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.
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 night (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
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-Arctic 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...
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). How-ever, this “lunar banding” within the ADCP data is only apparent for /C246 consecutive days over the 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).

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 Gli-wicz [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 re-sponses 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 micronecet 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...
least in fish, is likely to increase with retreating sea ice cover 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

<table>
<thead>
<tr>
<th>Geographical Area</th>
<th>Latitude Coordinates</th>
<th>Analysis of ADCP Data for Lunar-Month Periodicity (Days) at Three Depths</th>
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<td>Longitude</td>
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<td>71° 00.41' N</td>
<td>126° 04.46' W</td>
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<tr>
<td>Canadian Archipelago</td>
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<td>071° 56.37' W</td>
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<td>W. Greenland</td>
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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.
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 (ra-
dar) 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 zoo-
plankters. Radiative transfer modeling has shown that in the
top 75 m, solar irradiance in January exhibits a maximum wave-
length 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 pho-
tons m$^{-2}$ s$^{-1}$, suggesting that bright moonlight ($10^{-2}$ μmol pho-
tons 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 candi-
date 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 analog 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 influ-
enced by bioluminescence and non-visual tactic, chemosen-
sory, 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 esti-
mates ranging from 0.5 to 1.5 g C m$^{-2}$ y$^{-1}$ [16] and increased
provision of organic carbon to marine bacteria, considered cen-
tral to the carbon pump [43]. Further, it has been shown that that
lunar-induced migration exports carbon to depth by the con-
sumption 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 avoid-
ance 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 moon-
light-driven reality with major implications to real-world predator-
prey relations [30, 31], zooplankton phenology [45], fish/sea-
foraging patterns [22], and avian predation [4]. Finally, the impli-
cations of LVM on carbon sequestration [5, 46] need to be quan-
tified 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 migra-
tory 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/
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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. F.C. was a principle investigator (Pan-
archive: NE/H012524/1) and pan-Archive custodian and handled the study
design, interpretation, and manuscript review.

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