NOTE

Further evidence of diel vertical migration of copepods under Arctic sea ice during summer

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ABSTRACT: We examined diel vertical variability of acoustic backscatter under sea ice during the midnight sun season at high latitude in the Canada Basin of the Arctic Ocean. Acoustic backscatter demonstrated that the dominant Arctic copepods (*Calanus hyperboreus*) consistently performed a distinct diel vertical migration (DVM) synchronized with the solar radiation cycle. DVM was mainly observed between 2 distinctive pycnocline layers at 25 and 45 m above the subsurface chlorophyll maximum (SCM) within Pacific summer water. Picophytoplankton (<2 µm) were mainly distributed within the SCM layer, whereas diatoms (>20 µm) were above the SCM layer. This indicated that light variation is a potential trigger for the DVM of Arctic copepods under sea ice, whereas the vertical depth of occurrence was primarily controlled by water mass stratification and food. This vertical behavior is significant to understanding how Arctic copepods adjust to their habitats relative to sea ice, water masses, and food sources in the dynamic environmental changes in the Arctic Ocean.

KEY WORDS: Arctic copepod · Diel vertical migration · Pycnocline · Subsurface chlorophyll maximum · Acoustic Doppler current profiler

INTRODUCTION

Arctic copepods of the genus *Calanus*, the dominant herbivores among zooplankton communities in the Arctic Ocean, play a key role in controlling pelagic food webs (Kosobokova & Hopcroft 2010). Despite the ecological significance of Arctic copepods, our knowledge of their dynamics, especially vertical behavior under sea ice in high-latitude regions, is limited and reduces our ability to detect marine organisms with both net- and acoustic-based methods in the ice-covered regions of the Arctic Ocean.

Fortier et al. (2001) reported that herbivorous copepods such as *C. hyperboreus*, *C. glacialis*, and *Pseudocalanus acuspes* perform diel vertical migration (DVM) under sea ice of the Arctic Ocean in summer, during the midnight sun. The copepods migrate up into the chlorophyll *a* (chl *a*)-rich under-sea ice around the maximum relative rate of change in irradiance at dusk and descend to a deeper depth a few hours later. Wallace et al. (2010) identified an asynchronous zooplankton DVM under sea ice at Rijpfjorden fjord during summer, in contrast with the report by Fortier et al. (2001). They noted that the relatively thin sea ice and snow cover did not sufficiently reduce light levels for classical DVM, and low food availability also provided little incentive for vertical migration. Cottier et al. (2006) showed that feeding needs rather than external stimuli could cause uncoordinated vertical behavior in zooplankton during Arctic summer. There are still conflicting hypotheses for migration modulators, and the question of whether zooplank-

ton migrate daily under sea ice in the Arctic during periods of constant sunlight has not yet been resolved (Blachowiak-Samolyk et al. 2006). Moreover, the influence of hydrographic conditions on zooplankton DVM under sea ice has only been reported in a few studies (Falk-Petersen et al. 1999, Søreide et al. 2003).

In this study, we focused on copepod DVM in the high-latitude Canada Basin, which is one of the least studied marine ecosystems in the Arctic Ocean (Lee & Whitledge 2005). The Canada Basin has changed rapidly over the past decade, with decreasing sea ice extent and warmer ice-free water during summer (Stroeve et al. 2012). Increased ice melt has caused more fresh water at the sea surface, a deeper halocline, and increased water column stratification. The aim of our study was to provide supportive evidence for DVM of Arctic copepods under sea ice during the midnight sun period in summer at high-latitude regions of the Canada Basin. Acoustic backscatter pro-

vides a realistic representation of zooplankton vertical movement with high-resolution vertical profiles, and can resolve their vertical and temporal distribution (Cottier et al. 2006, Berge et al. 2009, Cisewski et al. 2010). Such information contributes to our understanding of zooplankton behavior and functioning under rapidly melting summer sea ice, which will have subsequent effects on the Arctic marine ecosystem.

MATERIALS AND METHODS

An ice-camp field campaign was performed in the Canada Basin of the Arctic Ocean from 9 to 14 August 2014. The site (initial position: 77° 36.741' N, 146° 6.072' W) was mostly (>75%) covered by sea ice with 0.8–4 m thickness (Fig. 1a). Ice breaker RV 'Araon' was anchored at the margin of a drifting ice floe. Ice-tethered moorings with an acoustic Doppler current profiler (ADCP; RDI Workhorse 300 kHz) and
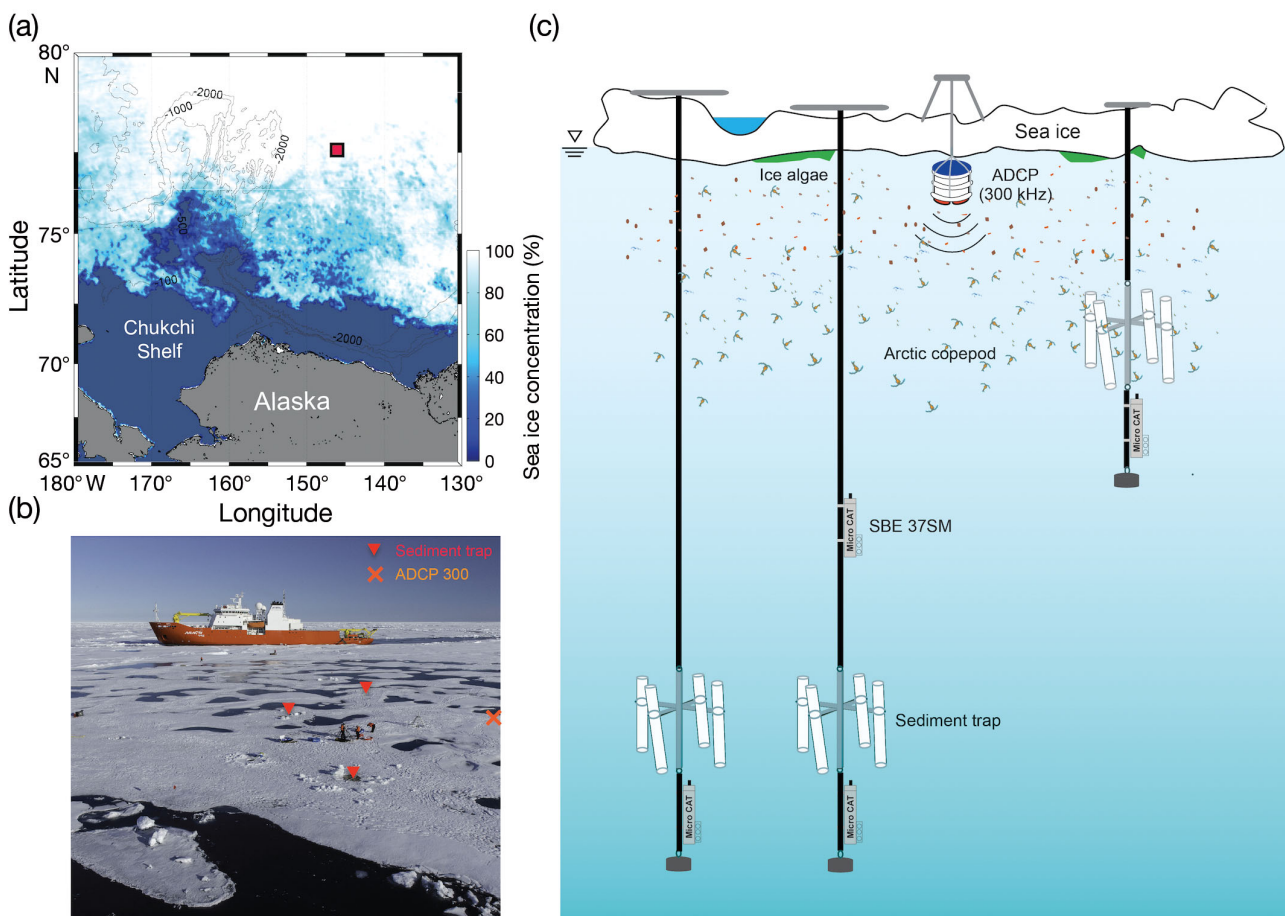

Fig. 1. (a) Sea ice distribution in the study area in the Canada Basin of the Arctic Ocean. Red square represents the ice-camp site. Sea ice concentration was measured by AMSR2 on 14 August 2014. (b) Photo taken at the mooring location where the sediment traps and acoustic Doppler current profiler (ADCP) were installed. (c) Schematic design of mooring systems with sediment trap and ADCP

3 sediment traps were installed near a melting pond approximately 200 m away from the 'Araon' (Fig. 1b,c). The downward-looking ADCP was mounted at a depth of 1.5 m from the sea surface to measure the vertical profiles of current velocity and acoustic intensity, which can estimate zooplankton abundance. ADCP has 4 beams that were oriented at a 20° angle from the vertical axis, and measured 84 m in depth with 1 m resolution. The angle was compensated to calculate each vertical depth from the transducers, and the relative acoustic intensity recorded by ADCP was converted to volume backscattering strength (S_V, dB re 1 m^{-1}) using the SONAR equation presented by Deines (1999). The sampling interval was set to 120 pings per ensemble every 3 min. ADCP data were post-processed using WinADCP®, filtering out data with beam correlations below 80. The absolute current velocities (eastward [U] and northward [V]) were calculated with GPS data from the ship, which could correct for the drift velocity of sea ice. The data below 50 m depth were removed because of low beam correlation.

Solar radiation was measured at 0.5 h intervals with a net radiometer (CNR1, Kipp and Zonen) installed at the bow of the 'Araon' to record the daily variation in light intensity. Vertical profiles of water column properties were measured with a calibrated conductivity-temperature-depth (CTD) system (SBE 911plus, Sea-Bird Electronics), dissolved oxygen sensor (SBE43, Sea-Bird Electronics), and a fluorometer (ECO FL(RT)D; WETLabs), and photosynthetically active radiation (PAR) was measured with a TriOS optical sensor (RAMSES; TriOS Mess) onboard at 2–12 h intervals throughout the field campaign. All data were 1 m averaged to remove noise. Water samples for chl *a* were collected with 10 l Niskin bottles at 5 depths (2, 8, 15, 25, and 60 m) through holes in the ice. To analyze size-fractionated chl *a* content, samples were sequentially passed through Whatman GF/F filters (24 mm) for total chl *a* concentrations, and then filtered further by size through 20 and 2 µm membrane filters. Chl *a* was measured using a fluorometer (TD-700; Turner Design) after filtration.

Zooplankton were collected with 3 cylinder-type sediment traps (7.56 cm diameter, aspect ratio of 1:10) and a Bongo net (mouth area of 0.5 m^{-2}, 330 µm mesh). The traps were filled with filtered seawater before deployment, and installed through the ice holes at 15 and 50 m depths under sea ice during the mooring period. The Bongo net was vertically towed within the upper 200 m of the water column from the 'Araon'. All zooplankton samples captured were preserved in 5% buffered formaldehyde for quantitative analyses. Subsampling was carried out with a Folsom plankton splitter and examined with a dissecting microscope in the laboratory to identify the lowest possible taxonomic level of zooplankton present in the samples. Abundance (ind. m^{-3}) was calculated with the revolution counts from a flow meter attached to the center of the net.

RESULTS

The physical and biogeochemical properties of the water column showed little temporal variation during the 5 d when the vessel was moored, reflecting the hydrodynamic stability of the study area (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m592p283_suppl.pdf). The upper 25 m surface layer was slightly isolated due to a strong summer halocline between the surface mixed water (SMW) and Pacific summer water (PSW) caused by surface ice melting. The second halocline layer was around 45 m, where the PSW encounters the Pacific winter water (PWW). The PSW from 45 to 80 m is relatively warm, ranging from −0.5 to 0.5°C, and while it is salty at 29 to 31.5 psu, it is fresher than the PWW below the PSW. The salinity gradually increased below 45 m, and the warmest water mass was at a depth of about 60 m. The density gradients clearly represent 2 distinctive layers of water masses for the summer and winter pycnocline at 25 and 45 m, respectively (Fig. 2c). The euphotic zone depth (1% of the sea surface PAR) was around 55–60 m (Fig. S1), and the subsurface chlorophyll maximum (SCM) was identified at 60 m within the PSW throughout the entire observation period.

Temporal variation in the vertical structure of the acoustic backscatter indicated that typical DVM of zooplankton was constantly present and associated with diel variation of incoming total solar radiation between 25 and 45 m under sea ice on 9–13 August (Fig. 3a,b). Downward movement occurred between 14:00 and 17:00 h UTC (hereafter all times are presented in UTC), when the total solar radiation was relatively high (100–150 W m^{-2}), while upward movement occurred between 03:00 and 06:00 h, late at night when the total solar radiation was relatively low (10–100 W m^{-2}). *Calanus hyperboreus* collected from the sediment trap at 15 m depth had a mean ± SD prosome length of 4.5 ± 0.12 mm (n = 25); no zooplankton was collected from the 2 sediment traps at 50 m depths. We identified 9 zooplankton groups, and calanoid copepods were the dominant taxa with the highest proportion (81%) from the net samples
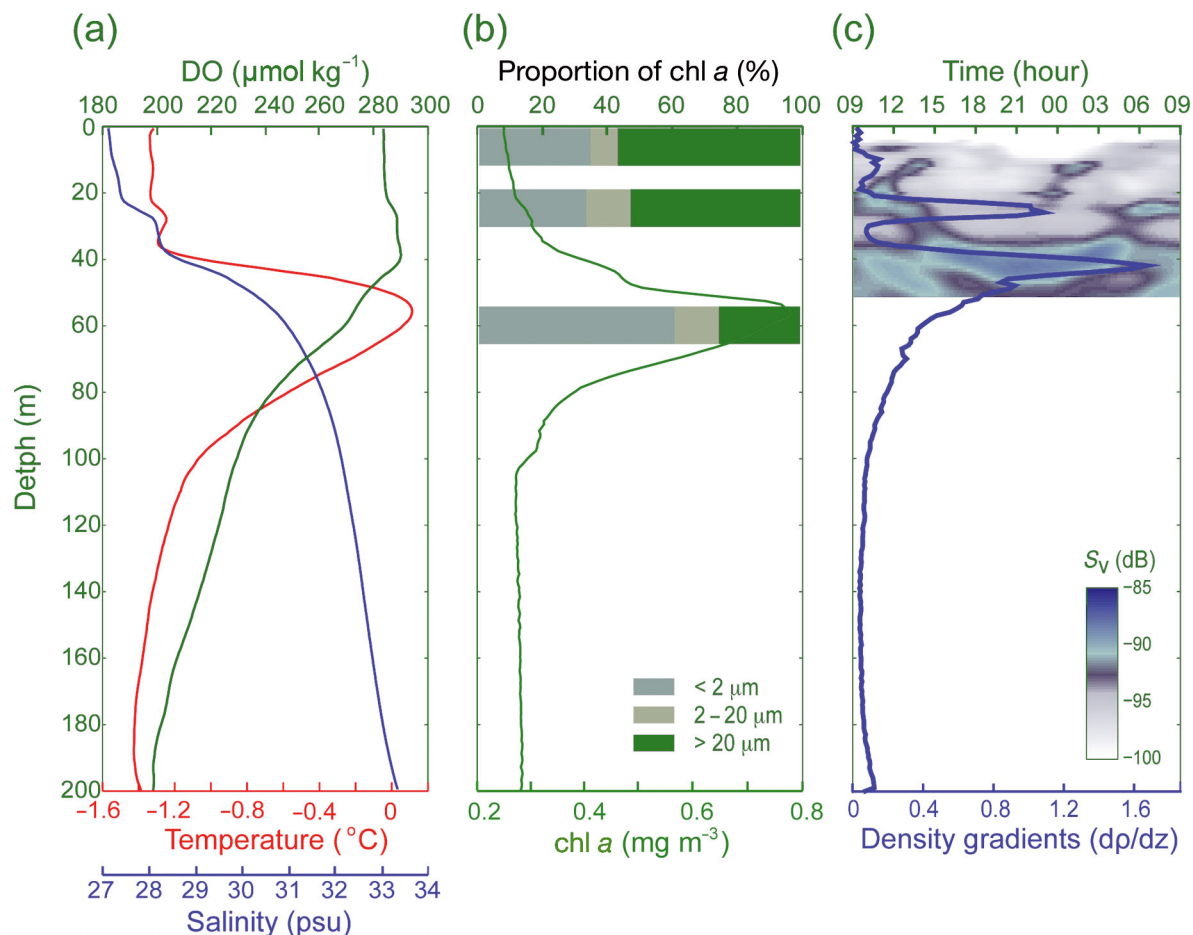
Fig. 2. (a) Vertical profiles of averaged potential temperature, salinity, and dissolved oxygen (DO). (b) Vertical profiles of chl *a* concentrations with the proportion of chl *a* in the different size fractions (>20, 2–20, and <2 μm). (c) Vertical profile of the density gradient and averaged daily variability of volume backscattering strength (S_V) between 09:00 h (UTC) on 9 August and 09:00 h on 13 August

(Table S2 in the Supplement). The occasionally high acoustic backscatter in the upper water column (<25 m) resulted from the generation of a high concentration of suspended particles below sea ice, which is controlled by the inertial motion of sea ice (Ha et al. 2015). Under sea ice, strong velocity shears were observed at around 25 and 45 m, which were consistent with the depths of the 2 constant pycnocline layers (Figs. 2c & 3c). Relatively stable and weak currents were observed between the summer pycnocline (25 m) and winter pycnocline (45 m). Temporal variability in acoustic backscatter, as shown by the frequency spectrum (cycles d^{-1}), was regular with respect to daily solar cycle (Fig. 3d). The frequency spectrum showed that the pronounced daily variation of copepods in a depth layer was related to the averaged diel cycle of solar radiation. Current speed exhibited a distinct temporal variability in an approximate 1 h cycle that was caused by the inertial motion under sea ice.

DISCUSSION

This study has characterized the acoustic backscatter pattern in the daily cycle of copepods' vertical behavior in the high-latitude Canada Basin of the Arctic Ocean. We discuss the migratory behavior of copepods in the Arctic Ocean that is associated with light, food, and water column stratification.

Variations in light intensity are essential in changing abundances and vertical distribution of plankton and fish (Aksnes et al. 2004). In the high-latitude Arctic Ocean, there are strong seasonal cycles in the migration behavior of zooplankton that vary seasonally with the sea ice conditions and light availability (Wallace et al. 2010). Zooplankton perform vertical migration in a day–night cycle in the spring and autumn when there is a distinctive difference in the levels of in-water light intensity. DVM behavior is absent when there is limited diurnal variability of light intensity during the midnight sun period of
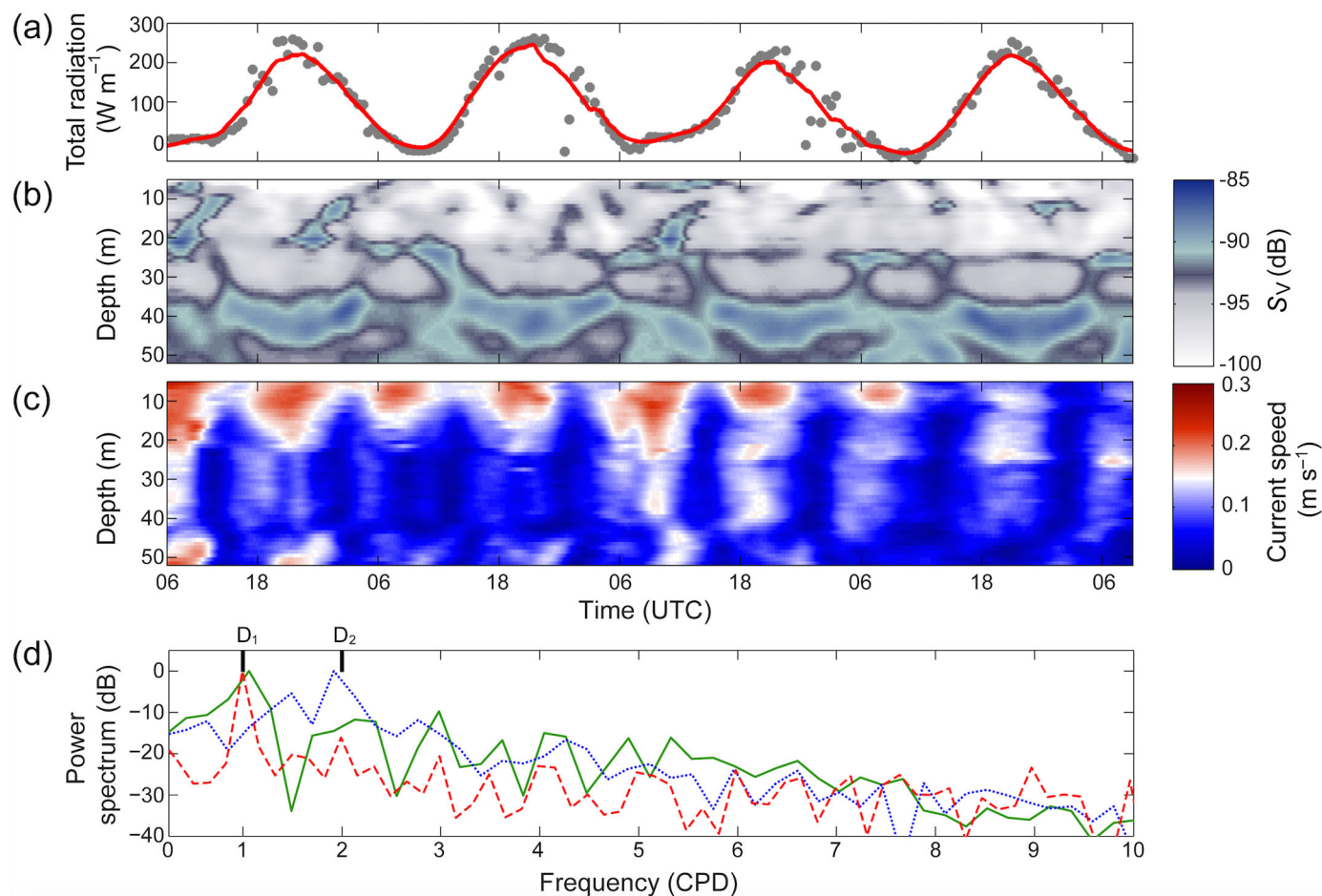
Fig. 3. Temporal variability of the (a) total net solar radiation, (b) vertical structure for volume backscattering strength (S_V), and (c) current speed (m s^{-1}) from 06:00 h (UTC) on 9 August to 23:00 h on 13 August. (d) Frequency (cycles d^{-1}, cpd) spectrum of the total net solar radiation (red dashed line), averaged S_V (green solid line), and current speed (blue dotted line) between 30 and 45 m. D_1 and D_2 indicate diurnal solar frequency and semidiurnal frequency, respectively

summer in both ice-free environments with continuous high illumination (Fischer & Visbeck 1993, Falkenhaug et al. 1997, Blachowiak Samolyk et al. 2006, Cottier et al. 2006, Geoffroy et al. 2016) and in ice-covered regions with thin sea ice and snow thickness (Fortier et al. 2001, Wallace et al. 2010). Some studies have reported the occurrence of zooplankton DVM in ice-covered regions during summer when light is sufficiently attenuated by sea ice, which stimulates vertical migration (Fortier et al. 2001, Wallace et al. 2010). In this study, a classical DVM pattern was observed under ~2 m thick sea ice that was synchronized with a distinctive daily contrast in the levels of solar radiation during the midnight sun period, even though the study was conducted at 77° N in mid-August. Only 20% of maximum PAR penetrated to 10 m under sea ice in our study region compared to PAR in open water (Fig. S2 in the Supplement). Copepods perform DVM in response to a

low variation of irradiance, i.e. 0.0005−0.5% that of the ambient irradiance during the polar night (Båtnes et al. 2015). This implies that copepods can sense the small variations in light intensity under sea ice and thus, continue DVM during summer, and the light conditions are considered to be the cue for the timing of their vertical migration.

Vertical migration is considered an efficient life strategy for zooplankton to adapt to the variable depth gradients in food availability. Therefore, the location and abundance of food sources may also affect the vertical distribution of copepods (Daase et al. 2008). Copepods distribute at the SCM layer where diatoms are a dominant fraction of the phytoplankton biomass, indicating a relationship between the depth of maximum chl *a* and the depth of maximum zooplankton biomass in the western Canada Basin (La et al. 2015). However, in the present study, the mean depth distribution of copepods indicated by

acoustic backscatter was not related to the chloro-phyll-richest water either during the day or night. The mean depth at which copepods were observed was about 30 m more shallow than the depth of maximum phytoplankton biomass. Copepods were mainly distributed within depths where large phyto-plankton (>20 µm) such as diatoms were most abun-dant (>40%) (Fig. 2c and Table S1 in the Supple-ment). Picophytoplankton (<2 µm) were mainly found (>50%) at the SCM layer within PSW. These results indicate that copepods located under sea ice in the Arctic Ocean could respond to biological cues associated with phytoplankton composition, and the maximum chlorophyll concentration does not always represent the maximum biomass of zooplankton.

The vertical distribution of copepods could be highly affected by the vertical distribution of water mass properties (Reiss et al. 2002), pycnocline layers (Lougee et al. 2002, Berge et al. 2014, Geoffroy et al. 2016), and current velocity and turbulence (Saiz & Alcaraz 1992). Copepods under sea ice associated with the depth of summer and winter pycnocline lay-ers showed typical DVM throughout the observation period (Figs. 2 & 3b). Water column stratification can indicate a physical barrier that sustains DVM within strong density gradient layers. Copepods might swim away from high turbulence and stay at depths with less turbulent areas. The Richardson number (Ri) represents the dynamic stability of a water column; in our study, the Ri values were >0.25 between 2 pyc-nocline layers, while strong vertical turbulent mixing was observed with Ri < 0.25 at depths of 0–25 m (Fig. S3 in the Supplement). These results exhibit a potential stability in low vertical mixing between 25 and 40 m, and a response to physical cues associated with the main vertical habit of copepods under sea ice. The population of copepods was consistently measured between 2 pycnocline layers, which exhib-ited a response to the stratified and homogeneous distribution of water masses in the vertical distribu-tion of copepods.

CONCLUSIONS

The results from this study support further evidence of copepod vertical migration that is responsive to so-lar radiation underneath sea ice in the high-latitude Arctic Ocean. The vertical depth of copepods was mainly distributed within a stable water column that had large-sized phytoplankton. Acoustic backscatter could enable measurement of the variation in the be-havior of zooplankton with fine vertical and temporal resolution. Vertical migration and distribution of copepods are different depending on location (lati-tude), time of day/year, and sea ice conditions in the Arctic Ocean. For the continued study of the vertical behavior of copepods, we recommend that future studies include long-term observations through the autumn and winter, which could evaluate potential seasonal behaviors associated with varying sea ice conditions. This would provide further insight into how copepods respond to the changing Arctic Ocean.

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