2009) and nekton (Webster et al., 2013), increased understanding of the microbial community structure and function (Rokkan Iversen and Seuthe, 2011), patterns of bioluminescence by pelagic organisms (Berge et al., 2012a; Johnsen et al., 2014), foraging by predators believed to rely at least in part on a visual search (Kraft et al., 2012; Berge et al., in press), and the ability to detect extreme low light levels in certain key zooplankton species (Båtnes et al., 2013; Cohen et al., 2015). These recent discoveries, in addition to the pioneering studies of Weslawski et al. (1991) and Melnikov (e. g. 1997), are currently representing a dramatic shift in our understanding of the marine system. We conclude, therefore, that in order to achieve a thorough and comprehensive understanding of the marine Arctic, it is no longer possible to ignore processes occurring during the polar night. For the benthic and sympagic habitats, however, little knowledge exists. There are also many types of cyclic activity in marine organisms that are highly synchronized within populations. It seems likely that marine zooplankton have a (circadian) biological clock entrained by the day/night cycle and that this clock is adaptive in initiating a migratory response even when external light cues are limited at depth. However, during the polar night, when the strongest source of illumination is no longer coming from the sun, moonlight probably plays an important role in entraining migratory behavior. Which species are implicated, and what the ultimate drivers are at this time, remains to be discovered. As shipping routes through the Northwest and Northeast Passage and the expanding oil, gas, fishery and mineral industries are increasingly active, the risk of environmental damage in the Arctic increases. There is a growing demand for sound management, decision-making, and governance guidelines that rely on a thorough research-based understanding of the ecosystem, not just snapshots from the bright part of the year. For example, we now know that many species across most phyla and trophic levels utilize the polar night for reproduction, hence increasing their potential vulnerability particularly during this part of the year. Knowledge of the patterns and processes that characterize the entire marine habitat during the polar night is, therefore, one of the most important gaps in knowledge preventing informed management of the Arctic.

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