Comparison of zooplankton vertical migration in an ice-free and a seasonally ice-covered Arctic fjord: An insight into the influence of sea ice cover on zooplankton behavior

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Abstract

We present observations of zooplankton diel vertical migration (DVM) over a period of 2 yr in an ice-free and a seasonally ice-covered Arctic fjord. The contrasting environments permitted assessment of the influences of physical and biological factors on temporal variability in DVM patterns and a test of the hypothesis that a reduction in summer sea ice extent and thickness following climatic warming will lead to changes in DVM via the loss of a shading effect on the pelagic marine environment. Acoustic backscatter and vertical velocity data from moored 300-kHz acoustic Doppler current profilers were used to derive DVM patterns, while measurements of sea ice and snow thickness enabled assessment of the underwater light environment and consideration of its potential to influence DVM. Pronounced differences in DVM between the sites emerged during summertime when intermittent synchronized DVM was observed at the ice-free site, whereas the ice-covered site was characterized by asynchronous behavior, thereby highlighting the influence of sea ice. Notably, the 0.8-m-thick sea ice cover was deemed important for its influence on water column properties such as food, turbidity, and zooplankton species composition, as indicated by biological samples from moored sediment traps, rather than a simple shading of the ocean and direct modification of zooplankton DVM. Loss of Arctic sea ice is likely to have an indirect but substantial effect on zooplankton DVM via modification of hydrography and composition of the pelagic community.

The diel vertical migration (DVM) of zooplankton is a ubiquitous feature of midlatitude oceans whereby populations remain at depth during daylight hours and move en masse to the surface under cover of darkness. It is generally accepted that zooplankton perform vertical migrations in an attempt to balance the need to feed close to the surface against the accompanying risk of being eaten in these shallow waters (Hayes 2003). Zooplankton use proximate cues to synchronize their behavior with the day–night cycle, with the rate of change in absolute or relative light intensity being the most commonly reported cues (Ringelberg 1995; Frank and Widder 1997). The influence of such cues is particularly revealed during exceptional events such as solar or lunar eclipses (Tarling et al. 1999; Stromberg et al. 2002).

A reliance on light-mediated proximate cues is potentially problematic in environments without strong daily changes in light levels. For instance, Blachowiak-Samolyk et al. (2006) noted that synchronized DVM was absent during the continuous illumination of the Arctic summer, while Cottier et al. (2006) identified an unsynchronized migration pattern during Arctic summer whereby individuals migrated up and down the water column in an uncoordinated manner. In that instance, the proximate cue for migration was deemed to be the feeding needs of the individual rather than any external stimulus. This suggests the existence of a hierarchy of migration modulators that enable individuals to adapt to local environmental conditions and seasonal cycles.

It is assumed that DVM behavior at high latitudes slows down or ceases during wintertime as food availability decreases and as some zooplankton species enter diapause (Conover 1988; Smetacek and Nicol 2005). However, the difficulties inherent in data collection at high latitudes during winter mean that data are sparse. Those that do exist are conflicting: a study in the Greenland Sea did not detect clear vertical migration from November to January (Fischer and Visbeck 1993), while a study in northern Svalbard identified DVM from October through to March, albeit with reduced synchronicity and vertical extent in midwinter (Berge et al. 2009).

Sea ice significantly reduces the penetration of downwelling irradiance into the ocean (typically by between 15% and 90%; Grenfell and Maykut 1977) through an increase in surface albedo and absorption and scattering of the transmitted light. Shading by ice algae can further reduce light penetration (Perovich et al. 1998). Nevertheless, the level of light under ice appears to be sufficient to act as a cue for DVM. Fortier et al. (2001) observed DVM in Arctic copepods under sea ice during periods of midnight sun. It remains uncertain whether and in what ways ice modifies the nature and extent of DVM.

This study focuses on Kongsfjorden and Rijpfjorden, two fjords in the Svalbard Archipelago (Fig. 1) located on the northwestern coast of Spitsbergen and the northern

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coast of Nordaustlandet, respectively. Both sites are well suited to the study of temporal variability in zooplankton vertical migration, as their locations at 79°N (Kongsfjorden) and 80°N (Rijpfjorden) mean that they experience nearly 4 months of continuous illumination and 4 months of continuous darkness during the annual cycle, and transit through “conventional” day–night cycles.

Kongsfjorden is open to the West Spitsbergen Shelf through a common mouth with Krossfjorden and is subject to intermittent exchange between the fjord and offshore Atlantic waters. It is dominated typically by cold, fresh Arctic waters for much of the year, with summertime intrusions of relatively warm, saline Atlantic-derived waters (Cottier et al. 2005). However, during the winter of 2005–2006, there was a major inflow of Atlantic Water (Cottier et al. 2007) that led to this fjord remaining free of sea ice from 2006 to 2008. The zooplankton community at this site includes both Atlantic and Arctic species, with the proportions of each varying with changes in oceanographic conditions (Kwasniewski et al. 2003). Calanoid copepods, which are known to exhibit vertical migration, are important in both communities (Kwasniewski et al. 2003; Willis et al. 2006). Calanus species have been identified as important indicators of the different oceanographic regimes, with Calanus finmarchicus being associated with Atlantic water and Calanus glacialis with Arctic water. Other migrating species can be expected to contribute to the DVM signal in Kongsfjorden. For instance, Metridia spp. exhibit more pronounced DVM than Calanus spp. (Hays 1995; Hays et al. 1997), while Themisto spp. are also important in Kongsfjorden (Willis et al. 2006; Berge et al. 2009).

Rijpfjorden runs roughly north to south and is open to the wide shelf to the northeast of Svalbard through a broad mouth to the east and through narrow channels between islands to the north. In contrast to Kongsfjorden, Rijpfjorden is covered by fast ice for 6–8 months of the year and experiences oceanographic conditions that are characteristically Arctic, with an accompanying Arctic zooplankton community. There is, however, an intermittent influence of Atlantic water on the system. One such occasion was August 2004, when a high proportion of C. finmarchicus was found in the fjord (Falk-Petersen et al. 2008). As at Kongsfjorden, vertically migrating species such as M. longa and amphipods including Themisto spp. are found in Rijpfjorden in addition to Calanus spp. (Berge et al. 2009).

In this study, we report on results obtained from the deployment of autonomous collecting devices to determine the nature and extent of zooplankton migratory behavior at Kongsfjorden and Rijpfjorden. Data were obtained continuously and at high levels of temporal resolution over almost 2 yr, from September 2006 to August 2008. The devices were a combination of 300-kHz acoustic Doppler current profilers (ADCPs), sediment traps, and environmental sensors, housed on a single mooring at each location. It has become increasingly common in recent years to employ ADCPs in the study of zooplankton behavior (Cottier et al. 2006; Berge et al. 2009), enabling insights into the vertical distribution and migration speeds of zooplankton. Sediment traps provide a qualitative
Table 1. Details of the Kongsfjorden and Rijpfjorden mooring deployments.

<table>
<thead>
<tr>
<th>Position</th>
<th>Depth (m)</th>
<th>Deployed</th>
<th>Recovered</th>
<th>Duration (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kongsfjorden</td>
<td>79°01.2’N</td>
<td>210 m</td>
<td>06 Jun 2006</td>
<td>25 Aug 2007</td>
</tr>
<tr>
<td></td>
<td>011°46.4’E</td>
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<td>28 Aug 2007</td>
<td>20 Aug 2008</td>
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<td>29 Aug 2006</td>
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</tr>
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<td>011°49.6’E</td>
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<td>21 Aug 2007</td>
<td>16 Aug 2008</td>
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<td>Rijpfjorden</td>
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<td>216 m</td>
<td>02 Feb 2007</td>
<td>(RRS James Clark Ross)</td>
</tr>
<tr>
<td></td>
<td>022°18.8’E</td>
<td>16 m</td>
<td>21 Aug 2007</td>
<td>(RRJ Jan Mayen)</td>
</tr>
<tr>
<td></td>
<td>80°18.8’N</td>
<td>216 m</td>
<td>21 Aug 2007</td>
<td>(R/V Lance)</td>
</tr>
<tr>
<td></td>
<td>022°19.6’E</td>
<td>200 m</td>
<td>25 Aug 2007</td>
<td>(R/V Jan Mayen)</td>
</tr>
</tbody>
</table>

Methods

Moorings—Deployment details for the Rijpfjorden and Kongsfjorden moorings are given in Table 1. Data used in this study were limited to those collected between 04 September and 15 August from 2006–2007 and 2007–2008, enabling direct comparison of uninterrupted time series from both sites. Each mooring was comprised of an upward-looking 300-kHz Teledyne RD Instruments ADCP at ~100-m depth, with a ParFlux sediment trap located 1 m below the ADCP. SeaBird Electronics MicroCats, recording temperature, conductivity, and pressure, were located at 27 m and 205 m at Rijpfjorden and 21 m and 199 m at Kongsfjorden. Both moorings included a SeaPoint fluorometer at the same depth as the upper MicroCat. Vemco temperature miniloggers were fixed at intervals of 3–30 m between depths of ~20 m and ~200 m.

The 300-kHz ADCPs are optimal for detecting scatterers a few millimeters in size and are thus suitable for the study of small mesozooplankton species. These ADCPs were configured to record data in 20-min ensembles over 30 4-m bins, ensonifying the water column from ~90 m depth to the surface. The upper four bins (~16 m to surface) of data were discarded in all cases because of acoustic contamination caused by side-lobe effects. Absolute volume backscatter (Sv, measured in decibels [dB]) was derived from echo intensity (Deines 1999) and, to facilitate comparison, Sv data from all deployments were normalized (by up to ±7 dB) so that mean values of all data sets were equal. The vertical velocity anomaly, w’, was derived following Tarling et al. (2002). Both Sv and w’ were processed using a 3-h low-pass filter. Sv and w’ data from contiguous 7-d ensembles were averaged to create a mean 24-h profile that was representative of each week in the 49-week data series from 04 September to 15 August (Figs. 2–5). Depth-averaged horizontal velocities were derived from the ADCP data for each 20-min ensemble and are included in Figs. 2–5.

Fluorescence and temperature were measured at hourly intervals. The raw fluorescence data were processed using a 3-h low-pass filter and, in the absence of water samples suitable for calibration, were normalized such that data from each time series ranged between 0 and 1, the purpose being simply to identify approximate timings of bloom events. Linear interpolation between temperature sensors was used to derive a low-resolution (10-m) water column profile from 20-m to 200-m depth for each time point.

The sediment traps were configured and the samples analyzed as described by Willis et al. (2006). Data from the 2006–2007 deployments have been published previously (Berge et al. 2009, online data supplement). Trap samples from the 2007–2008 deployment in Rijpfjorden are not presently available for publication, and the Kongsfjorden deployment failed because of a blockage forming in the trap funnel.

Meteorological data—Hourly measurements of photo-synthetically active radiation (PAR; μmol m–2 s–1) were obtained from weather stations at Rijpfjorden and Ny Ålesund using Kipp and Zonen ParLite photosynthetic active radiometers, with an effective lower irradiance detection limit of 1 μmol m–2 s–1. Data from Rijpfjorden were available only from 02 February 2007 (station deployed) until 07 August 2008 (station failed). Gaps of several hours occur in the Rijpfjorden time series throughout the year, and data were missing from November 2007 to March 2008. A calibration problem was noted for the Rijpfjorden sensor, giving rise to a large offset in the PAR data compared to those measured at Ny Ålesund, though both stations showed similar patterns of diurnal and seasonal variability. Accordingly, PAR values for both
fjords were normalized between 0 and 1. Calculations requiring accurate PAR data (the irradiance profile model described below) used measurements from Ny Ålesund. PAR time series were processed with a 3-h low-pass filter and averaged to produce 49 mean 24-h periods for each week of data corresponding to those in the ADCP data. Air temperature data were collected at Rijpfjorden using a PT100 Platinum Resistance Thermometer from Pico Technology.

Sea ice and snow observations—Approximately monthly in situ measurements of sea ice thickness and associated snow cover were made at various sites (between 0.1 km and 7.2 km apart) in Rijpfjorden between March and June 2007. Both ice formation and breakup were observed directly during 2007, but no direct observations were available for 2008. Duration of the sea ice cover in 2008 was estimated from ADCP data following the method of Hyatt et al. (2008). Daily observations from the research station at Ny Ålesund indicated that sea ice was absent from the main basin of Kongsfjorden throughout our study period.

Irradiance profile model—A one-dimensional model was used to investigate the contrast in light levels between open waters in Kongsfjorden and ice-covered waters in Rijpfjorden. The albedo of sea ice varies widely (Perovich 1998); snow-free white ice typically has an albedo of 0.7, increasing to 0.9 with a fresh snow cover and as low as 0.15 in the presence of melt ponds (Grenfell and Maykut 1977). Attenuation of light in snow and ice through absorption and scattering is a function of wavelength, with the 490–550-nm range (green-yellow) experiencing the least
Attenuation coefficients \( k_{\text{ice}} \) measured in sea ice vary between 1.1 m\(^{-1}\) and 1.5 m\(^{-1}\) (Grenfell and Maykut 1977). Attenuation in snow is generally much greater with \( k_{\text{snow}} \) varying from 4.3 m\(^{-1}\) in dense snow to 40.1 m\(^{-1}\) in fresh snow (Grenfell and Maykut 1977).

The effect of attenuation by snow-covered sea ice on the downwelling irradiance can be estimated from

\[
I = I_0 e^{-k_{\text{ice}}z}
\]

where \( I \) is the transmitted downwelling irradiance, \( I_0 \) is the incident downwelling irradiance, \( k_{\text{ice}} \) is the wavelength dependent attenuation coefficient for the snow or ice, and \( z \) is the thickness of the snow or ice (Grenfell and Maykut 1977).

For ease of viewing, each week of PAR, \( S_v \), and \( w' \) is represented as 1 d averaged from that week’s data (thus, each “month” marked on the time axis comprises approximately four of these average days, and “midnight” is signified by a tick mark).

The attenuation of light within the ocean is largely dependent on the concentration of dissolved and suspended matter (Tyler 1961). An attenuation coefficient for water \( k_{\text{water}} \) of 0.0444 m\(^{-1}\) has been derived for optically uniform waters under sea ice in the Canadian Arctic in
May (Smith 1973). This value is in general agreement with prebloom measurements of Aas and Berge (1976) in the Norwegian and Barents Seas. PAR measurements from Kongsfjorden in May 2008, after the beginning of the summer bloom when concentrations of suspended matter were considerably higher than during springtime, yielded a higher value of 0.12 m$^{-1}$ (E. Leu pers. comm.), which is similar to measurements made by Hanelt et al. (2001) in Kongsfjorden from May to September 1995–1998. Therefore, we used the value of 0.0444 m$^{-1}$ obtained by Smith (1973) for prebloom calculations of light attenuation.

**Results**

The mooring and meteorology data are presented in four composite figures for both fjords for the years 2006–2007 and 2007–2008 (Figs. 2–5). They show the mean 24-h profiles of $S_v$ and $w'$ (with each profile derived from 1 week of data) plotted for each of the 49 consecutive weeks (04 September–15 August). These enable direct comparison of vertical migration patterns over an annual cycle between the two sites and the 2 yr. The inclusion of PAR time series, also averaged into mean 24-h periods, facilitates the identification of seasonal patterns of vertical migration associated with changes in light cues. The fluorescence, depth-mean horizontal velocity, temperature, and sea ice data presented in these figures enable identification of environmental differences between the sites. Our task was to disentangle those changes in DVM due to seasonal factors from those arising as a result of the differing environments. We tackled this by describing the seasonal development of DVM over the course of 2 yr and identifying commonalities and differences between the two locations. We then examined environmental and
biological data from each site in order to identify possible forcing mechanisms for the observed differences. In this analysis, seasons were defined as follows: spring from 01 March to 30 April, summer from 01 May to 31 August, autumn from 01 September to 31 October, and winter from 01 November to 28–29 February.

*Inference of vertical migration from ADCP data*—Two principal periods of classic DVM were evident in the $S_v$ data from September to early November (approximating to autumn) and late February to early April (approximating to spring) at both fjords (Figs. 2–5). These were characterized by a conspicuous scattering layer migrating vertically in the water column, with an increase in $S_v$ at shallow depths centered around midnight: this is interpreted as the synchronized motion of animals, during which the bulk of the biomass moved toward the surface at midnight and sank to depth during the day. This signal type was observed throughout the entire depth range sampled by the ADCPs for much of both autumn and spring, indicating that vertical migration was taking place over distances of 80 m or more. The day–night cycle was most pronounced at these times, as evidenced by the PAR time series. Notably, these patterns of classic DVM appeared and died away at both locations at approximately the same time each year despite the presence of sea ice at Rjåfjorden during spring. Absolute levels of $S_v$ were lower during spring than autumn, indicating a difference in the biological communities: fewer or smaller animals, different species compositions, or a combination of these factors may have led to a decrease in $S_v$, and these effects cannot be distinguished using ADCP data. These periods of pronounced DVM...
were also characterized by $w'$ of order ± 2–5 mm s$^{-1}$ associated with the vertical motion of the scattering layer.

From late November until early January, no clear $S_v$ pattern was observed. Berge et al. (2009) studied this time period using a method of DVM detection that was optimized to identify weak signatures of migration, and reported that weak DVM occurred at both fjords during midwinter. However, in the context of the annual patterns of migratory behavior shown here, that wintertime DVM is a much more subtle signal (in terms of backscatter strength and depth range) than we observed in spring and autumn and will not be discussed further in this study. This time period was characterized by strong fluctuations in $w'$ (particularly pronounced at Kongsfjorden during 2006–2007; Fig. 4) that did not appear to bear any relation to $S_v$. These $w'$ fluctuations had a period ranging from 1 h to 6 h and thus were reduced but not removed by the 3-h low-pass filter used here.

Following the spring DVM, $S_v$ and $w'$ patterns at the two sites diverged, and the main features of each are summarized in Fig. 6. No clear synchronous signal was observed in either $S_v$ or $w'$ at Rijpfjorden from May until August 2007 and May until early July 2008 (Figs. 2, 3); $w'$ was close to zero (< ± 1.5 mm s$^{-1}$) throughout most of this period, with the notable exception of an event in mid-July 2007, where strongly negative $w'$ above ~ 30 m was associated with high $S_v$ values below this depth. In late July and August 2008, $S_v$ increased throughout much of the water column around midnight, indicating the onset of autumn DVM, although there was no $w'$ signal associated with this. No other distinctive pattern was identified over this time period.

Both $S_v$ and $w'$ were more variable at Kongsfjorden between May and August of both years (Figs. 4, 5). The 2008 spring DVM continued through April and into early May, and both 2007 and 2008 saw the initiation of autumn DVM during late July or early August. There were also periods of a few weeks in summertime when a synchronous signal appeared in $S_v$ (e.g., May to late June 2007 and mid-June to July 2008). These “weak summertime DVM” signals were less pronounced than the autumn and spring DVM, with higher background levels of $S_v$ and therefore less contrast between “midday” and “midnight.” Additionally, the synchronous signals were often detectable only over limited depth ranges in the water column (see Fig. 6) and were interspersed with periods during which no synchronous signal could be identified in $S_v$ (e.g., July 2007 and mid-May to mid June 2008). $S_v$ was generally more intense at Kongsfjorden than at Rijpfjorden, indicating some difference between the biological communities.
Sea ice and zooplankton migration

During both summers at Kongsfjorden, through periods of asynchrony, weak synchrony, and emergent autumn DVM, a distinctive signal was observed in $w'$ throughout much of the water column, with relatively high ($2-3 \text{ mm s}^{-1}$), positive $w'$ centered around midnight and values close to zero ($< \pm 1 \text{ mm s}^{-1}$) at midday. The $w'$ distributions during July 2008 also shared similarities with the distinctive “foray-type behavior” pattern identified by Cottier et al. (2006) at Kongsfjorden in 2002, with positive $w'$ in the lower water column and negative $w'$ closer to the surface. However, Cottier et al. (2006) did not observe the weak 24-h cycle that we identified in both $w'$ and $S_v$, and their $S_v$ data yielded the highest values close to the surface, whereas our observations showed $S_v$ to be lowest in near-surface waters.

These observations have served to highlight that zooplankton in both fjords showed a pronounced seasonal signal in vertical migration behavior, with DVM being apparent during autumn and spring each year at both locations, when the day–night cycle was strongest. There was no clearly identifiable divergence in migration behaviors between the two sites that could be readily attributed to the presence of ice at Rijpfjorden. The largest contrast between the sites was observed during summer, where the signal at Rijpfjorden, which remained ice covered until July (2007) or August (2008), appeared to be entirely asynchronous, while periods of weak synchrony were observed at Kongsfjorden at this time. The characteristics of the observed summertime asynchrony differed between the two sites, with $w'$ at Rijpfjorden remaining close to zero throughout the water column for virtually the entire summer, while $w'$ at Kongsfjorden exceeded 2 mm s$^{-1}$ for much of the day and often showed a weak diurnal signal.

Sea ice observations—The annual sea ice cycle at Rijpfjorden was offset with respect to the seasonal cycle, with ice onset occurring during late winter and ice cover persisting until mid- to late summer. In 2007, ice onset was observed on 01 February and breakup on 15 July, with a sea ice thickness of the order of 0.8 m throughout much of the sea ice season that year. Snow overlying the sea ice was approximately 0.05 m thick during the sea ice growth phase and accumulated to approximately 0.1 m later in the sea ice season.

The results of the ADCP method of sea ice identification are shown in Fig. 7. In 2007, our ADCP-derived estimate for ice onset was 09 February (8 d later than observed), and that for breakup was 06 July (9 d earlier than observed), implying that this method is suitable for the identification of consolidated sea ice. In 2008, the ADCP method yielded 26 January as the date of ice onset, so it is likely that the ice began to grow roughly a week earlier. Ice breakup was rapid in 2008, with an ADCP-derived estimate of 12 August, 2 d before a cruise on the RRS James Clark Ross (JR210) entered the area and found the fjord virtually clear of ice. At that time, sea ice was densely packed on the shelf to the north of the fjord, implying that the Rijpfjorden sea ice had moved northward out of the fjord rather than melting in situ. This interpretation was confirmed by satellite imagery.

Irradiance profile model—We applied the irradiance profile model to two situations: late February, with the reemergence of both the day–night cycle and classic DVM in the water column, and early April, with sea ice and snow cover in Rijpfjorden approaching its maximum thickness and with both the pronounced contrast between day and night and the classic DVM behavior beginning to die away.

Values for midday incident irradiance, attenuation coefficients, albedo, and snow and ice thickness used in the model are given in Table 2. In late February, air temperatures at Rijpfjorden were typically in the range from $-20^\circ \text{C}$ to $10^\circ \text{C}$, and sea ice was growing, so we can assume reasonably that meltwater ponds (which reduce albedo) were absent. Observations indicated that snow cover (which increases albedo) was also absent at this time, so we used a gray ice albedo of 0.20 (Allison et al. 1993) for the young sea ice. Because of the presence of snow cover in April, we used a higher albedo of 0.80 (Perovich 1998). This value agreed well with unpublished PAR measurements from Rijpfjorden in late April 2007 (E. Leu pers. comm.). These PAR measurements also yielded attenuation coefficients for snow ($k_{snow}$) and ice ($k_{ice}$) of 18.0 and 1.6 m$^{-1}$, respectively. The latter value is high compared with the range from 1.1 to 1.5 m$^{-1}$ measured in previous studies (Grenfell and Maykut 1977), which can be attributed to an observed ice algae bloom during April (E. Leu pers. comm.). In the absence of measurements from February, we were unable to assess the quality of the model for early spring. However, observations from Rijpfjorden indicated that no substantial ice algae cover was present at that time (E. Leu pers. comm.), so we deemed it reasonable to use a lower value of $k_{ice} = 1.3 \text{ m}^{-1}$. As the sea ice cover was very thin in early February, errors associated with $k_{ice}$ were an order of magnitude smaller than the lowest light levels of interest and thus were not considered further.

Fluorescence data (Figs. 2–5) confirmed that prebloom conditions prevailed in both fjords during the selected model periods, which supported our decision to use the water attenuation coefficient of Smith (1973). Furthermore, the ADCPs at both locations dropped a high proportion of data from the upper water column at this time of year (see $w'$ in Figs. 2–5), indicating that concentrations of partic-
ulate matter were low and suggesting that the waters were optically clear compared with May 2008, when the PAR measurements in Kongsfjorden yielded a higher attenuation coefficient (E. Leu pers. comm.).

The output of the irradiance profile model is presented in Fig. 8. In late February, differences between the ice-free and ice-covered systems were negligible, indicating that thin, gray ice has little effect on light attenuation. Synchronized vertical migration was active at this time (Figs. 2–5), and these observations together suggest that DVM may have been cued by light levels as low as \(10^{-4}\) \(\mu\text{mol m}^{-2} \text{s}^{-1}\).

In early April, the difference in irradiance between the ice-free and ice-covered systems was more pronounced, with irradiance in ice-free waters being roughly 100 times that under ice. The major contributor to this difference was the greater albedo of the snow-covered surface. Critically, in Rijpfjorden the water column irradiance in early April, beneath snow-covered 0.8-m-thick sea ice, was only three to four times higher than that in late February, when ice cover was negligible, whereas at Kongsfjorden the irradiance in the water was two orders of magnitude larger in April than in February.

**Hydrography**—Temperature data from the two sites show the contrasting hydrography between the two study sites, with Rijpfjorden experiencing several months of consistently low temperatures (approx. \(-1.8^\circ\text{C}\)) during the sea ice season. The July sea ice melt in 2007 permitted subsequent surface warming (to \(3.5^\circ\text{C}\)) during that summer, whereas the persistent sea ice cover in 2008 led to an almost 8-month-long period of low temperatures from January until August. In contrast, temperatures at Kongsfjorden reached a winter minimum of \(0^\circ\text{C}–1^\circ\text{C}\), with these conditions persisting throughout the water column for roughly 4 months in 2007 and 6 months in 2008 and then followed by summertime temperatures in excess of \(5^\circ\text{C}\).

The horizontal velocity data also highlighted contrasts between the two fjords, with Kongsfjorden experiencing strongly directional (northwest to southeast) currents throughout both years, indicating that the mooring site was constantly flushed with warm Atlantic water flowing in from the shelf. Flow directions at Rijpfjorden showed far more variability, suggesting that recirculation of water within the fjord was far more important at this site.

**Primary productivity**—The fluorescence data showed that chlorophyll concentrations were low (close to zero) throughout both years, indicating that the mooring site was constantly flushed with warm Atlantic water flowing in from the shelf. Flow directions at Rijpfjorden showed far more variability, suggesting that recirculation of water within the fjord was far more important at this site.

### Table 2. Values of parameters for Eq. 1 used to model downwelling irradiance.

<table>
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<tr>
<th>Source</th>
<th>Late Feb</th>
<th>Early Apr</th>
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<td>(I_0) (\mu\text{mol m}^{-2} \text{s}^{-1})</td>
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<td>Snow Thickness (m)</td>
<td>Measurements</td>
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<td>(I) ((\mu\text{mol m}^{-2} \text{s}^{-1}))</td>
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<td>200 m</td>
<td>1 (\times) (10^{-4})</td>
</tr>
</tbody>
</table>

Fig. 8. Modeled irradiance in ice-covered and ice-free waters. The left-hand panels show the irradiance values as a function of depth with incident radiation being 1 \(\mu\text{mol m}^{-2} \text{s}^{-1}\) in late February and 300 \(\mu\text{mol m}^{-2} \text{s}^{-1}\) in early April. The right-hand panel shows the log\(_{10}\) profile of irradiance.
in both fjords for most of the year. In both 2007 and 2008, Kongsfjorden experienced an increase in fluorescence from April to August, which can be interpreted as a summer phytoplankton bloom. At Rijpfjorden, the fluorescence increase occurred 3 months later, in July and persisted for less than 1 month in both years. Water samples confirmed that these increases were due to pelagic blooms rather than to ice algae release events from the melting sea ice cover (J. Søreide unpubl.). Both Rijpfjorden and Kongsfjorden experienced unexpected increases in fluorescence during September 2007. While these could not be independently verified with water samples, such late bloom events have been described previously in the Arctic (Gislason and Astthorsson 1998; Arrigo and van Dijken 2004).

Species composition—The sediment trap samples collected in both fjords in 2007 included a wide range of species, of which the most numerous are presented in Fig. 9. All of these animals are in the size range we expect a 300-kHz ADCP to detect. The only organisms to be collected in the sediment traps throughout the year were *Calanus* spp., although their numbers varied immensely both between sites and between sampling periods. Although *Calanus* was the only group present consistently in the sediment traps, they dominated the samples only during late spring and summer months, with *Metridia longa* being important at Kongsfjorden during winter and the amphipods *Themisto* spp. and *Gammarus wilkitzkii* dominating numerically at Rijpfjorden during winter. The latter is one of six common ice-associated amphipods in the area (Arndt and Swadling 2006; MacNaughton et al. 2007), and is thus unlikely to be found in Kongsfjorden. Total numbers of animals collected at Kongsfjorden were consistently higher than at Rijpfjorden (Fig. 9).

Discussion

We have identified and characterized the dominant S, and w' patterns in the annual cycle of Arctic zooplankton vertical migration and have shown that the zooplankton communities at both Kongsfjorden and Rijpfjorden exhibited distinct phases of vertical migration throughout the year. DVM patterns at the two locations were similar from autumn to spring, but there was a divergence in vertical migration behavior during the summer months. The data thus support our prediction that differences in sea ice cover will lead to differentiated patterns of vertical migration. However, this simplistic hypothesis “test” does not complete the story. The response may be subtle and multifaceted, so exploration of the detail, as below, is warranted.

A strong seasonal cycle in migratory behavior was observed in both fjords, with classic DVM apparent in spring and autumn. DVM at such times was closely synchronized with the clear day–night regime. There was a great contrast in the levels of in-water irradiance between the two localities in late spring, with light penetration being diminished in Rijpfjorden through snow-covered sea ice. The fact that DVM built up and died away in both fjords at very similar times indicates that the relative change in irradiance is important for stimulating and synchronizing vertical migration. This supports previous findings by Ringelberg (1995), Tarling et al. (2002), and Cottier et al. (2006). Furthermore, patterns were similar between the two fjords despite differences in the composition and abun-
dance of zooplankton species. Differences in vertical migration behaviors emerged during summertime, with no synchronous signal observed at Rijpfjorden, whereas Kongsfjorden exhibited both asynchronous and weakly synchronous patterns.

**Rijpfjorden summertime asynchrony**—The lack of synchronized DVM observed under ice at Rijpfjorden during summer contrasts with the observations of Fortier et al. (2001), who found copepods performing DVM under ice during the period of midnight sun. They concluded that sea ice reduced light levels sufficiently to inhibit visual predation at “night” such that performing normal DVM benefited the zooplankton despite the 24-h daylight. Fortier et al. (2001) did not observe DVM in ice-free environments during periods of midnight sun and suggested that there was no inhibition of visual predation because light levels were continuously high. The absence of any apparent synchrony at Rijpfjorden during summer indicates some important difference(s) between our ice-covered site and that of Fortier et al. (2001). One factor is the contrast in sea ice and snow cover between the two sites. With sea ice in the Fortier et al. (2001) study being approximately twice as thick and snow cover two to three times thick as at Rijpfjorden, we might expect differences in under-ice irradiance of one to two orders of magnitude between the two locations (the actual difference would depend on the physical properties of the media and any ice algae cover). Therefore, although our results showed that shading of the ocean by sea ice at Rijpfjorden was pronounced, the effect may have been insufficient to inhibit visual predation or trigger coordinated DVM during Arctic summer. Differences in food availability may also have been important, in that primary production was restricted at Rijpfjorden, as evidenced by our fluorescence data and the work of J. Søreide (unpubl.), leading to low food availability for much of the season. This may have led to little incentive for migration since there would have been a minimal food gradient through the water column. Certainly, w’ was close to zero at Rijpfjorden for most of both summers, which could imply that the animals were not performing vertical migrations, although this is not the only possible interpretation (as discussed below). Different species compositions and, hence, different predator–prey interactions may also have played a role. Atkinson et al. (1999) observed that copepod abundances and vertical migration behavior at South Georgia were directly influenced by competition for food and predation by other zooplankton species, and such mechanisms are likely to play a role here. Further investigation of these factors would require detailed knowledge of the under-ice light environment during summer, food availability, species composition, and the effects of in-water light levels on the behaviors of relevant predators.

**Kongsfjorden summertime vertical migration**—Both the weakly synchronous and asynchronous S, patterns observed at Kongsfjorden were associated with nonzero w’, indicating that the animals were performing vertical migration throughout the summer. We note that our w’ measurements could, on occasion, be interpreted in the context of foray-type behavior (Cottier et al. 2006), such as during July 2008, where positive w’ in the lower water column was overlain by negative w’ and synchronized S, signals were weak and restricted to ~25–40-m depth. However, the feature requiring most discussion is the intermittent weak synchrony, which implied that the animals did, on occasion, respond to diurnal light variability during periods of midnight sun. This observation contrasts with the results of previous studies, which failed to identify coordinated zooplankton migration during periods of midnight sun (Blachowiak-Samolyk et al. 2006).

**Comparison of vertical migration behavior**—We are thus faced with the challenge of explaining the observation of synchronized migration under the midnight sun in an open-water environment, while such behavior was absent at an ice-covered site, even though we might expect the respective in-water light environments to induce the opposite, given the shading effect of a sea ice cover. Disregarding the unlikely explanation that incident solar radiation was significantly lower at Kongsfjorden than Rijpfjorden for continuous periods of several weeks during both summers, we are left with the possibilities that (1) light attenuation was stronger in Kongsfjorden than Rijpfjorden for periods of a few weeks at a time, leading to lower in-water irradiance and intermittent coordinated vertical migration at the former site; (2) differences in the vertical distribution of food between the two sites were sufficient to induce markedly different behavior in the zooplankton populations; and (3) predator–prey interactions differed between the two sites, again leading to differences in vertical migration patterns. These possibilities are addressed in turn.

Hanelt et al. (2001) found that increased turbidity associated with the influx of glacial water in Kongsfjorden led to a strong increase in light attenuation in near-surface waters, with summertime values of $k_w$ ranging between ~0.1 m$^{-1}$ and ~1 m$^{-1}$, depending on the sediment load of the water. Assuming that Rijpfjorden, under 0.8 m of fast ice and 0.1 m of white snow cover (as in 2007), did not experience a large summertime sediment influx, there may have existed a significant contrast in attenuation in which $k_w$ at Rijpfjorden was of the order of 0.1 m$^{-1}$ while that at Kongsfjorden was of the order of 1 m$^{-1}$. Under this scenario, using the attenuation coefficients for ice and snow given in Table 2, the in-water irradiance below 5-m depth would be higher at Rijpfjorden than Kongsfjorden. Certainly the large quantities of mud that blocked the sediment trap soon after deployment in Kongsfjorden in the autumn of 2007 indicated that the concentrations of suspended particulate matter were high at that time. However, to explain our observations of intermittent weak synchrony in this manner, highly turbid conditions would have to persist for weeks at a time in Kongsfjorden. Furthermore, ice algae at Rijpfjorden would have increased the light attenuation at that location, so it seems unlikely that in-water light levels at Kongsfjorden would have been lower than those at Rijpfjorden for extended periods of time.

As we have already discussed, zooplankton at Rijpfjorden may not have performed vertical migration in summertime because of low food availability (J. Søreide unpubl.) and thus little incentive for the behavior. In contrast, at Kongsfjorden phytoplankton blooms appeared...
in May of both years and persisted throughout much of the summer, providing a near-surface food source for zooplankton species and an incentive for vertical migration. For this to be a plausible explanation for the intermittent synchronized vertical migration, diurnal changes in in-water irradiance would have to be sufficient to trigger coordinated DVM, at least for limited periods of time. As discussed in the first argument, turbidity changes could have a pronounced effect on the in-water light environment. However, the advantage of the present argument is that it does not require light levels at Kongsfjorden to be lower than those at Rijpfjorden because of the crucial difference in food availability. Intermittency in coordinated DVM could also arise from changes in the incentive (i.e., the vertical distribution of food) for that behavior throughout the summer (Pearce 2003). The intermittent occurrence of conditions conducive to coordinated DVM under the midnight sun has the potential to deliver conflicting conclusions as to whether synchronized DVM is in fact active in the Arctic (Blackowiak-Samolyk et al. 2006).

The third argument requires there to be differences in predator and prey species between Rijpfjorden and Kongsfjorden that can account for the observed differences in vertical migration behaviors. We previously explained the lack of synchrony and near-zero \( w' \) at Rijpfjorden in terms of the absence of vertical migration, but an alternative explanation is that the zooplankton community composition at this site led to one group of animals (size or species group) moving downward in response to the upward movement of a different group, resulting in net zero vertical velocities. For instance, both *Calanus* and *Themisto* were present at Rijpfjorden in relatively large numbers during the early summer and, given that *Calanus* is a common prey for *Themisto* (Scott et al. 1999; Auel et al. 2002), it is reasonable to expect *Calanus* species to avoid *Themisto* where possible, which could have given rise to a canceling out of vertical velocities. Given that *Themisto* is less abundant at Kongsfjorden, we would not necessarily expect this particular mechanism to be important at that site.

As another example, *M. longa* was more numerous at Kongsfjorden than Rijpfjorden in May and August 2007, when the most pronounced synchrony was observed at the former site. *Metridia* spp. are less able to evade visual predators than *Calanus* spp. and therefore exhibit more pronounced vertical migration than the latter (Hays et al. 1997). It is possible that light levels at both fjords were sufficiently low during midsummer (because of sea ice at Rijpfjorden and sediment load at Kongsfjorden) that *M. longa* would have benefited from DVM at both locations, but that we simply failed to see this behavior at Rijpfjorden because the species was not present in large enough numbers for an identifiable coordinated DVM signal to emerge. These two examples serve to illustrate that interactions between species of differing abundances have the potential to influence observed patterns of vertical migration, but we emphasize that additional species that were not collected in our sediment traps undoubtedly contributed to the predator–prey interactions at each site.

In the absence of midsummer PAR profiles and a comprehensive understanding of the food web at each site, we are unable to investigate further the applicability of our arguments to the two fjords. However, we note that the consideration of food availability and predator–prey interactions as controls on vertical migration behavior in the second and third arguments is consistent with the results of Atkinson et al. (1999).

An additional feature of the summertime migration signal at Rijpfjorden was the observation of strong negative \( w' \) above \( \sim 30 \) m and high \( S \). below this depth during mid-July 2007. This coincided with the summer increase in fluorescence, and the signals in both \( w' \) and \( S \) can be attributed to flocculations of phytoplankton material sinking out of surface layers. Such processes have been observed under both laboratory (Kiorboe et al. 1990) and marine (Fabricius and Wolanski 2000) conditions.

The pronounced vertical velocity fluctuations observed during winter in both fjords are difficult to interpret. Such variability has been observed in ADCP data at other sites (Tarling et al. 2002), but its origins remain unclear, and there is no apparent relationship between this variability and \( S_w \).

What emerges from this two-site comparison is that synchronized DVM behavior is a robust phenomenon whose broad features are linked to the presence or absence of a pronounced day–night cycle. In the absence of such a signal during midsummer, a pronounced synchronized DVM pattern is almost completely absent. However, a difference exists between the ice and snow–covered fjord, where any vertical migration is wholly asynchronous, and the open fjord, where some weak synchrony in DVM persists. We propose that the presence of 0.8-m-thick sea ice and 0.1-m-thick snow cover does not directly alter DVM through shading of the ocean but rather, in conjunction with the hydrographic environment, is an important control on food availability, turbidity, and species composition, all of which are contributory factors to patterns of vertical migration. Future changes in the thickness and distribution of sea ice in the Arctic are likely to alter zooplankton vertical migration behavior, particularly during the midsummer months.

**Acknowledgments**

Thanks to the crew and scientists on board the British Antarctic Survey’s RRS *James Clark Ross* and the Norwegian Polar Institute’s R/V *Lance* and R/V *Jan Mayen* for assistance with the mooring deployments and recoveries; Trond Svene of the Norwegian Polar Institute, Tromsø, Norway, for providing photosynthetically active radiation (PAR) data from Ny Ålesund; and Eva Leu of the Norwegian Polar Institute, Tromsø, Norway, for Rijpfjorden PAR data and information regarding subsea ice blooms in 2007. The analysis was funded under a Natural Environment Research Council (NERC) Strategic Ocean Funding Initiative (SOFI) grant (NE/F012381/1) to Andrew S. Brierley, Geraint A. Tarling, and Finlo R. Cottier, in partnership with Jørgen Berge at the University of Norway in Svalbard (UNIS). Finlo R. Cottier’s contribution was further supported through the European Regional Development Fund, under the Addressing Research Capacity (in the Highlands and Islands) project. The Rijpfjorden mooring was funded by the Norwegian Research Council under the Climate Effects on Planktonic Food Quality and Trophic Transfer in Arctic Marginal Ice Zones (CLEOPATRA) project (178766/S30), the StatoilHydro Ice Edge program, and the ConocoPhilips ArcWin program. During 2006–2007, the Kongsfjorden mooring was funded through Research Council of...
Norway (MariClim 165112/S30) and in 2007–2008 was funded by NERC Oceans 2025 Theme 10.

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Associate editor: Luc De Meester

Received: 06 May 2009
Accepted: 08 October 2009
Amended: 17 November 2009