

Current Biology

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

Highlights

- The polar night is not a time of biological quiescence
- Biological rhythms and activity levels are retained during the polar night
- Seabirds are overwintering and actively foraging throughout the polar night
- Ecological processes across most phyla and trophic levels remain high

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In Brief

Berge et al. provide evidence that challenges the classical paradigm of biological quiescence during the Arctic polar night. Instead of an ecosystem that has entered a resting state, they document a system in which diversity, activity levels, and biological interactions across most trophic levels and phyla remain high during the winter.

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

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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*)

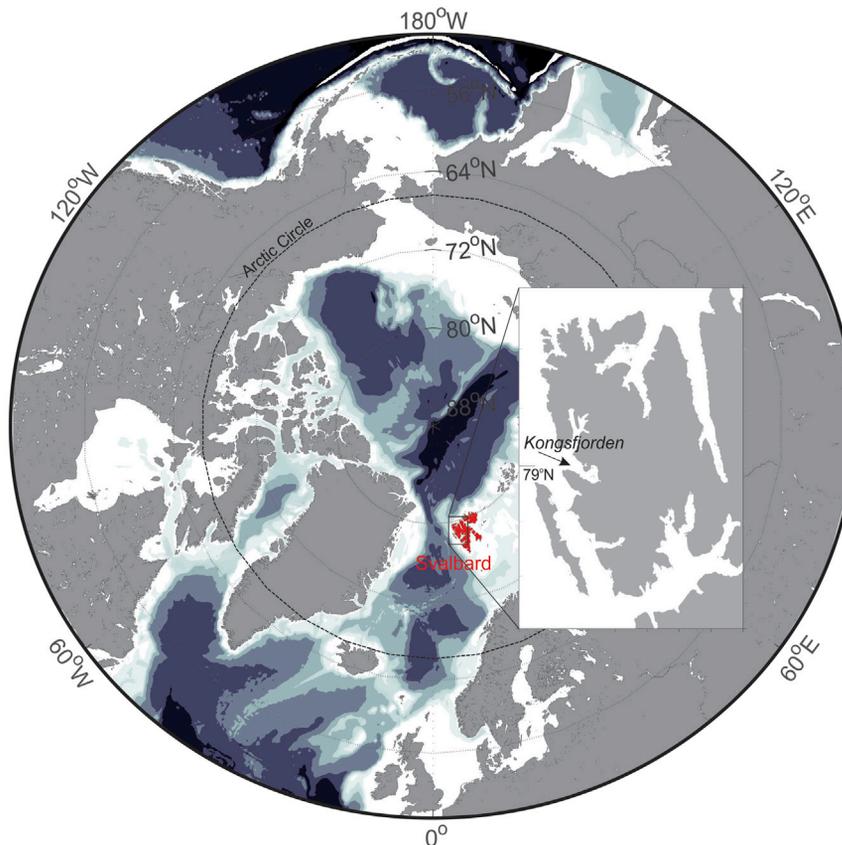


Figure 1. Study Area

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

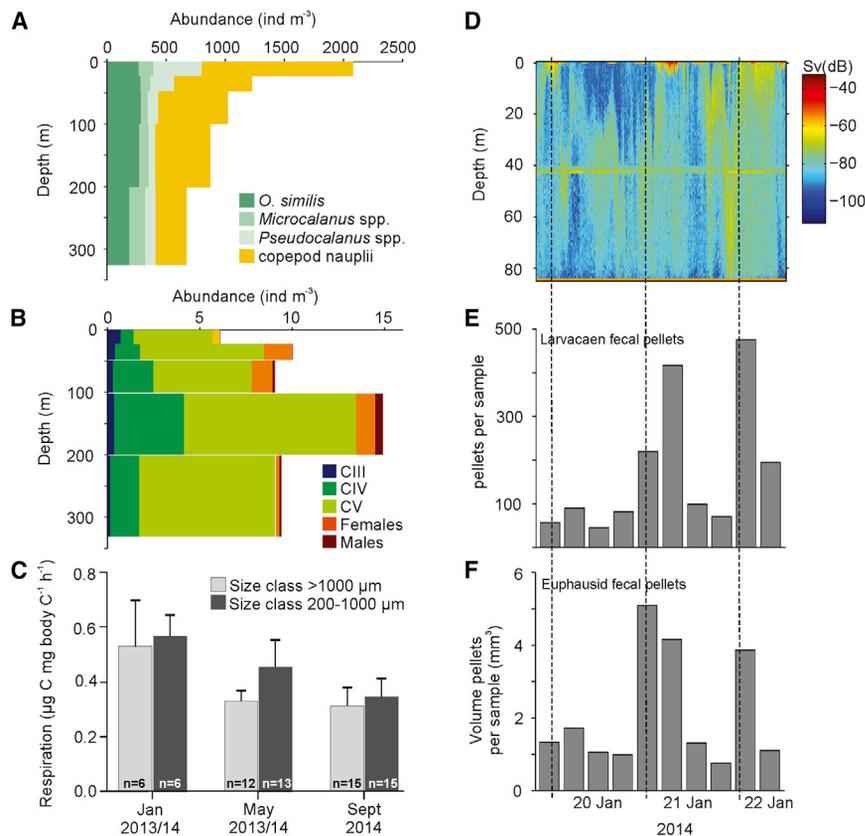


Figure 2. Pelagic Processes in Kongsfjorden during the Polar Night

(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 μm) and small (200–1,000 μm) 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) Larvacean (E) and euphausiid (F) fecal pellets in sediment traps from of January 20–22, 2014.

of benthic communities on the highly seasonal, pelagic primary producers [31].

Abundance and biodiversity of fauna associated with the kelp *Saccharina latissima* 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 m^{-2} , approximately an order of magnitude greater than values re-

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 m^{-2} in January) did not differ significantly from that recorded in other seasons (from 6,300 to 8,880 individuals 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

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

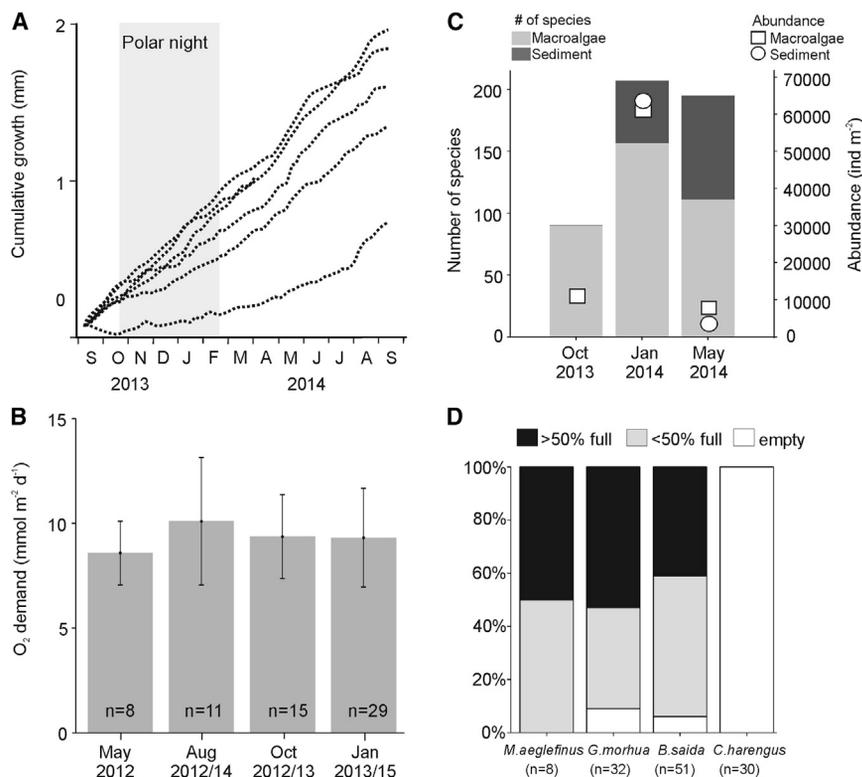


Figure 3. Processes in Benthic and Fish Communities in Kongsfjorden during the Polar Night

(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>Cepphus 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.

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Current Biology

Supplemental Information

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

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Supplemental Data

Supplemental figures and tables

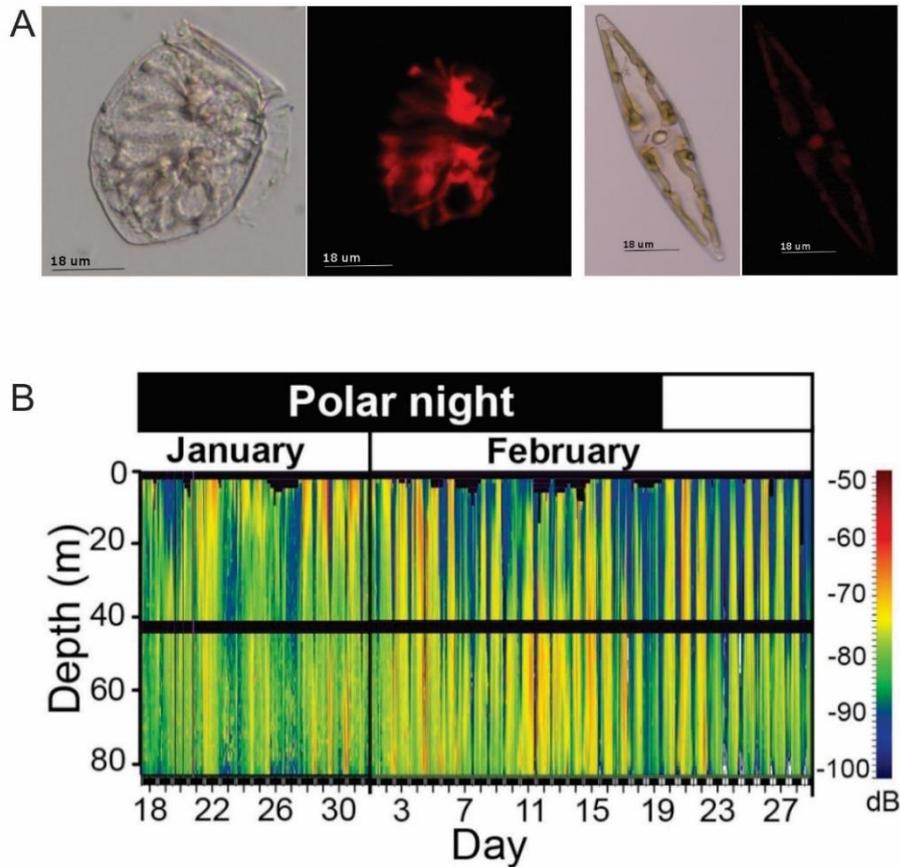


Figure S1: Microscopy and autofluorescence of (left) *Dinophysis* sp. and (right) *Pleurosigma* cf. *stuxbergii* (a). Time series of absolute volume backscatter (S_v) in decibel (dB) in the upper 80 m in Kongsfjorden from January-February 2014 (b); warmer colors indicate higher biomass (scale bar to the right). Vertical bands represent sound scattering layers. These bands become gradually stronger across the entire water column towards the end of the period, and represent migrating scattering layer. From January 27th the clear bands appear in the surface (0-30m), and from 4th of February they extend all the way down to 80m. Black horizontal line at about 40m depth represent a sediment trap (data deleted due to artificially high backscatter from the metal frame of the sediment traps). Related to Figure 2 and Table S1.

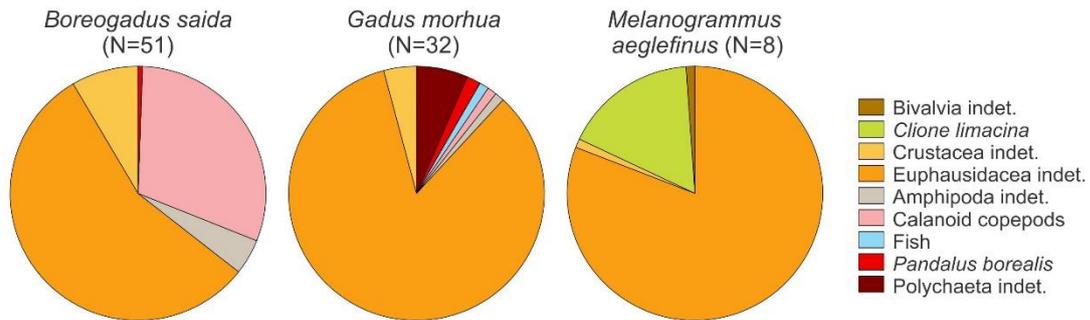


Figure S2: Prey species composition in the stomachs of three gadoid fish species caught in a single trawl in Kongsfjorden in January 2015. Data present relative contribution of prey items from each category. Related to Figure 3.

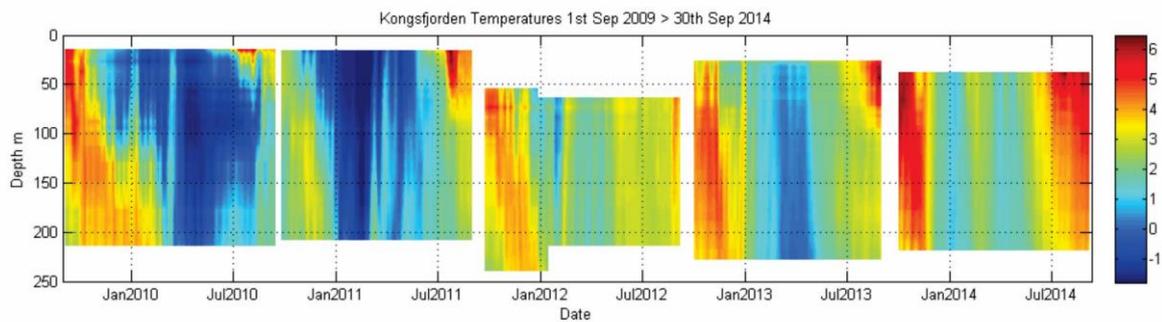


Figure S3: Temperature profile measured in Kongsfjorden from 2009-2014 by a mooring equipped with temperature loggers (37-SM MicroCAT, Sea-Bird Electronics and Vemco temperature mini loggers) spaced through the water column (for details on the mooring see [S1]). Related to Figure 1.

Table 1: Diel activity cycles in benthic bivalves (valve movements) and zooplankton during the polar night. Related to Figure 3.

Time period	Circadian period		P value
	Scallops	Zooplankton	
26 th Aug - 21 st Oct 2013	24.0 hrs	no data	p <0.0001
21 st Oct - 17 th Feb 2014	24.0 hrs	23.8 hrs	p <0.0001
17 th Feb – 16 th April 2014	23.9 hrs	23.8 hrs	p <0.0001

Supplemental information: Methods

Study area

Kongsfjorden is a glacial, west-facing fjord on the island of Spitsbergen in the Svalbard archipelago at 79°N. Water flow in the fjord is under geostrophic control [S2], and there is no distinct shallow sill at the fjord’s mouth. It is, therefore, directly linked to the shelf and slope along West Spitsbergen and as such, it provides a large “mesocosm environment” in which we may examine a variety of biotic parameters of relevance for larger oceanographic regions and processes. Consequently, Kongsfjorden is one of the most thoroughly studied marine ecosystems in the Arctic [S3, 4] including long-term observation of zooplankton, soft and rocky bottom benthos, and seabirds (e.g. [S3, 5, 6]). The majority of the research in Kongsfjorden, however, has been conducted during the Arctic light season (April-September). At 79°N the polar night is defined as *Nautical polar night* when the sun is at most 12.4° below the horizon. Levels of ambient downwelling irradiance (PAR, E) measured in air at noon when the sun is 9° below the horizon (medio January) is on the order of 10^{-5} $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, rendering levels of ambient light at depth in the water several orders of magnitude lower [S7].

Primary producers and epifluorescence

Samples were collected with a plankton net (20 μm mesh size) close to the sea surface, and pre-screened through 63 μm mesh to eliminate large grazers. Chl *a*-specific net primary production (NPP) was determined in 24h incubations both *in situ* as well as in the laboratory directly after sampling and after 2 days of exposure to low light (6 ± 1 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; 14 hours daylength). After addition of a 20 μCi (0.37 MBq) spike of $\text{NaH}^{14}\text{CO}_3$ (PerkinElmer, 53.1 mCi mmol^{-1} stock), duplicate samples (seawater pH_{NBS} of 8.04 at *in situ* temperature) were immediately placed in a culture room at 1.6 ± 0.4 °C and 6 ± 1 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Another set of samples was incubated in the fjord at 0.5 m water depth. After 24h, samples were filtered

onto GF/F-filters, acidified with 6N HCl and left to degas overnight. Filters were then transferred back into scintillation vials, to which 10 mL of scintillation cocktail was added (Ultima Gold AB, PerkinElmer). After 2h, the samples were measured on a liquid scintillation counter (DPM_{sample}; Tri-Carb, PerkinElmer), using automatic quench correction and a maximum counting time of 5 minutes. For blank determination (DPM_{0%}), one extra sample per treatment and measurement day was filtered and acidified immediately after addition of the ¹⁴C spike. To determine the total amount of NaH¹⁴CO₃ (DPM_{100%}) added, filtered seawater was spiked with 1 µCi mL⁻¹ NaH¹⁴CO₃. From these samples, 10 different 0.5 mL aliquots were immediately removed and mixed with 10 mL of scintillation cocktail. These samples were directly measured after 2h of reaction time with the cocktail. Chlorophyll *a* concentrations at the start of the incubation period were measured fluorometrically after extraction overnight in 90% acetone (Trilogy Fluorometer, Turner Designs). The initial amount of dissolved inorganic carbon (DIC) of HgCl₂-fixed subsamples was measured colorimetrically using a QuAAtro autoanalyzer (Seal; (46)). NPP rates [µg C (µg Chl)⁻¹ d⁻¹] were calculated as:

$$\text{NPP} = ([\text{DIC}] * (\text{DPM}_{\text{sample}} - \text{DPM}_{0\%}) * 1.05) / (\text{DPM}_{100\%} * t * [\text{Chl}])$$

where [DIC] and [Chl] denote the concentrations of dissolved inorganic carbon and Chl *a* in the sample, respectively. DPM_{sample} denotes the disintegrations per minute (DPM) in the samples, DPM_{0%} reflects the blank value, DPM_{100%} denotes the DPM of the total amount of NaH¹⁴CO₃ added to the samples, and t is the duration of the incubation.

Phytoplankton autofluorescence was measured on samples fixed with buffered formalin and glutaraldehyde. Pictures were taken with a Nikon DS Camera (DS-5M & DS-L1) on a Nikon converted microscopy (Eclipse TE300) equipped with a Super High Pressure Mercury Lamp (C-SHG1).

Zooplankton sampling

Zooplankton were sampled by vertical hauls (towing speed 0.5 m s⁻¹) from close to the seafloor to the surface using a multiple opening/closing net (Multinet, Hydrobios, Kiel, mouth opening 0.25 m²). *Calanus* spp. were sampled using a mesh size of 200 µm, smaller copepods and nauplii were collected using a mesh size of 64 µm. Samples were preserved in a 4% formaldehyde-in-seawater solution until analysis under a Leica stereomicroscope. Samples were examined by sub-sampling with aliquots obtained with 5 ml automatic pipette, with the pipette tip cut at 5 mm diameter to allow free collection of mesozooplankton. Large (total length > 5 mm) organisms were removed before taking sub-samples. The number of subsamples

analyzed was chosen so that at least 150 *Calanus* and 300 small copepods were counted from each sample. Samples with low abundance were examined in their entirety.

Zooplankton respiration

Additional multinet casts were made to catch live mesozooplankton for respiration and biomass measurements at station KB3 (78°57N, 11°56E, 330 m) in January, May and September 2014. Each of the five nets of the sampler was fitted with a 2-L rigid cod-end with filtration apertures at the top of the cylinder to keep the animals in sufficient water until collection. Upon retrieval, each sample was diluted in cold filtered (0.2-0.7 μm GF/F) seawater (FSW) and the potential few large macrozooplankton (e.g. large amphipods, euphausiids, medusae) were removed. In a temperature-controlled room set at *in situ* temperature (1-4°C), the live sample was poured into a funnel fitted with a 1-mm sieve inside and a gate valve to obtain two mesozooplankton size classes for incubation. The large size class was maintained in the top part of the device while the small zooplankton was gently evacuated through the sieve by adding cold oxygenated FSW and collected delicately in a container. Each size class was introduced in a separate airtight glass bottle (110-280 mL capacity) that was then filled to the brim with cold oxygenated FSW and capped. For each experimental setup, control bottles without zooplankton were prepared in triplicates. Oxygen-sensitive optical sensors (optodes) were glued on the inner-wall of the incubation bottles. Oxygen consumption was monitored by optode respirometry with a 10-channel respirometer (Oxy-10 Mini, PreSens Precision Sensing GmbH, Regensburg Germany) every 2 hours for 8-12 h. At termination of the experiment, the condition of the animals was verified before they were carefully blotted in absorbing material and preserved in cryovial at -20°C. On land, the samples were transferred to pre-weighed plastic cups and dried in an oven at 60°C for 48 h prior to weighing on a microbalance ($\pm 1\mu\text{g}$). Respiration rates were calculated by determining the slope of the decrease of oxygen over time and subtracting the mean value for the controls. Oxygen consumption rates were transformed to respiratory carbon using a respiratory quotient of 0.75 in January, assuming a winter metabolism mainly by lipid reserves [S8], and 0.97 in May and September with a metabolism primarily based on proteins [S9].

Mooring with Acoustic Zooplankton Fish Profiler (AZFP) and sediment trap

A mooring with a sediment trap and a multifrequency AZFP (125, 200, 455, 769 kHz) was deployed at approximately 200 m depth in Kongsfjorden during 2014. The AZFP, installed at 84 m depth, sampled the 80 m between surface and the instrument. The sediment trap, illustrated by the dark thick strip below 40 m in Figure S2 collected sinking particles from the

top 40 m of the water column. The transducers of the AZFP transmit an acoustic pulse through the water column and record the echo. The intensity of the backscattered signal returning from each discrete depth interval (bins) is related to the zooplankton biomass present within each bin. From the start of the deployment on 16 January, the sampling rate was 1 ping per 10 seconds (0.1 Hz). At 09:42 on 22-Jan, the resolution reduced to 0.05 Hz until recovery on 9 September 2014. An AZFP software within the instrument processes the raw echo counts, using information from the manufacturer's calibration, to provide absolute volume backscatter (Sv, dB) as direct output. The 125 kHz frequency we used would detect zooplankton from large copepods (>5 mm) to macrozooplankton. The sampling bottles in the sequential carousel of the sediment trap were pre-programmed to sample 6 hrs each. The trap sample bottles were pre-filled with filtered seawater containing NaCl to provide a density discontinuity relative to ambient seawater, and 2% formalin buffered with sodium borate to preserve the deposited material. After samples were retrieved, the contents were gently sieved through a 60 μ m net. The contents in the sieve were further analysed for abundance of larger fecal pellets of larvaceans and euphausiids. Cylindrical pellets produced by euphausiids were not preserved intact. In order to compare the abundance of these fecal pellets among samples, the sample was concentrated to a known volume (20-100 ml). A 5 ml subsample was taken using a pipette with an enlarged opening. The subsample was placed in a petri dish with a pre-etched grid. The petri dish was placed under a stereomicroscope equipped with a mounted digital camera. 10-15 pictures were taken at 1.6x magnification, each picture captured fecal pellets within 2 squares of the grid (equal to 7 mm², petri dish size 2206 mm²). If the concentration of fecal pellets was so dense that many pellets lay on top of each other, a second subsample of 5 ml was taken and the procedure repeated. The images were used to measure the length (l) and width (w) of each fecal pellet piece using ImageJ, an open source graphic program (<http://rsb.info.nih.gov/ij/>). Volume (V) of the fecal pellets was calculated assuming a cylindrical shape ($V = \text{Pi} (0.5w)^2 h$). Total volume of fecal pellets was calculated from the number of measured squares, petri dish area, and subsample volume.

Growth of scallops

Fifteen Icelandic scallops *Chlamys islandica* (53.6 ± 1.2 cm length, 48.9 ± 1.1 cm width from 26/08/2013 to 16/04/2014 (233 days of data) were placed in a cage, with at least 3 m of overlying seawater, on the bottom under the Old Pier of Ny-Ålesund (78° 56' N, 11°56' E). The growth rate and the valve movement behaviour of the scallops were measured by high-frequency non-invasive valvometry [S10]. The technique involves gluing one lightweight

electromagnet on each valve, and then continuously measuring, at 0.6 Hz per the distance between the valves. In bivalve molluscs, calcification takes place in the mantle cavity, over the shell's internal surface. As a result, the consequence of daily growth is an increase in the minimal distance between electrodes when the valves close. To obtain a growth rate, we isolate these daily values and plot them as a function of time providing data on the stability, reduction, acceleration or cessation of growth.

Diel activity of scallops and zooplankton

To describe cyclic activity of valve movements we calculated the mean hourly valve opening amplitudes. Chronobiological analyses were made with the software Time Series Analysis Serial Cosinor 6.3 (<http://www.euroestech.net/mainuk.php>). Validating a rhythm in the scallop required a series of steps [S11, 12]. Briefly, to check the quality of the data set the absence of randomness using the autocorrelation diagram and the absence of a stationary character were determined by a Partial Autocorrelation Function (PACF) calculation [S13]. The periodicities in the recorded data were tested with the spectral method of the Lomb and Scargle periodogram [S14]. These methods give a threshold of probability ($p = 0.95$) defining the limit below which the signal can be regarded as "noise". We calculated the confidence interval of the period using Halberg's method [S15]. The cycle was modelled with the Cosinor model, which uses a cosine function calculated by regression [S16]. To validate the model two tests are necessary: the elliptic test [S16] must be rejected and the probability (p -value) for the null amplitude hypothesis must be lower than 0.05 (Table 2). Analysis of diel rhythms in zooplankton (Table 2) follow the methods outlined in Berge et al. [S17], and is based upon an acoustic dataset from Kongsfjorden, covering the same period as for the scallops (Table 2). Activity patterns are defined as sound scattering layers migrating in the water column, and are derived from acoustic (ADCP) data comparable to those used in Berge et al. [S17].

Benthic respiration and macrofauna density

Sediments were collected with a single corer at two stations in the middle of the fjord (Station B 78°56.902N, 11°55.691E 300 m and Station C 78°59.094N, 11°31.762E 300 m) in May 2012, August 2012 and 2014, October 2012 and January 2013 and 2015. For each station and each date, five replicate cores (12 cm diameter, 20-25 cm deep) containing sediments and overlying bottom water from the station were incubated in a cold room at 2°C, in the dark, for 24h, to measure total respiration by benthic community inhabiting sediment cores. Cores were sealed using tops that provided constant stirring of the overlying water [S18]. Parallel to sediment core incubation, control cores without sediment but with similar volume of bottom

water were incubated simultaneously to evaluate the effect of seawater microorganisms on oxygen and nutrient fluxes [S19, 20]. These values were used as blanks and were subtracted from the values obtained with sediment incubations. Oxygen concentrations were monitored every 2 hours using a microelectrode (Unisense A/S; Aarhus, Denmark) inserted into a small sampling port in the core top without introducing any air. Incubations were terminated after 24h when 15–20% of the oxygen had been consumed [S21] and sediment oxygen demand (SOD) was measured as the (negative) slope of the regression line between oxygen concentration and time, subtracting the mean control values[S22]. Oxygen consumption rates were converted into sediment carbon demand (SCD) by assuming a 1:1 stoichiometric relationship between oxygen and carbon consumption, and then applying a respiratory coefficient of 0.85 [S22]. Three van Veen grabs (of 0.1 m² sample area) were collected at each station/ each occasion alongside core sampling. The samples were sieved on 0.5 mm sieves and preserved with formalin. At the laboratory all individuals were identified to the lowest possible taxonomic level and enumerated.

Sampling of fauna associated with the macroalgae Saccharina latissima and fauna of sediments around the algae

In October 2013, January and May 2014 SCUBA divers collected 10 sample sets in Kongsfjorden (near Marine Lab in Ny-Ålesund) at 2 m depth. Each sample set included: (1) a whole individual of *Saccharina latissima* (together with the attached stone) which was packed underwater in a sampling net with 0.5 mm mesh to prevent loss of motile fauna, and (2) a sediment sample taken by cogged grab (areas sampled= 0.025 m²) near *S. latissima* individuals. Sediment samples were washed through a sieve (0.5 mm mesh). All organisms retained on the sieve were identified to the lowest possible taxonomic level (except Nemertea), counted and wet-weighted with accuracy of 1 mg. To calculate densities of sessile species, we measured the area of each substrate type (blade and holdfast of *S. latissima* as well as stones). We also measured the holdfast's attachment area to calculate densities of motile fauna within a holdfast.

Scavenging fauna observed with time-lapse photography

To study the presence and composition of shallow-water scavenging fauna during the polar night, bait consisting of a 300g Atlantic Cod (*Gadus morhua*) was deployed by divers at 12 m depth in close vicinity of the Ny-Ålesund harbour. A custom-made time-lapse camera system fitted with a Canon 1100D (T3 Rebel) took photographs every 15 minutes for four days

(Supplemental data time-lapse video). The whole setup was additionally equipped with a bait-trap containing 30g of Atlantic Cod meat.

Fish and bird stomach content

Fishes were collected using a Campelen bottom trawl from R/V *Helmer Hanssen* inside Kongsfjorden during both 2014 and 2015. Trawling time was standardised to 10 min bottom time for all trawl hauls (>10 trawls). The opening of the trawl is 60 m across and the trawling speed was 2kt. The diet of four fish species caught in a single trawl are displayed in Figure S3. Although fish species diversity varied among trawls, the stomach fullness and content of dominating species were similar. All specimens in the haul were identified, counted, and weighed. Stomachs of all specimens of the dominant species (*Boreogadus saida*, *Gadus morhua*, *Clupea harengus* and *Melanogrammus aeglefinus*) were dissected and weighed before being preserved in 70% Ethanol. Identification to the lowest taxonomic level possible of stomach contents was carried out in the lab under a Leica dissecting microscope (4-50x magnification). Prey species were weighed and each individual counted whenever possible. Birds were sampled from a small open boat and with permission from the local authorities. Stomachs were dissected and treated in a similar fashion to the fish stomachs (Table 1).

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