ARTICLE IN PRESS

Progress in Oceanography xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

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

Jørgen Berge [a,b,*], Paul E. Renaud [b,c], Gerald Darnis [c], Finlo Cottier [d], Kim Last [d], Tove M. Gabrielsen [b,e], Geir Johnsen [b,f], Lena Seuthe [a], Jan Marcin Weslawski [g], Eva Leu [c,h], Mark Moline [i], Jasmine Nahrgang [a], Janne E. Søreide [b], Øystein Varpe [b,c], Ole Jørgen Lønne [b], Malin Daase [a], Stig Falk-Petersen [a,c]

[a] Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, 9037 Tromsø, Norway
[b] The University Centre in Svalbard, N-9171 Longyearbyen, Norway
[c] Akvaplan-niva, Fram Centre for Climate and the Environment, N-9296 Tromsø, Norway
[d] Scottish Association for Marine Sciences, Scottish Marine Institute, Oban, Argyll PA37 1QA, Scotland, UK
[e] University of Bergen, Institute of Biology, Pb 7803, N-5020 Bergen, Norway
[f] Dept. of Biology, Applied Underwater Robotics Laboratory, Norwegian University of Science and Technology (NTNU), N-7491 Trondheim, Norway
[g] Institute of Oceanology Polish Academy of Sciences, Powstancow Warszawy 55, 81-712 Sopot, Poland
[h] Alfred-Wegener-Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany
[i] School of Marine Science and Policy, University of Delaware, DE, USA

ARTICLE INFO

Article history:
Available online xxxx

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

* Corresponding author at: Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, 9037 Tromsø, Norway.
E-mail address: Jorgen.berge@uit.no (J. Berge).

http://dx.doi.org/10.1016/j.pocean.2015.08.005
0079-6611/© 2015 Published by Elsevier Ltd.

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., this issue). 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., this issue) 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

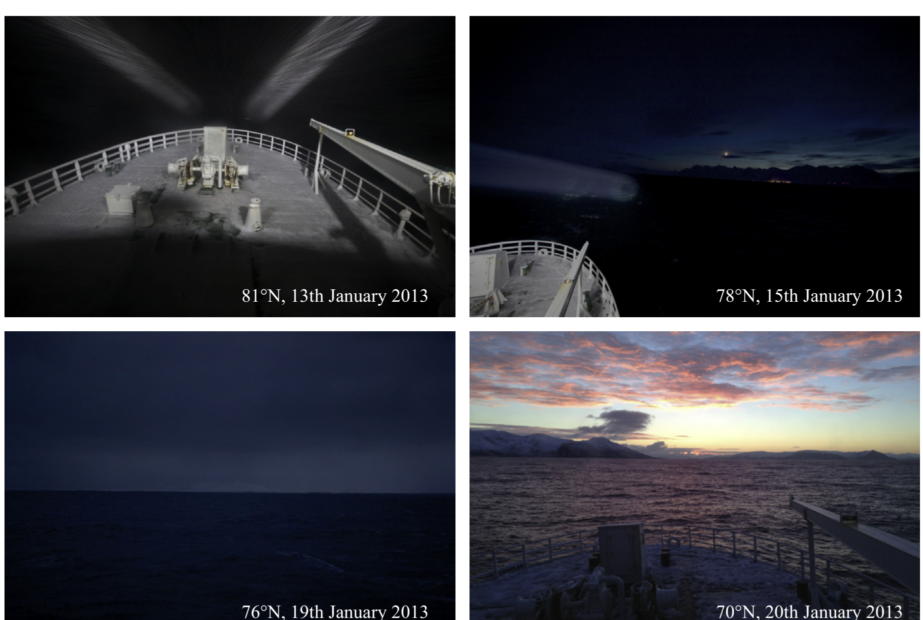

Fig. 1. Light levels as seen by the human eye during the polar night at 81° (upper left, Rijpfjorden), 78° (upper right, Longyearbyen), 76° (lower left, Bear Island), and 70° (lower right, Tromsø) North. All pictures were taken onboard the RV *Helmer Hanssen* at local sun noon within one week in January 2013. Photo: G Johnsen.

Please cite this article in press as: Berge, J., et al. In the dark: A review of ecosystem processes during the Arctic polar night. Prog. Oceanogr. (2015), http://dx.doi.org/10.1016/j.pocean.2015.08.005