

# Unexpected Levels of Biological Activity during the Polar Night Offer New Perspectives on a Warming Arctic

Jørgen Berge,<sup>1,2,\*</sup> Malin Daase,<sup>1</sup> Paul E. Renaud,<sup>2,3</sup> William G. Ambrose, Jr.,<sup>3,4</sup> Gerald Darnis,<sup>3</sup> Kim S. Last,<sup>5</sup> Eva Leu,<sup>3</sup> Jonathan H. Cohen,<sup>6</sup> Geir Johnsen,<sup>2,7</sup> Mark A. Moline,<sup>6</sup> Finlo Cottier,<sup>1,5</sup> Øystein Varpe,<sup>2,3</sup> Natalia Shunatova,<sup>8</sup> Piotr Bałazy,<sup>9</sup> Nathalie Morata,<sup>10</sup> Jean-Charles Massabuau,<sup>11,12</sup> Stig Falk-Petersen,<sup>1,2</sup> Ksenia Kosobokova,<sup>13</sup> Clara J.M. Hoppe,<sup>14</sup> Jan Marcin Węśławski,<sup>9</sup> Piotr Kukliński,<sup>9</sup> Joanna Legeżyńska,<sup>9</sup> Daria Nikishina,<sup>8</sup> Marine Cusa,<sup>1</sup> Monika Kędra,<sup>9</sup> Maria Włodarska-Kowalczyk,<sup>9</sup> Daniel Vogedes,<sup>1,2</sup> Lionel Camus,<sup>3</sup> Damien Tran,<sup>11,12</sup> Emma Michaud,<sup>10</sup> Tove M. Gabrielsen,<sup>2</sup> Andrei Granovitch,<sup>8</sup> Anya Gonchar,<sup>8</sup> Rupert Krapp,<sup>1</sup> and Trine A. Callesen<sup>2</sup>

<sup>1</sup>Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, 9037 Tromsø, Norway

<sup>2</sup>University Centre in Svalbard, Pb 156, 9171 Longyearbyen, Norway

<sup>3</sup>Akvaplan-niva, Fram Centre for Climate and the Environment, 9296 Tromsø, Norway

<sup>4</sup>Department of Biology, Bates College, Lewiston, ME 04240, USA

<sup>5</sup>Scottish Marine Institute, Scottish Association for Marine Science, Oban PA37 1QA, UK

<sup>6</sup>School of Marine Science and Policy, University of Delaware, Lewes, DE 19958, USA

<sup>7</sup>Trondheim Biological Station, Norwegian University of Science and Technology, 7491 Trondheim, Norway

<sup>8</sup>Department of Invertebrate Zoology, Biological Faculty, Saint Petersburg State University, Universitetskaya nab. 7/9, St. Petersburg 199034, Russia

<sup>9</sup>Institute of Oceanology Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland

<sup>10</sup>Laboratoire des Sciences de l'Environnement Marin, LEMAR, UMR 6539, CNRS-IRD-UBO-Ifremer, IUEM, Technopôle Brest-Iroise, Rue Dumont d'Urville, 29280 Plouzané, France

<sup>11</sup>EPOC, UMR 5805, University Bordeaux, 33400 Talence, France

<sup>12</sup>CNRS, EPOC, UMR 5805, 33400 Talence, France

<sup>13</sup>Institute of Oceanology, Russian Academy of Science, 117997 Moscow, Russia

<sup>14</sup>Alfred Wegener Institute – Helmholtz Center for Polar and Marine Research, 27570 Bremerhaven, Germany

\*Correspondence: [jorgen.berge@uit.no](mailto:jorgen.berge@uit.no)

<http://dx.doi.org/10.1016/j.cub.2015.08.024>

## SUMMARY

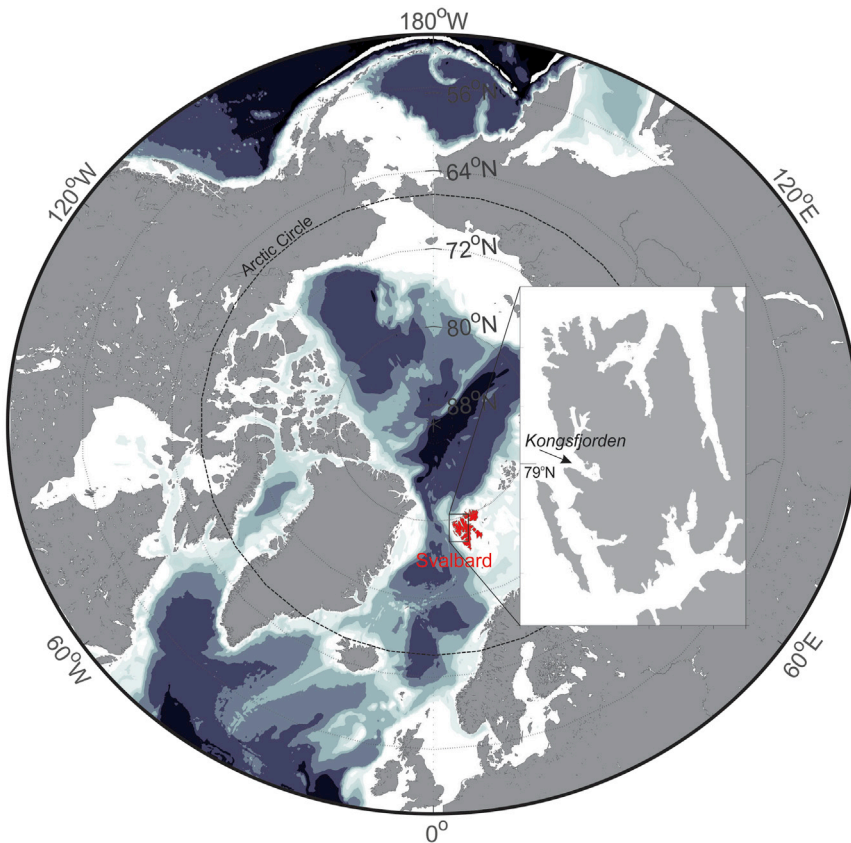
The current understanding of Arctic ecosystems is deeply rooted in the classical view of a bottom-up controlled system with strong physical forcing and seasonality in primary-production regimes. Consequently, the Arctic polar night is commonly disregarded as a time of year when biological activities are reduced to a minimum due to a reduced food supply. Here, based upon a multidisciplinary ecosystem-scale study from the polar night at 79°N, we present an entirely different view. Instead of an ecosystem that has entered a resting state, we document a system with high activity levels and biological interactions across most trophic levels. In some habitats, biological diversity and presence of juvenile stages were elevated in winter months compared to the more productive and sunlit periods. Ultimately, our 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 [1].

## RESULTS AND DISCUSSION

During three consecutive winters (January 2013–January 2015), we conducted sampling in Kongsfjorden, Svalbard (79°N 11°E; Figure 1). Our aim was to study biodiversity, biological activity, and ecosystem functions from microalgae to avian top predators, in both pelagic and benthic realms (Figures 2 and 3). We targeted the second half of the 117-day-long polar night when biological activity was expected to be at or near the minimum. Compiling observations from across most phyla and trophic levels allows us to draw conclusions at a scale of biological organization not achievable from more narrow studies [2] and to unequivocally oppose the classical paradigm of an ecosystem in resting mode. This paradigm has recently been challenged for the pelagic ecosystem of the Canadian Arctic [3, 4]. Among our most striking results were continuous growth in bivalves, actively foraging seabirds, and a persistent circadian cycle in both zooplankton and benthos throughout the polar night. Although several prior studies have examined selected aspects of Arctic marine ecosystems from a winter perspective [3–7], none have focused on the darkest period of the year and with an ecosystem perspective.

### Pelagic Communities

Mid-winter studies from Kongsfjorden [8, 9] and elsewhere in the Arctic [5, 10] have described a microbial community dominated by heterotrophic bacteria and flagellates, with chlorophyll *a* (Chl *a*)



**Figure 1. Study Area**

Map showing Svalbard (red) and the study area (Kongsfjorden) inserted.

virtually undetectable. Indeed, Chl *a* concentrations measured in January 2014 and 2015 ( $0.01\text{--}0.02\ \mu\text{g L}^{-1}$ ) were 2–3 orders of magnitude lower than during the spring bloom [11]. Nonetheless, diatom and dinoflagellate cells with high pigment concentration and exhibiting strong Chl autofluorescence were detected in surface waters (Figure S1). In situ photosynthetic rates were below detection limits ( $0.003 \pm 0.002\ \mu\text{mol C (Chl } a)^{-1}\ \text{d}^{-1}$ ). However, when transferred to artificially illuminated conditions at in situ temperatures, primary production was measurable at an irradiance of  $0.5\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$  ( $0.465 \pm 0.004\ \mu\text{mol C (Chl } a)^{-1}\ \text{d}^{-1}$ ), indicating that the phytoplankton community was primed to take advantage of the returning light by the end of the polar night (mid-February) when ambient surface irradiance reaches levels between  $0.1$  and  $1\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$  in Kongsfjorden [12].

Despite no measurable pelagic primary production in January, herbivorous and omnivorous mesozooplankton species were present throughout the water column (Figures 2A and 2B), albeit in lower abundance than during the summer and autumn (i.e., [9, 13, 14]). Contrary to the common conception that polar organisms synchronize their reproduction with the spring bloom [15], we found evidence of winter reproduction in a range of zooplankton, including herbivorous, omnivorous, and carnivorous taxa. Copepod nauplii were the most abundant organisms in the zooplankton community (Figure 2A), indicating reproduction of planktic cyclopoids (e.g., *Oithona similis*) and some calanoids (e.g., *Microcalanus* spp., *Metridia longa*). Juvenile stages of ctenophores (*Mertensia ovum*) and pteropods (*Clione limacina*, *Lima-cina* spp.), as well as meroplanktic larvae (Nudibranchia, Bivalvia, Polychaeta, Bryozoa) were observed. Moreover, male *Calanus* co-

pepods, largely absent from the population during the light season [14, 16], were observed in high proportions during the polar night at depths between 50 and 200 m (sex ratio 1:4 in favor of females), together with females bearing spermatophores. Such observations confirm the importance of the polar night as the major mating period for this key component of Arctic ecosystems.

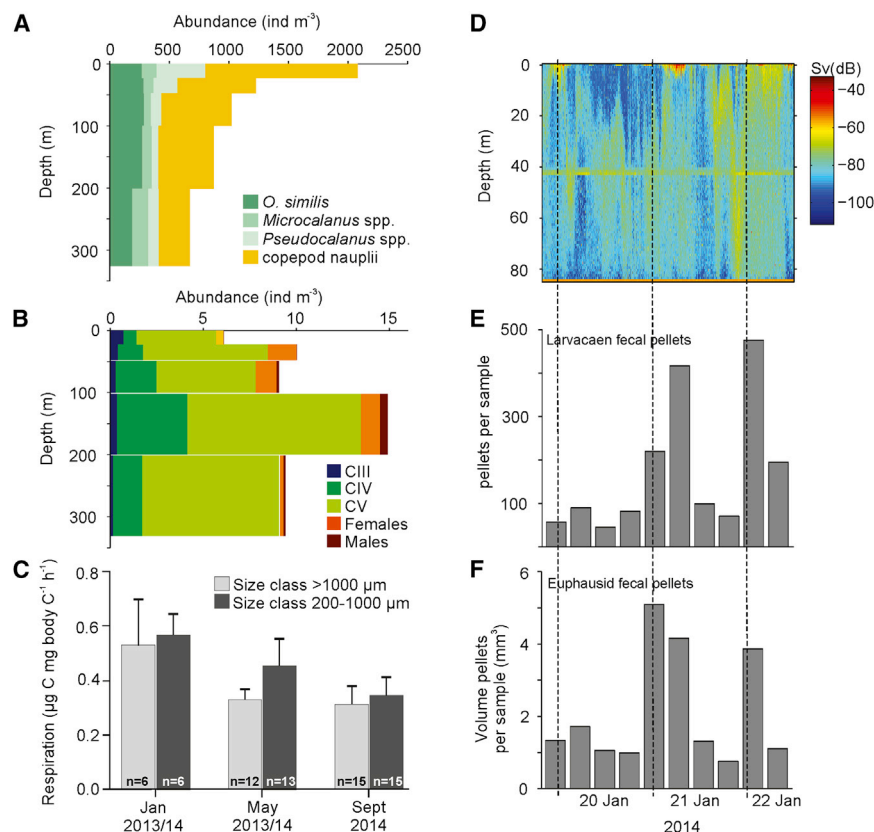
In general, the *Calanus* life cycle includes an overwintering period during which certain developmental stages descend toward the bottom where they spend the winter in a state of diapause [15, 17]. We, however, found overwintering stages of *Calanus* spp. distributed throughout the entire water column (Figure 2B). Those *Calanus* specimens inhabiting deep oceanic waters (>500 m) may exhibit a more profound form of dormancy during winter [18–20] than in shallow waters (<500 m water depth), perhaps since shallow-water populations

may need to be more active to counteract buoyancy forces [21]. However, *Calanus* can successfully overwinter in shelf and coastal waters (<500 m), and they are usually found at greater depth during autumn and winter [22–24], with their ascent related to ice breakup and the onset of the spring bloom [22, 23]. Our results reveal not only that *Calanus* commence their ascent long before light and food become abundant but also that zooplankton respiration rates per unit biomass in the uppermost 100 m of water column in Kongsfjorden were *higher* in January than in May or September (Figure 2C) and within the range of measurements made in July north of Svalbard [25]. It is unclear how this activity may be sustained.

Acoustic measurements from mid-January to February (Figure S1) obtained using a 125-kHz Acoustic Zooplankton and Fish Profiler (AZFP) confirm previous reports of diurnal vertical migration (DVM) during the polar night [12, 26]. The pattern is weak in mid-January (Figure 1D) but becomes more pronounced from late January onward (Figure S1) as the day-night cycle intensifies. Furthermore, the occurrence of euphausiid and larvacean fecal pellets in sediment traps (Figures 2E and 2F) indicates feeding in surface waters during the polar night. The importance of this winter DVM and feeding for the pelagic carbon flux should be assessed to better understand biogeochemical cycling of carbon in high Arctic marine ecosystems characterized by an extensive dark season.

### Benthic Communities

Biodiversity, abundance, growth, and reproduction in habitats studied were at similar or higher levels than during seasons



**Figure 2. Pelagic Processes in Kongsfjorden during the Polar Night**

(A) Abundance of small copepods and copepod nauplii (average of five replicate samples). (B) Abundance of copepodite stages of *Calanus* spp. (average of four replicate samples). (C) Respiration rates per unit mass of large (>1,000  $\mu\text{m}$ ) and small (200–1,000  $\mu\text{m}$ ) mesozooplankton size classes. Values were higher in January compared to May and September (Kruskal-Wallis test;  $p < 0.0157$  and  $p < 0.0007$  for large and small mesozooplankton, respectively). Error bars are SDs of  $n$  replicates. (D) Absolute volume backscatter ( $S_v$ , in dB) in the upper 80 m from January 20–22, 2014. (E and F) Larvacen (E) and euphausiid (F) fecal pellets in sediment traps from of January 20–22, 2014.

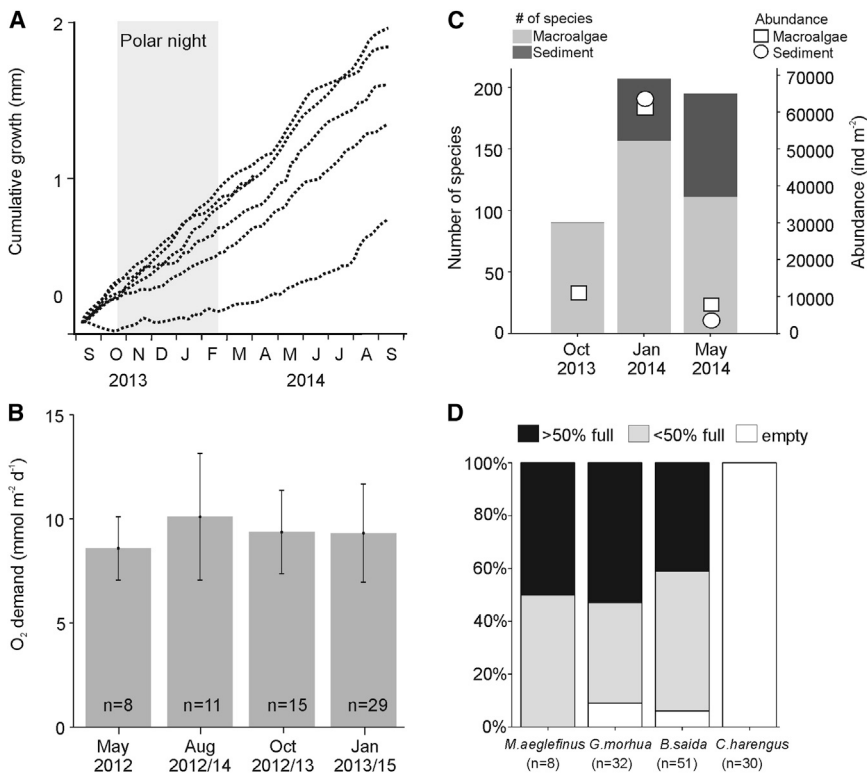
with substantial primary productivity (Figures 3A–3D). Strikingly, growth rates in the filter-feeding bivalve *Chlamys islandica* did not slow during the polar night compared to the rest of the year (Figure 3A). This observation is contrary to seasonal reductions in growth for many bivalve species around the world, especially at high latitudes [27, 28]. Based on these results, we suggest that filter-feeding bivalves likely use resuspended detrital material when fresh phytoplankton is not available. If this material is of lower quality, it could still lead to the occurrence of growth rings (caused by seasonal differences in shell growth), but it raises questions as to the generality of seasonal growth patterns. The recorded winter density of benthic macrofauna in Kongsfjorden sediments (mean 9,830 individuals  $\text{m}^{-2}$  in January) did not differ significantly from that recorded in other seasons (from 6,300 to 8,880 individuals  $\text{m}^{-2}$  on average), a pattern also noted in shallower habitats [29]. While this was expected for multi-year and infaunal non-migratory organisms, it was surprising that sediment community respiration rates measured in January were on par with those measured at the same stations at different times of the year (Figure 3B) and other Arctic locations during summer [30]. In January 2013, temperatures close to the bottom were 3–5 degrees lower than during summer and autumn (Figure S3). Both bivalve feeding and community respiration results may be explained by recent findings documenting that fjord benthos incorporate significant amounts of macroalgal detritus into their diets [31]. As macroalgae abundance in polar regions is generally predicted to increase with increasing temperatures [32, 33], this trophic link may increase ecosystem resilience to climate change by reducing the reliance

of benthic communities on the highly seasonal, pelagic primary producers [31]. Abundance and biodiversity of fauna associated with the kelp *Saccharina latisima* and surrounding sediments were considerably higher in January compared to October and May at the same location (Figure 3C). Average densities of invertebrates in January reached more than 60,000 individuals  $\text{m}^{-2}$ , approximately an order of magnitude greater than values recorded in May and October. Some of this pattern was caused by prolific settlement by a number of benthic species such as *Margarites helicinus*, *Capitella capitata*, and *Circeis armoricana*. Baited traps with time-lapse cameras revealed an abundant, active and species-rich shallow-water scavenging community, dominated by gastropods (*Buccinum* spp.), amphipods (*Anonyx* spp. and *Onisimus* spp.), and crabs (*Hyas araneus*) (Movie S1). Thus, rates of growth, respiration, and reproduction for the examined benthic organisms were not lower during the polar night compared to other times of the year. In addition, measurements of a potential circadian cycle (24 hr) in both *Chlamys islandica* valve opening and vertical migration of zooplankton indicated that, despite 4 months of apparent darkness, activity cycles remain entrained to the existing but weak diurnal cycles [34] and cues (Table S1).

### Seabird and Fish Communities

Kongsfjorden hosts large seabird colonies with a marked seasonal peak in abundance during spring and summer as they migrate south or to the open ocean during winter [35]. Nevertheless, a number of seabird species were observed foraging in Kongsfjorden (Table 1), although in much lower numbers than during the summer, including little auks (*Alle alle*), black guillemots (*Cepphus grylle*), Brünnich's guillemots (*Uria lomvia*), northern fulmars (*Fulmarus glacialis*), black legged kittiwakes (*Rissa tridactyla*), and glaucous gulls (*Larus hyperboreus*). Most examined individuals showed evidence of recent feeding (Table 1). The most abundant food items were fish, euphausiids (*Thysanoessa* spp.), and benthic amphipods (*Anonyx nugax*). Actively foraging seabirds under continuously dark conditions have not previously





**Figure 3. Processes in Benthic and Fish Communities in Kongsfjorden during the Polar Night**

(A) Cumulative growth of *Chlamys islandica* specimens (five out of ten examined).

(B) Benthic respiration rates measured at two sites in January (2013, 2015), May (2012), August (2012, 2014), and September (2012, 2013). Error bars are SDs of n replicates.

(C) Number and abundance of species on *Saccharina latissima* ("Macroalgae") and in the surrounding sediment ("Sediment") in October 2013, January 2014, and May 2014.

(D) Percentage of empty, <50%, or >50% full stomachs of four fish species caught in a single trawl in January 2015.

been reported, although one study from 69°N [36] did report cormorants foraging throughout the winter. Importantly, however, at 69°N, there is still considerable ambient light during the daytime [4]. While a dedicated study of how seabirds might detect their prey was not performed, the low degree of digestion in most of the examined stomachs allows us to conclude that they had been foraging locally and thus under continuously dark conditions. Further, most examined birds appear to have selected just one type of prey, not a random selection of available prey items (Table 1). Some of the prey items such as *Thysanoessa* spp. (krill) are known to be bioluminescent [37], which might act as a cue for detecting these organisms in the dark [37–39]. However, there are clearly other search mechanisms that need to be investigated, such as acoustic and/or tactile mechanisms, as suggested for cormorants and petrels [36, 40].

Active predation by fish was similarly apparent from stomach analyses of specimens collected from both pelagic and bottom trawls at depths down to 250 m (Figure 3D). Interestingly, the more boreal and planktivorous herring (*Clupea harengus*) did not show evidence of feeding, while approximately half of the investigated individuals of polar cod (*Boreogadus saida*), haddock (*Melanogrammus aeglefinus*), and Atlantic cod (*Gadus morhua*) exhibited a stomach fullness over 50% (Figures 2D and S2). All of these observations confirm active feeding by top predators in the system and raise the question as to how species known to be visual predators other times of the year are able to find their prey during the polar night.

### Outlook and Implications

Irradiance (E) is extremely low during the winter polar night period [34], resulting in primary production rates close to zero

Kongsfjorden during the polar night contradict this paradigm. We describe a system in which most taxa and trophic levels are active either earlier than expected or throughout the polar night. In the absence of photosynthetic production, trophic interactions and metabolic rates remained high for most examined consumers, indicating that organisms are able to sustain their activities on alternative food sources or stored reserves. Primary producers were physiologically active and able to rapidly commence photosynthesis as soon as E reached 0.5  $\mu\text{mol photons s}^{-1}\text{m}^{-2}$ , a level occurring (at this site) 2–3 weeks before the sun rises above the horizon (J.H.C., unpublished data). High activity by grazing zooplankton could be linked to the observation that phytoplankton are physiologically able to rapidly commence photosynthesis when even very low light levels return. Ultimately, the ability to take advantage of primary production as soon as it occurs may counteract the potential costs of being active during the polar night. Furthermore, predation by many Arctic species does not seem to be as visually oriented as expected, even for fish and birds (Figure 3D; Table 1). Successful prey detection results in continued feeding during the polar night by a large proportion of both pelagic and benthic predators (Figures 2 and 3). Finally, opportunism (or quick response to environmental cues) may be an important strategy for many species, as evidenced by our findings of classical pelagic-feeding seabirds found with stomachs full of benthic prey, rapid response of the benthic scavengers to food-fall items that become available in the environment, and continuous growth of a suspension feeder. We therefore suggest a working hypothesis of a top-down, as opposed to bottom-up, control of polar marine ecosystems during the polar night. Understood in a strictly classical meaning of the term, this implies that the timing and magnitude of the Arctic

**Table 1. Stomach Contents and Morphometrics of Seabirds Caught in Kongsfjorden in January 2014 and 2015**

Species	Total Weight (g)	Bill Length (cm)	Tarsus Length (cm)	Date of Collection	Stomach Contents
<i>Alle alle</i>	230	1.50	2.84	January 21, 2014	digested remains, mostly empty
<i>Alle alle</i>	182	1.40	2.75	January 21, 2014	digested remains of crustaceans, mostly empty
<i>Alle alle</i>	176	1.54	2.77	January 23, 2014	digested remains of crustaceans, mostly empty
<i>Alle alle</i>	204	1.30	2.51	January 25, 2015	104 <i>Thysanoessa</i> spp.
<i>Alle alle</i>	158	1.12	2.53	January 25, 2015	1 large <i>Anonyx nugax</i> (full stomach)
<i>Uria lomvia</i>	728	3.33	4.75	January 21, 2014	fish otoliths and digested remains, no fresh food
<i>Uria lomvia</i>	660	3.66	3.81	January 21, 2014	1 <i>Thysanoessa</i> spp., 11 <i>Anonyx nugax</i>
<i>Uria lomvia</i>	802	3.40	4.32	January 23, 2014	>200 <i>Thysanoessa</i> spp., vertebrae/otoliths
<i>Cephus grylle</i>	374	3.63	3.51	January 23, 2015	10 <i>Anonyx nugax</i>
<i>Fulmaris glacialis</i>	–	–	–	January 21, 2014	digested remains, potentially waste from boat
<i>Larus hyperboreus</i>	1,582	5.91	8.75	January 22, 2014	2 <i>Hiatella arctica</i> , 3 pieces of plastic

spring bloom may not be the ultimate driver for biological interactions and processes during the entire year but rather that governance of ecosystem structure and function is shifted toward higher trophic levels during the polar night. This further implies that, in the absence of primary production, the activities and trophic interactions reported herein were maintained based on stored, recycled, and/or advected energy.

Most of the Arctic seas (including the Arctic Ocean itself) are advective systems dominated by the in- or through-flow of Atlantic water [44, 45]. Our study area both is located well within the high Arctic region and is a region that has undergone significant changes during the last decade. Kongsfjorden has been largely ice-free all year since 2006, and intrusions of Atlantic water have influenced both its general oceanography [46, 47] and biology [48, 49]. As a result, winter temperatures during the last three winters were generally 2°C–3°C higher compared to the preceding two winters (Figure S3), rendering the fjord a more Atlantic-influenced and warmer location than previously. As such, it provides a relevant and realistic projection of what the pan-Arctic domain may look like in the relative near future. Some of our individual findings (Figure 2) are in agreement with previous studies, including activity and reproduction of small mesozooplankton in mid-winter [3, 6, 50], ascent of *Calanus* spp. by January [51, 52], and reproduction and settlement of benthic species throughout the winter [53]. They are, however, in contrast with several other studies that found no evidence of early ascent in *Calanus* [23, 54] and low respiration rates of benthos and zooplankton in mid-winter [55, 56]. Some of the concurring studies [50, 51] are from regions strongly influenced by Arctic water and heavy seasonal sea ice, suggesting that low ice cover and warm water temperatures alone do not explain our observations. Nevertheless, the most dramatic change likely to occur in the Arctic is that currently ice-covered regions will become seasonally ice-free, leading to a larger and more productive Marginal Ice Zone [42]. The annual minimum ice extent

occurs in September and only reaches its maximum in March [57]. Since the polar night is initiated in October at high latitudes, it follows that larger areas of ice-free seas will “experience” the polar night in the future. Thus, our results documenting activity levels across most major phyla from an ice-free Kongsfjorden will likely be highly relevant for broader areas of Arctic ecosystems in the future.

In order to understand how the Arctic Ocean and its ecosystems are changing, attention needs to be directed toward a more factual understanding of today’s biological patterns, processes that occur during the polar night, and the mechanisms responsible for them. Since most biological surveys have ignored the polar night under the old paradigm that activity is low, there are no available comprehensive ecosystem studies that may be used in comparison with ours. However, our conclusion that the ecosystem is not dormant during the polar night is supported by the findings in a recent study of the heterotrophic pelagic food web of the Canadian Arctic [3] and recent case studies mainly from Svalbard [4]. Based on this, and in accordance with our proposed working hypothesis of increased top-down control of Arctic ecosystems during the polar night, a new perspective emerges—a system less orchestrated by production regimes than previously assumed and where the timing of annual routines is not primarily linked with the onset of the spring bloom. The immediate implication of this is that knowledge-based management of a region experiencing enhanced environmental change must begin to consider processes taking place during the polar night.

#### EXPERIMENTAL PROCEDURES

This study was performed according to and within the regulations enforced by the Norwegian Animal Welfare authorities, and no specific permissions were required, except for hunting of seabirds, which was conducted with

permission from the Governor of Svalbard, given in accordance with the environmental protection regulations for Svalbard. The R/V Helmer Hanssen is owned by the University of Tromsø and has all necessary authorization from the Norwegian Fisheries Directorate to use a bottom trawl to collect fish for scientific purposes. Methods and any associated references are available in the [Supplemental Information](#).

### SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, one table, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.08.024>.

### AUTHOR CONTRIBUTIONS

J.B.: principle investigator, study design, acoustics, fish and bird sampling, interpretation, and manuscript preparation; M.D.: zooplankton sampling and analysis, sediment trap analysis, interpretation, and manuscript and figure preparation; P.E.R.: study design, interpretation, and manuscript preparation; W.G.A.: scallop growth, interpretation, and manuscript preparation; G.D.: zooplankton sampling and analysis, zooplankton respiration, interpretation, and manuscript review; K.S.L.: acoustics, interpretation, and manuscript review; E.L. and C.J.M.H.: primary production measurements, epifluorescence, interpretation, and manuscript preparation and review; J.H.C.: study design, interpretation, and manuscript review; G.J.: study design, interpretation, and manuscript review; M.A.M.: study design, interpretation, and manuscript review; Ø.V.: bird and fish sampling and stomach analysis, interpretation, and manuscript review; N.S. and D.N.: analysis of infauna and epifauna on macroalgae; P.B.: benthic scavengers and time-lapse video; N.M. and E.M.: benthic respiration measurements, fauna sampling, and manuscript review; J.-C.M.: scallop growth and activity measurements; S.F.-P.: study design, interpretation, and manuscript review; K.K.: zooplankton analysis and manuscript review; J.M.W.: study design, interpretation, and manuscript review; P.K., J.L., M.K., and M.W.-K.: benthic macrofauna sampling and analyses and manuscript review; M.C.: fish sampling and stomach analysis and manuscript review; D.V.: zooplankton and bird sampling, instrumentation, interpretation, and manuscript review; L.C. and D.T.: scallop growth and activity analysis; T.M.G.: interpretation and manuscript review; F.C.: acoustics, interpretation, and manuscript review; A. Granovitch: study design, benthic analyses, and manuscript review; A. Gonchar: bird sampling and analyses; R.K.: bird sampling and analyses; T.A.C.: zooplankton sampling and analysis.

### ACKNOWLEDGMENTS

This study is a contribution to the Norwegian Research Council (NRC) funded projects Circa (NRC 214271) and Marine Night (NRC 226417). The first author was financially supported through the EWMA project (NRC 195160) funded by NRC and ENI Norge AS, whereas other authors received funding from AMOS CoE at NTNU (NRC 223254), Talking Clam (NRC 208974), EMAP (NRC 233635), Russian Foundation for Basic Research (project number 13-04-00551), Russian Scientific Foundation (project number 14-50-00095), Statoil, National Science Foundation (PLR-141763), and the Polish Ministry of Science and Higher Education (W157/Norway/2013). The benthic macrofauna study was supported by the French National Agency under the retour Post Doct program (ECOTAB project: ANR 11 PD0C 018 01) and Norwegian Arctic Field grant (WIMBA project). Benthic taxonomy work was funded by the Laboratoire d'Excellence LabexMER (ANR-10-LABX-19) and co-funded by a grant from the French government under the program Investissements d'Avenir. Also, the EU DEVOTES project and Svalbard Science Forum have co-financed part of the work. Jasmine Nahrgang, Pierre Ciret, Mohamedou Sow, Rudolph Corvaisier, Emilie Courtecuisse, and Zofia Smola are acknowledged for their help and Joanne Muratori for editorial assistance. We are grateful to two anonymous reviewers for their constructive comments on an earlier version of the manuscript.

Received: June 15, 2015

Revised: July 15, 2015

Accepted: August 10, 2015

Published: September 24, 2015

### REFERENCES

- Comiso, J.C., Parkinson, C.L., Gersten, R., and Stock, L. (2008). Accelerated decline in the Arctic Sea ice cover. *Geophys. Res. Lett.* **35**, L01703.
- Boyd, P.W. (2013). Framing biological responses to a changing ocean. *Nat. Clim. Chang.* **3**, 530–533.
- Darnis, G., Robert, D., Pomerleau, C., Link, H., Archambault, P., Nelson, R.J., Geoffroy, M., Tremblay, J.E., Lovejoy, C., Ferguson, S.H., et al. (2012). Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. *Clim. Change* **115**, 179–205.
- Berge, J., Renaud, P., Darnis, G., Cottier, F., Last, K., Gabrielsen, T., Johnsen, G., Seuthe, L., Weslawski, J.M., Leu, E., et al. In the dark: a review of ecosystem processes during the Arctic polar night. *Prog. Oceanogr.* Published online August 28, 2015. 10.1016/j.pocean.2015.08.005.
- Węśławski, J.M., Kwasniewski, S., and Wiktor, J. (1991). Winter in a Svalbard fjord ecosystem. *Arctic* **44**, 115–123.
- Hirche, H., and Kosobokova, K. (2011). Winter studies on zooplankton in Arctic seas: the Storfjord (Svalbard) and adjacent ice-covered Barents Sea. *Mar. Biol.* **158**, 2359–2376.
- Legeżyńska, J., Kędra, M., and Walkusz, W. (2012). When season does not matter: summer and winter trophic ecology of Arctic amphipods. *Hydrobiologia* **684**, 189–214.
- Iversen, K.R., and Seuthe, L. (2010). Seasonal microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): I. Heterotrophic bacteria, picoplankton and nanoflagellates. *Polar Biol.* **34**, 731–749.
- Seuthe, L., Rokkan Iversen, K., and Narcy, F. (2011). Microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): II. Ciliates and dinoflagellates. *Polar Biol.* **34**, 751–766.
- Horner, R., and Schrader, G.C. (1982). Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of Beaufort Sea. *Arctic* **35**, 485–503.
- Leu, E., Falk-Petersen, S., Kwaśniewski, S., Wulff, A., Edvardsen, K., and Hesse, D.O. (2006). Fatty acid dynamics during the spring bloom in a high Arctic fjord: importance of abiotic factors versus community changes. *Can. J. Fish. Aquat. Sci.* **63**, 2760–2779.
- Berge, J., Cottier, F., Last, K.S., Varpe, Ø., Leu, E., Søreide, J., Eiane, K., Falk-Petersen, S., Willis, K., Nygård, H., et al. (2009). Diel vertical migration of Arctic zooplankton during the polar night. *Biol. Lett.* **5**, 69–72.
- Kwaśniewski, S., Hop, H., Falk-Petersen, S., and Pedersen, G. (2003). Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *J. Plankton Res.* **25**, 1–20.
- Walkusz, W., Kwaśniewski, S., Falk-Petersen, S., Hop, H., Tverberg, V., Wieczorek, P., and Węśławski, J.M. (2009). Seasonal and spatial changes in the zooplankton community of Kongsfjorden, Svalbard. *Polar Res.* **28**, 254–281.
- Falk-Petersen, S., Mayzaud, P., Kattner, G., and Sargent, J. (2009). Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.* **5**, 18–39.
- Kosobokova, K.N. (1999). The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. *Polar Biol.* **22**, 254–263.
- Conover, R.J. (1988). Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* **167**, 127–142.
- Hirche, H.J. (1996). Diapause in the marine copepod, *Calanus finmarchicus* - a review. *Ophelia* **44**, 129–143.
- Ingvardsdottir, A., Houlihan, D.F., Heath, M.R., and Hay, S.J. (1999). Seasonal changes in respiration rates of copepodite stage V *Calanus finmarchicus* (Gunnerus). *Fish. Oceanogr.* **8**, 73–83.
- Jonasdottir, S.H. (1999). Lipid content of *Calanus finmarchicus* during overwintering in the Faroe-Shetland Channel. *Fish. Oceanogr.* **8** (Suppl. 1), 61–72.
- Pond, D.W., and Tarling, G.A. (2011). Phase transitions of wax esters adjust buoyancy in diapausing *Calanoides acutus*. *Limnol. Oceanogr.* **56**, 1310–1318.

22. Madsen, S.D., Nielsen, T.G., and Hansen, B.W. (2001). Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. *Mar. Biol.* **139**, 75–93.
23. Darnis, G., and Fortier, L. (2014). Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean). *J. Plankton Res.* **36**, 1092–1108.
24. Clark, K.A.J., Brierley, A.S., and Pond, D.W. (2012). Composition of wax esters is linked to diapause behavior of *Calanus finmarchicus* in a sea loch environment. *Limnol. Oceanogr.* **57**, 65–75.
25. Alcaraz, M., Almeda, R., Calbet, A., Saiz, E., Duarte, C.M., Lasternas, S., Agusti, S., Santiago, R., Movilla, J., and Alonso, A. (2010). The role of Arctic zooplankton in biogeochemical cycles: respiration and excretion of ammonia and phosphate during summer. *Polar Biol.* **33**, 1719–1731.
26. Wallace, M.I., Cottier, F.R., Berge, J., Tarling, G.A., Griffiths, C., and Brierley, A.S. (2010). Comparison of zooplankton vertical migration in an ice-free and a seasonally ice-covered Arctic fjord: an insight into the influence of sea ice cover on zooplankton behavior. *Limnol. Oceanogr.* **55**, 831–845.
27. Lutz, R.A., and Rhodes, D.C. (1980). Growth patterns within the molluscan shell: an overview. In *Skeletal Growth of Aquatic Organisms*, R.A. Lutz, and D.C. Rhodes, eds. (Plenum Press), pp. 203–254.
28. Ambrose, W.G., Renaud, P.E., Locke, W.L., Cottier, F.R., Berge, J., Carroll, M.L., Levin, B., and Ryan, S. (2012). Growth line deposition and variability in growth of two circumpolar bivalves (*Serripes groenlandicus* and *Clinocardium ciliatum*). *Polar Biol.* **35**, 345–354.
29. Kędra, M., Kulinski, K., Walkusz, W., and Legeżyńska, J. (2012). The shallow benthic food web structure in the high Arctic does not follow seasonal changes in the surrounding environment. *Estuar. Coast. Shelf Sci.* **114**, 183–191.
30. Jørgensen, B.B., Glud, R.N., and Holby, O. (2005). Oxygen distribution and bioirrigation in Arctic fjord sediments (Svalbard, Barents Sea). *Mar. Ecol. Prog. Ser.* **292**, 85–95.
31. Renaud, P.E., Lokken, T.S., Jørgensen, L.L., Berge, J., and Johnson, B.J. (2015). Macroalgal detritus and food-web subsidies along an Arctic fjord depth gradient. *Front. Mar. Sci.* **2**, 31.
32. Krause-Jensen, D., Marba, N., Olesen, B., Sejr, M.K., Christensen, P.B., Rodrigues, J., Renaud, P.E., Balsby, T.J.S., and Rysgaard, S. (2012). Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. *Glob. Change Biol.* **18**, 2981–2994.
33. Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P.E., Rodrigues, J., Lonne, O.J., and Gulliksen, B. (2012). Climate-driven regime shifts in Arctic marine benthos. *Proc. Natl. Acad. Sci. USA* **109**, 14052–14057.
34. Cohen, J.H., Berge, J., Moline, M.A., Sørensen, A.J., Last, K., Falk-Petersen, S., Renaud, P.E., Leu, E.S., Grenvald, J., Cottier, F., et al. (2015). Is ambient light during the high Arctic polar night sufficient to act as a visual cue for zooplankton? *PLoS ONE* **10**, e0126247, <http://dx.doi.org/10.1371/journal.pone.0126247>.
35. Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwaśniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Włodarska-Kowalecuk, M., et al. (2002). The marine ecosystem of Kongsfjorden, Svalbard. *Polar Res.* **21**, 167–208.
36. Grémillet, D., Kuntz, G., Gilbert, C., Woakes, A.J., Butler, P.J., and le Maho, Y. (2005). Cormorants dive through the Polar night. *Biol. Lett.* **1**, 469–471.
37. Johnsen, G., Candeloro, M., Berge, J., and Moline, M. (2014). Glowing in the dark: discriminating patterns of bioluminescence from different taxa during the Arctic polar night. *Polar Biol.* **37**, 707–713.
38. Berge, J., Båtnes, A.S., Johnsen, G., Blackwell, S.M., and Moline, M.A. (2012). Bioluminescence in the high Arctic during the polar night. *Mar. Biol.* **159**, 231–237.
39. Haddock, S.H.D., Moline, M.A., and Case, J.F. (2010). Bioluminescence in the sea. *Annu. Rev. Mar. Sci.* **2**, 443–493.
40. Martin, G.R., and Prince, P.A. (2001). Visual fields and foraging in procelariiform seabirds: sensory aspects of dietary segregation. *Brain Behav. Evol.* **57**, 33–38.
41. Tremblay, J.E., Robert, D., Varela, D.E., Lovejoy, C., Darnis, G., Nelson, R.J., and Sastri, A.R. (2012). Current state and trends in Canadian Arctic marine ecosystems: I. Primary production. *Clim. Change* **115**, 161–178.
42. Wassmann, P., and Reigstad, M. (2011). Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. *Oceanography (Wash. D.C.)* **24**, 220–231.
43. Kaartvedt, S. (2008). Photoperiod may constrain the effect of global warming in arctic marine systems. *J. Plankton Res.* **30**, 1203–1206.
44. Carmack, E., and Wassmann, P. (2006). Food webs and physical-biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. *Prog. Oceanogr.* **71**, 446–477.
45. Carmack, E., Barber, D., Christensen, J., Macdonald, R., Rudels, B., and Sakshaug, E. (2006). Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. *Prog. Oceanogr.* **71**, 145–181.
46. Nilsen, F., Gjevik, B., and Schauer, U. (2006). Cooling of the West Spitsbergen Current: isopycnal diffusion by topographic vorticity waves. *J. Geophys. Res.- Oceans* **111**, C08012.
47. Cottier, F.R., Nilsen, F., Inall, M.E., Gerland, S., Tverberg, V., and Svendsen, H. (2007). Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. *Geophys. Res. Lett.* **34**, L10607.
48. Nahrgang, J., Varpe, O., Korshunova, E., Murzina, S., Hallanger, I.G., Vieweg, I., and Berge, J. (2014). Gender specific reproductive strategies of an arctic key species (*Boreogadus saida*) and implications of climate change. *PLoS ONE* **9**, e98452.
49. Berge, J., Hegglund, K., Lønne, O.J., Cottier, F., Hop, H., Gabrielsen, G.W., Nottestad, L., and Misund, O.A. (2015). First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard archipelago, Norway, with possible explanations for the extension of its distribution. *Arctic* **68**, 54–61.
50. Ussing, H.H. (1938). The biology of some important plankton animals in the fjords of east Greenland. *Medd. Grøn.* **100**, 1–108.
51. Daase, M., Varpe, Ø., and Falk-Petersen, S. (2014). Non-consumptive mortality in copepods: occurrence of *Calanus* spp. carcasses in the Arctic Ocean during winter. *J. Plankton Res.* **36**, 129–144.
52. Błachowiak-Samolyk, K., Wiktor, J., Hegseth, E., Wold, A., Falk-Petersen, S., and Kubiszyn, A. (2015). Winter Tales: the dark side of planktic life. *Polar Biol.* **38**, 23–36.
53. Kukliński, P., Berge, J., McFadden, L., Dmoch, K., Zajackowski, M., Nygård, H., Piwosz, K., and Tatarek, A. (2013). Seasonality of occurrence and recruitment of Arctic marine benthic invertebrate larvae in relation to environmental variables. *Polar Biol.* **36**, 549–560.
54. Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M., and Van Keuren, D. (2003). Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **50**, 1235–1261.
55. Renaud, P.E., Riedel, A., Michel, C., Morata, N., Gosselin, M., Juul-Pedersen, T., and Chiuchio, A. (2007). Seasonal variation in benthic community oxygen demand: a response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? *J. Mar. Syst.* **67**, 1–12.
56. Seuthe, L., Darnis, G., Riser, C.W., Wassmann, P., and Fortier, L. (2007). Winter-spring feeding and metabolism of Arctic copepods: insights from faecal pellet production and respiration measurements in the southeastern Beaufort Sea. *Polar Biol.* **30**, 427–436.
57. Barber, D., Hop, H., Mundy, C.J., Brent, E., Dmitrenko, I.A., Tremblay, J.É., Ehn, J.K., Assmy, P., Daase, M., Candlish, L.M., et al. Selected physical, biological and biogeochemical implications of a rapidly changing Arctic Marginal Ice Zone. *Prog. Oceanogr.* Published online September 12, 2015. [10.1016/j.pocean.2015.09.003](https://doi.org/10.1016/j.pocean.2015.09.003).