Report

Moonlight Drives Ocean-Scale Mass Vertical Migration of Zooplankton during the Arctic Winter

Highlights

- During the Arctic winter, moonlight drives zooplankton migrations

- Lunar vertical migrations (LVMs) occur across the entire Arctic domain

- LVMs have periodicities of 24.8 hr (LVM-day) and 29.5 days (LVM-month)

- The extent of LVM suggests that the behavior is conserved and adaptive

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In Brief

Last et al. provide evidence for lunar influence on Arctic zooplankton communities during the dark polar night. During full moon periods, zooplankton migrations are driven by moonlight in synchrony with the altitude and phase of the moon. Such newly termed lunar vertical migrations (LVMs) occur throughout the Arctic, in fjord, shelf, slope, and open sea.

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Moonlight Drives Ocean-Scale Mass Vertical Migration of Zooplankton during the Arctic Winter

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SUMMARY

In extreme high-latitude marine environments that are without solar illumination in winter, light-mediated patterns of biological migration have historically been considered non-existent [1]. However, diel vertical migration (DVM) of zooplankton has been shown to occur even during the darkest part of the polar night, when illumination levels are exceptionally low [2, 3]. This paradox is, as yet, unexplained. Here, we present evidence of an unexpected uniform behavior across the entire Arctic, in fjord, shelf, slope and open sea, where vertical migrations of zooplankton are driven by lunar illumination. A shift from solar-day (24-hr period) to lunar-day (24.8-hr period) vertical migration takes place in winter when the moon rises above the horizon. Further, mass sinking of zooplankton from the surface waters and accumulation at a depth of ~50 m occurs every 29.5 days in winter, coincident with the periods of full moon. Moonlight may enable predation of zooplankton by carnivorous zooplankters, fish, and birds now known to feed during the polar night [4]. Although primary production is almost nil at this time, lunar vertical migration (LVM) may facilitate monthly pulses of carbon remineralization, as they occur continuously in illuminated mesopelagic systems [5], due to community respiration of carnivorous and detritivorous zooplankton. The extent of LVM during the winter suggests that the behavior is highly conserved and adaptive and therefore needs to be considered as "baseline" zooplankton activity in a changing Arctic ocean [6–9].

RESULTS AND DISCUSSION

Migrations by Arctic zooplankton persist during the winter and are driven not by sunlight but by moonlight. Data from moored acoustic instruments, deployed cumulatively for >50 years,

show that wintertime lunar vertical migration (LVM) is modulated by both the moon's altitude above the horizon and its phase and that this response occurs across the entire Arctic Ocean. We infer that moonlight plays a central role in structuring predator-prey interactions and possibly carbon sequestration during the Arctic winter.

Diel vertical migration (DVM) of zooplankton occurs in virtually all water bodies and is possibly the largest daily migration by biomass in the natural world [10]. DVM provides metabolic and demographic advantages to the migrants [11] and enables them to avoid predation by visually hunting near-surface predators [12, 13]. Understanding the magnitude and timing of DVM is essential for balancing oceanic carbon budgets [5, 14–16] because the daily migrations are an important step on the ladders of migration transporting surface-fixed carbon into the ocean interior.

The most important proximate factor driving DVM is the change in underwater light climate over the course of a day [17]. High-latitude environments have discrete day/night light regimes during the spring and autumn, and at this time "classical" highly synchronized DVM occurs [18]. However, during midsummer and mid-winter in polar regions, light regimes are almost invariant day to day (known as the midnight sun and the polar night), at least to the human eye. During the polar night for example, when the sun is 6–12 degrees below the horizon (nautical twilight), only a faint glow may be perceived at midday, becoming almost imperceptible when the sun sinks ≥12 degrees (astronomical twilight) below the horizon (depicted graphically in Figure S1).

During these times, the Arctic seas can be considered similar to the mesopelagic zone (200–1,000 m) elsewhere in the world ocean where even small variations in light have been shown to provide the necessary stimulus for DVM [19, 20]. It is therefore important to understand the possible effect of moonlight on vertical migration of polar pelagic marine organisms, which, in winter, inhabit an otherwise permanently dark ocean.

Zooplankton Migrations during the Polar Night
Acoustic Doppler current profiler (ADCP) data were obtained from locations across the Arctic (see Figure 1) and cataloged in an archive (the "pan-Archive"). The derived acoustic mean volume backscattering strength (MVBS) from the pan-Archive was double
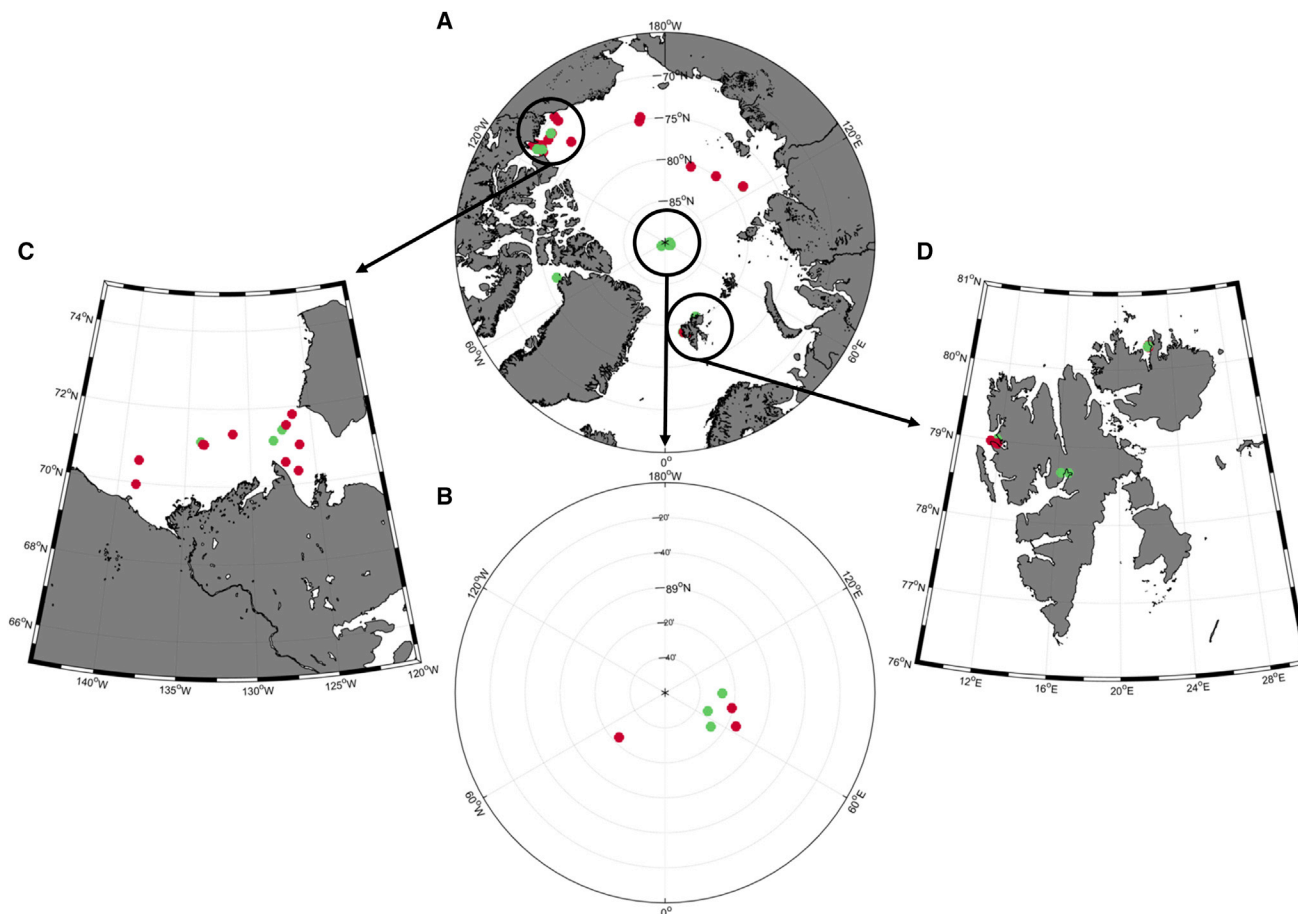
Figure 1. ADCP Mooring Locations across the Arctic Ocean

(A–D) Maps showing the following: locations of the ADCP stations across the Arctic Ocean; all mooring sites are ≥ 69°N spanning a wide range of latitudes and levels of solar illumination during the polar night (A) (see also Figure S1). Increased scale is shown for those centered around; the North Pole (B); the Beaufort Sea (C); and the Svalbard archipelago (D). ADCP stations colored as green dots were used for period analysis of both the LVM-day and LVM-month, while red stations were used for LVM-day analysis only as deployment times at other stations were too short for chronobiological analysis or did not incorporate the depths required.

plotted as actograms and used as a proxy for changes in zooplankton abundance with an example shown in Figure 2 (three central panels). The data are centered approximately on the winter solstice when the sun is continuously below the horizon (in this example 79°N, Kongsfjorden, Svalbard) for several months. In the autumn and spring when there is "normal" day/night variation in the solar altitude above the horizon, a classical pattern of synchronized DVM is observed with lower MVBS values (shown in light/dark blue) during the day versus higher values during the night (shown in orange/red). Further, higher MVBS values, representing higher biomass, are seen for a few hours at dawn and dusk as more intense bands, especially at 58 m depth in the autumn and spring, which implies active synchronized vertical migrations, where populations are moving through these layers, but not remaining in them for long periods of time.

As the autumn progresses toward winter and the days become shorter (decreasing photophase), the DVM signal becomes constrained in a "V" shape in that there is more nocturnal activity over the diel cycle. This mirrors the solar altitude actogram in Figure 2 (far right panel). DVM persists beyond the period

when the sun is above the horizon at local noon and is seen to occur, in the case illustrated here, until the beginning of December. This is due to reflected sunlight still visible at noon until the sun falls ≥ 12 degrees below the horizon. At this time, classical DVM is not manifested but is re-initiated at the start of January when the sun is still only 11 degrees below the horizon. The pattern of DVM initiation is that of an inverted V with a reduction in backscatter initially centered near noon, then progressively tracking the increasing photophases into spring with reducing nocturnal activity over the diel cycle, again as in the autumn, mirroring solar altitude (Figure 2, far right panel).

The autumn/spring pattern of backscatter depicted in Figure 2 is replicated across the pan-Archive in line with solar altitude and conforms to what is already a well-described behavior of zooplankton [17, 21] and some of their predators, such as polar cod [22].

Lunar-Month Vertical Migrations

Across the DVM pattern shown in Figure 2 (three central panels) are regular "bands" of consecutive days where there is a
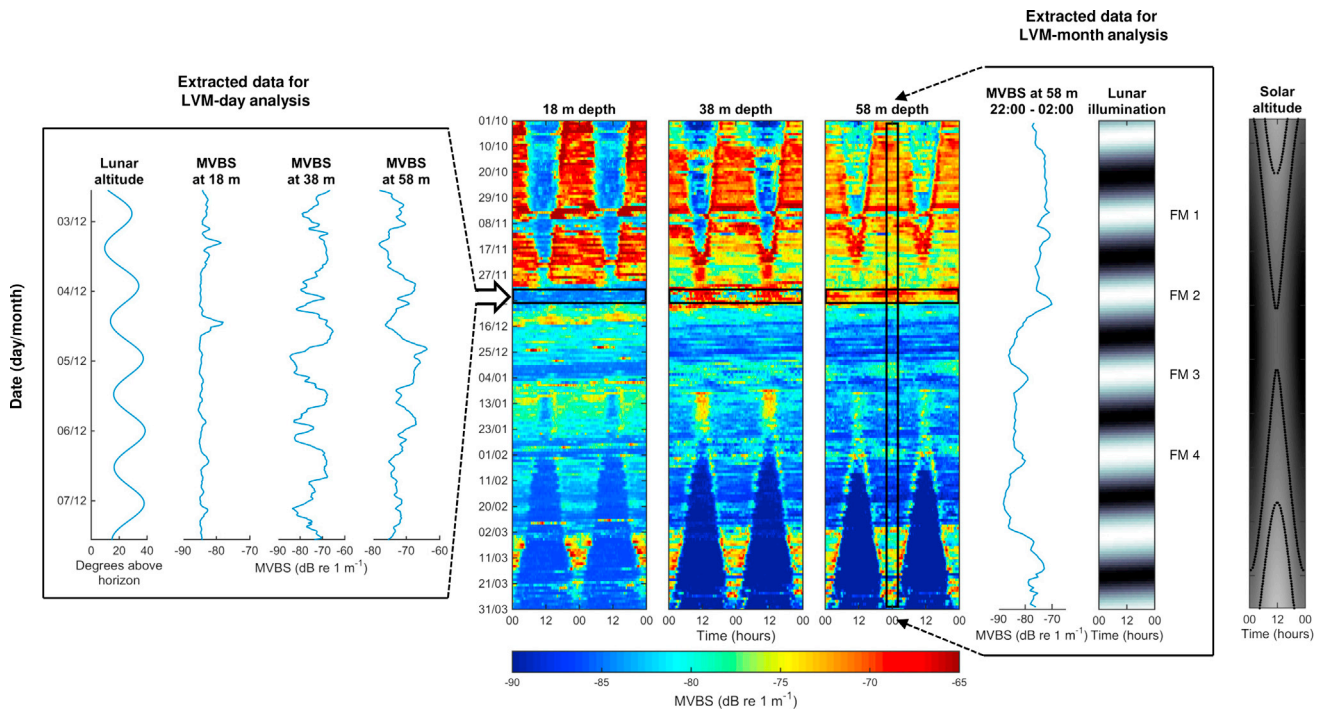
Figure 2. Methodological Approach to Determine the Lunar Influence on Zooplankton Migrations

The three central panels show double-plotted actograms of mean volume backscatter (MVBS) at three depths representing data over 6 months (10/01/2006–03/31/2007), from Kongsfjorden, Svalbard at 79°N (see also Figure S2). The actograms are centered about the winter solstice as highlighted by the solar altitude actogram in the far right panel where the outer contour lines represent sun at 0 degrees, and inner contours represent sun at −12 degrees below horizon. MVBS data were extracted from the actogram to analyze for LVM-month (right box) and LVM-day (left box) periodicity. The right box contains a single plotted actogram of lunar phase (as a proxy for lunar illumination) as grayscale, where white equates to full moon and black equates to new moon, with the four periods of the full moon (FM) over the winter labeled (FM 1–4). Data were extracted from 58 m where MVBS were calculated from data 2 hours either side of midnight. It can be seen that with increasing lunar illumination, there is corresponding increase in MVBS, i.e., increased backscatter at this depth especially at FM 2–4. The left box focused on only a single full moon event, in this case on 12/05/2006 to determine LVM-day periodicity. Here, lunar altitude cycles are presented 3 days either side (12/02/2006–12/07/2006) of full moon with MVBS data extracted at three depths. When the moon is at its lowest altitude, there is a brief increase in MVBS at 18 m, at least for the first two lunar-day cycles. Similarly, at 38 m there is an increase in MVBS as the moon sinks, and as it rises, the two cycles are in antiphase. At 58 m, the MVBS cycle is once again in phase with lunar altitude. Using this approach of data extraction, it is possible to carry out a chronobiological analysis to determine the most significant periods that explain any cyclic activity within the MVBS pan-Archive data. All times are local (corrected for longitude).

disruption of the DVM signal, both in the autumn and the spring, i.e., the timing of dusk/dawn DVM migrations are disrupted. Further, in December and early January, there are bands of reduced (seen as blue) backscatter in surface layers (18 m) but with increased backscatter at depth (38 and 58 m) (yellow/orange/red). The timing of these bands coincides precisely with the time of the four winter full moon (FM 1–4) periods, the periods with greatest lunar illumination (Figure 2, right box). However, this "lunar banding" within the ADCP data is only apparent for ~6 consecutive days over the full moon period when the moon is typically between waxing and waning gibbous (20% of time over the lunar month). Occurrence of lunar-month periodicity within the pan-Archive was determined by averaging MVBS data across midnight to remove any residual effect of the solar cycle (in this example from 58 m depth) between 22:00 and 02:00 over 6 months, shown in Figure 2, right box. Data for period analysis have been collected from stations in Figure 1 (red dots only, see Supplemental Experimental Procedures). Significant periodicity in the lunar-month range (between 24.5 and 34.5 days) spanning the sidereal and synodic lunar month was detected at any one or more depths (depth bins

closest to 20, 40, and 60 m) at all locations (Table 1). We term this behavior lunar-month vertical migration (LVM-month) and highlight that LVM-month cannot be explained by increased tidal flow as a result of the spring/neap cycle since there is no corresponding behavior at new moon spring tides.

Although a number of studies have recognized the response of zooplankton to moonlight or moon phase, accounts have been from discrete locations. Dietz [23] showed that zooplankton migrate upward after the setting of a full moon at night, while Gliwicz [24] demonstrated that freshwater copepods have different nocturnal vertical positions in the water column depending on the relative timing of moonrise and sunset. Some species such as the sergestid shrimp, *Acetes intermedius*, show migratory responses to changing lunar phase [25], and Benoit-Bird et al. [26] showed fortnightly vertical and horizontal (away from shore) migrations correlated with lunar phase in micronecton off Hawai'i. In very clear oceanic water, the lunar signal has been shown to drive migrations to bathypelagic depths (~1,000 m) with the suggestion that this is a cascade response, with deeper-living organisms responding to movements of shallower-living, surface-synchronized populations [27]. The findings presented

Table 1. Summary Table for Data from the Pan-Archive ADCP Moorings Used to Analyze for LVM-Month

Geographical Area	Geographical Coordinates		Analysis of ADCP Data for Lunar-Month Periodicity (Days) at Three Depths		
	Latitude	Longitude	20 m	40 m	60 m
Canadian Archipelago	71° 00.41′ N	126° 04.46′ W	29.5*	29.5*	
Canadian Archipelago	71° 04.81′ N	133° 37.75′ W	ns	25.71	25.58
Canadian Archipelago	71° 05.15′ N	133° 43.27′ W	29.5*		
Canadian Archipelago	71° 32.27′ N	127° 01.46′ W		ns	25.58
W. Greenland	76° 17.38′ N	071° 56.37′ W	26.53		29.5*
W. Greenland	76° 17.60′ N	071° 55.63′ W	29.5*		
Laptev Sea	78° 27.99′ N	125° 40.91′ E	29.5*	29.5*	29.5*
Svalbard	78° 39.76′ N	016° 11.25′ E	29.5*		29.5*
Svalbard	78° 57.44′ N	011° 49.60′ E		26.67	27.58
Svalbard	78° 57.75′ N	011° 45.55′ E		27.47	
Svalbard	78° 57.75′ N	011° 45.56′ E	29.5*	29.5*	29.5*
Svalbard	78° 57.75′ N	011° 45.56′ E	29.5*	29.5*	
Svalbard	78° 59.18′ N	011° 20.93′ E	33.78	29.5*	29.5*
Svalbard	79° 01.20′ N	011° 46.42′ E	26.60	29.5*	29.5*
Laptev Sea	79° 55.10′ N	142° 21.15′ E	26.24	27.25	33.33
Svalbard	80° 16.89′ N	022° 18.90′ E		29.5*	29.5*
Svalbard	80° 17.03′ N	022° 18.15′ E	29.5*	29.5*	26.04
Svalbard	80° 17.22′ N	022° 15.45′ E	29.5*	30.581	
Svalbard	80° 17.60′ N	022° 18.80′ E	29.5*		29.5*
Svalbard	80° 18.01′ N	022° 17.66′ E	29.5*	29.5*	29.5*
Svalbard	80° 18.08′ N	022° 17.44′ E	29.5*		32.79
Svalbard	80° 18.42′ N	022° 17.50′ E	29.5*	29.5*	
N. Pole	89° 15.17′ N	064° 41.51′ E		29.5*	
N. Pole	89° 20.81′ N	077° 07.21′ E		34.48	
N. Pole	89° 23.34′ N	046° 01.15′ W			26.88
N. Pole	89° 27.29′ N	089° 19.74′ E	29.5*	29.5*	ns
N. Pole	89° 27.46′ N	053° 31.26′ E		ns	29.5*
N. Pole	89° 33.41′ N	066° 38.82′ E	ns	26.18	

TSA Cosinor analysis of 6 months of data at the closest depth bin to 20 m, 40 m, and 60 m and spanning the polar winter was used to detect 29.5-day lunar-month periods. Initial tests were run at this period and if significant are defined as 29.5*. Otherwise, the most significant period was found using periodogram analysis and displayed if within the lunar-month range, defined as 24.5–34.5 days in line with analysis for the circadian range (±16% of the lunar-month period). All results are at the $p < 0.05$ level unless stated as non-significant (ns). Empty cells represent results outside of the lunar-month range.

here are not isolated but ubiquitous across the Arctic Ocean and typically under a sea ice cover, where the influence of the sun has been reduced and the importance of the moon in structuring populations identified.

As with classical DVM, we suggest that the adaptive reason behind LVM-month is in the avoidance of light-mediated visual predators. Moonlight has been shown to increase nocturnal hunting in some terrestrial predators [28] and will influence zooplankton capture success of freshwater predatory fish [12]. Indeed, both Gliwicz [24] and subsequently Hernández-León et al. [29] demonstrated that changes in zooplankton density were correlated with lunar phase where moonlight was attributed to driving predatory grazing. Recent observations have shown that birds and fish can forage successfully during the polar night [4], and behavioral modeling has shown that foraging success, at least in fish, is likely to increase with retreating sea ice cover and increased light penetration onto the water column [30]. Although it is not well understood how important visual predation is at high latitudes during the winter, some evidence indicates that the planktonic amphipod predator *Themisto libellula* is able to detect its calanoid prey even at 80°N during the darkest part of the polar night [31].

Lunar-Day Vertical Migrations

Analysis of MVBS data have further revealed 24.8-hr periodicity, which is synchronized to the altitude of daily lunar cycles as illustrated in Figure 2, left box. We term this new behavior of zooplankton lunar-day vertical migration (LVM-day). When data are combined from the pan-Archive for stations from Figure 1 (green and red dots; see Supplemental Information) and analyzed for significant periodicity, we can identify a shift of mean periodicity centered at 24 hr during the autumn and spring
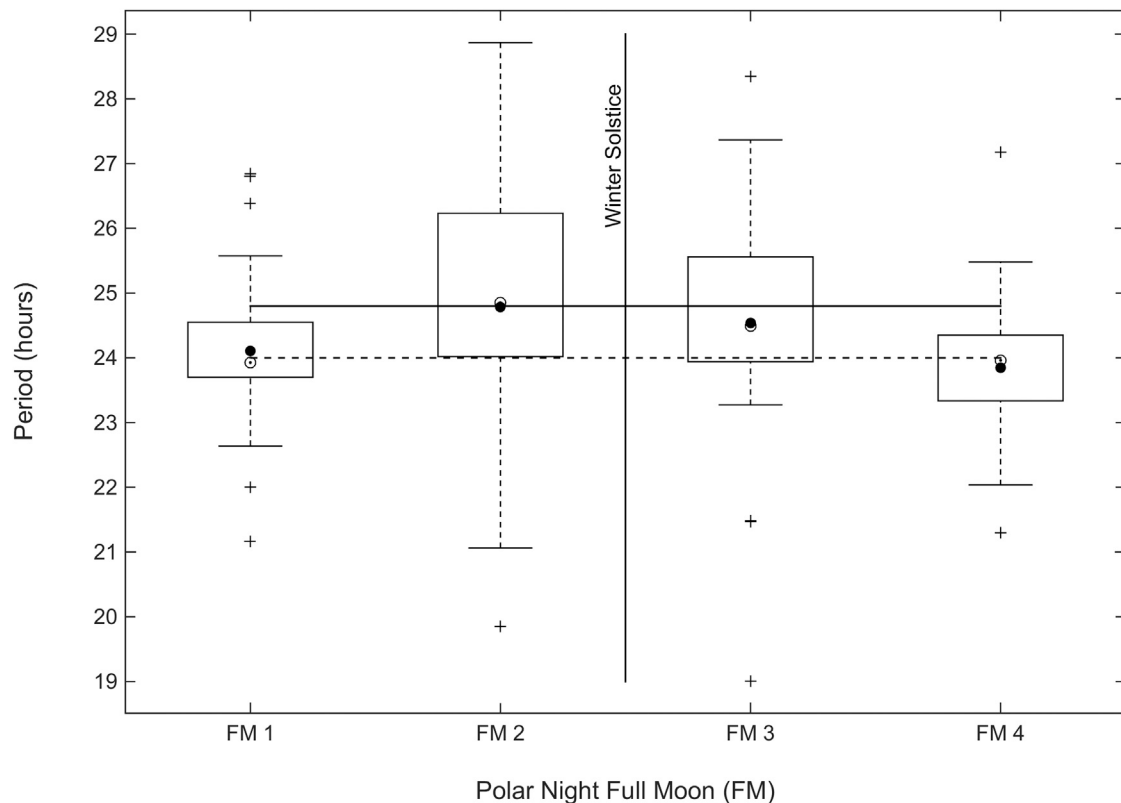
Figure 3. Period Analysis of Zooplankton Migrations across the Winter Full Moons

Mean significant periods over 6 days across four full moons (FM 1–4) where FM 1–4 refer to the four full moons seen in the 60 days either side of winter solstice (absolute dates vary between years). The central solid vertical line shows the relative timing of the winter solstice (on average, at the midpoint of FM 2 and FM 3). 24-hr (solar-day) periodicity is defined by the horizontal dashed line, and 24.8-hr (lunar-day) periodicity is defined by the horizontal solid line. The mean period for each full moon is shown by solid circles and median period by targets. The 25% and 75% quartiles are defined by the box edges, with data points within ± 50% of this range included in the whiskers. Crosses show all individual data points outside these boundaries. Number of data values for each full moon varied (FM 1 = 40, FM 2 = 30, FM 3 = 28, FM 4 = 29).

full moon times (FM 1 and FM 4) to mean periodicity centered close to 24.8 hr during the two full moons either side of the winter solstice (FM 2 and FM 3) as depicted in Figure 3. The implication of this is that vertical migrations are driven by the changes in lunar irradiance over the course of (approximately) a day. This is manifested as a slope in the actograms, i.e., MVBS data are not centered on 24 hr (as with classical DVM), but, instead, the data "slant" to the right where the periodicity is > 24 hr, implying lengthening of period from 24 hr. This is illustrated in Figure 2 for the full moon period approximately between 01/01/2007 and 01/05/2007 at 38 m and 58 m depth (FM 2), with greater detail and further examples shown in Figure S2. To our knowledge, this response, cued directly by changes in lunar altitude and hence illumination, has never been described for any migratory behavior other than that controlled by the interaction between the tidal and day/night cycles, usually in intertidal inhabitants [32, 33]. At the proximate level, zooplankton are responding to subtle changes in light level, presumably to avoid predation, where the migratory response is exogenously driven, and this behavior remains intact over the winter period.

Astronomical constants are such that lunar phase is consistent across all latitudes. Lunar altitude, however, is not, and it is

apparent that the rising or setting of the moon, even when not full, can play a significant role in driving vertical migrations. Closer investigation of the central panel actograms in Figure 2 (see also magnification of actograms in Figure S2) between 11/02/2006 and 11/11/2006 at all depths reveal phase disruption to the DVM migratory pattern due to the rising of the moon. At this time, the moon is just rising above the horizon and provides sufficient moonlight to delay the ascent of zooplankton to the surface from 18 m, but not from deeper layers. Since the rising of the moon above the horizon occurs earlier each day, the time that zooplankton initiate the upward dusk migration to the surface layers is delayed until such a time when the moon is bright, or high enough, to suppress DVM completely, which, in this example, occurs from 11/06/2006 onward. Indeed, changes in the light field and the disruption of migrations have been documented for both lunar [34] and solar eclipses [35], the suggestion being that even subtle changes of light, such as the 77% eclipse documented by Strömberg et al. [35], were sufficient to trigger migrations in krill, even at ∼80 m depth. Changes in light climate, such as from the masking effect of clouds, may explain the subtle variation in the lunar migrations between months and years seen within the pan-Archive. However, since cloud cover is

spatially and temporally highly variable and meteorological (radar) data are limited in this region, it was not deemed appropriate to assess as part of this broad-scale study.

Mechanisms, Consequences, and Summary of Zooplankton LVM during the Polar Night

There is limited information on the visual acuity of Arctic zooplankters. Radiative transfer modeling has shown that in the top 75 m, solar irradiance in January exhibits a maximum wavelength at 485 nm, which, for the commonly occurring krill *Thysanoessa inermis*, means limited detectability to only 20–30 m depth [36]. For *Calanus* spp., a phototactic response was determined at 455 nm with an intensity of only 10^{-8} μmol photons m^{-2} s^{-1}, suggesting that bright moonlight ($\sim 10^{-2}$ μmol photons m^{-2} s^{-1}) would be of biological relevance down to 120–170 m with highest sensitivity to blue and green light [37]. Copepods, the main constituents of zooplankton communities, are therefore likely to be well adapted to perform LVM during the polar night, when intensity and diurnal variation of ambient solar irradiance is low.

It is probable that zooplankton migrations (DVM, LVM-month, and LVM-day) are ultimately underpinned by biological clocks [38], though the responses to moonlight described here are probably exogenously driven. As argued by Berge et al. [2], the spontaneous onset of strict 24-hr DVM observed during January requires an exogenous trigger, or Zeitgeber. Since most candidate triggers are either continuous (e.g., tides) or do not match the circadian period (e.g., temperature), the suggestion by the authors was that migrations were triggered by "imperceptible" variations in illumination. Although our understanding of non-circadian "enigmatic clocks" remains limited [39], a recent study has demonstrated that a dedicated lunar clock, entrained by moonlight, appears to be operating, at least in the polychaete *Platynereis dumerillii* [40], and it remains to be determined, with laboratory studies, whether this is also evident in zooplankton.

The moon's influence on zooplankton migrations results in monthly accumulations of animals at ~50 m across the Arctic. At such times there is insufficient irradiance at this depth for many predatory species to detect their prey and vice versa [4, 36, 37]. In this respect, an analogy can be drawn between the polar night pelagic ecosystem and the North Atlantic meso-pelagic (twilight) zone, in that primary production is absent, and for much of the winter, predator-prey interactions become influenced by bioluminescence and non-visual tactic, chemosensory, or chance encounters [41, 42]. The consequences of LVM-month to carbon sequestration is unknown, but DVM has been shown to significantly enhance the gravitationally mediated flux of material into the deep ocean by up to 53% [15] with estimates ranging from 0.5 to 1.5 g C m^{-2} y^{-1} [16] and increased provision of organic carbon to marine bacteria, considered central to the carbon pump [43]. Further, it has been shown that that lunar-induced migration exports carbon to depth by the consumption and transport of epipelagic zooplankton and that this is on the order of the mean gravitational export [9]. It remains to be tested whether there is increased carnivory within the zooplankton community associated with LVM-month, thereby potentially enhancing the transport of particulate organic carbon (POC) and dissolved organic carbon (DOC) to depth due to the respective production and breakdown of fecal pellets [44].

In summary, we present compelling evidence of zooplankton migrations during the polar night across the Arctic Ocean, in fjords, on the shelf, slope, and open sea across 21 degrees of latitude. This finding is consistent at all locations of the pan-Archive. The LVM-month behavior is coincident with the time of the full moon and typically involves movement to deeper water for a few days, the reason for which is hypothesized to be avoidance of visual predators capable of utilizing the lunar illumination to hunt. In addition, we describe LVM-day behavior, which is coincident with lunar elevation above the horizon near the time of the full moon. Both LVM-month and LVM-day can disrupt or mask classical DVM migrations when the sun is still just above or just below the horizon. Collectively, these data show that there is a robust zooplankton response to what might be considered very subtle changes in illumination, a response that was until now unexpected but alluded to in single-site observations in the Arctic [2, 4]. As with the hunting behavior of mythical werewolves that is driven by moonlight, our data reveal a moonlight-driven reality with major implications to real-world predator-prey relations [30, 31], zooplankton phenology [45], fish/seal foraging patterns [22], and avian predation [4]. Finally, the implications of LVM on carbon sequestration [5, 46] need to be quantified with field data, which may then inform the budgeting of Arctic biogeochemical models.

EXPERIMENTAL PROCEDURES

A standard chronobiological toolkit was used to visualize and quantify migratory periodicity (time series analysis [TSA] Cosinor 6.3 package) of zooplankton. Details of study areas, moorings, environmental parameters, and statistical approaches and magnified details of LVM-day actograms are given in the Supplemental Information.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and two figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.11.038.

AUTHOR CONTRIBUTIONS

K.S.L. handled the study design, methodological approach, interpretation, and manuscript preparation. L.H. performed data analysis, interpretation, and manuscript review. A.S.B. performed interpretation and manuscript review. J.B. was a principle investigator (Circa: 214271) and carried out study design, interpretation, and manuscript review. F.C. was a principle investigator (Panarchive: NE/H012524/1) and pan-Archive custodian and handled the study design, interpretation, and manuscript review.

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