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An abrupt decline in springtime zooplankton diel vertical migration due to a shift in stratification regime

Jay A. Austin[a],*, Thomas R. Hrabik[b], Donn Branstrator[b]

[a] Large Lakes Observatory and Department of Physics and Astronomy, University of Minnesota, Duluth, United States
[b] Department of Biology, University of Minnesota, Duluth, MN 55812, United States

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ABSTRACT

Returned signal strength intensity measurements from an acoustic Doppler current profiler deployed at an open-water site in Lake Superior from May-July 2019 were used to estimate the scattering intensity over the top 50 m of the water column. It displayed a strong diel signal, with higher scattering intensity at night, consistent with the normal diel vertical migration of planktonic organisms. However, the intensity of the nocturnal scattering signal decreased abruptly on 10 June, coincident with the end of winter stratification (cold water on top of warmer water) and the beginning of the neutrally stratified period. We hypothesize that the sudden change in zooplankton behavior is due the availability of phytoplankton deep in the water column after the transition, made possible by radiatively driven convection mixing the entire water column on time scales of hours.

Introduction

Diel vertical migration (DVM) of zooplankton is a common feature in many aquatic ecosystems and is commonly observed in Lake Superior (Jensen et al., 2009; Ahrenstorff et al., 2011; Oliver et al., 2015). Vertical distributions may vary seasonally (Ahrenstorff et al., 2011), and variability in thermal stratification has a strong influence on the phenology of zooplankton species composition, distribution and predator–prey interactions generally (Tessier and Welser, 1991; Gerten and Adrian, 2002; MacPhee et al., 2011). Thermal stratification is central to the onset of seasonal zooplankton dynamics in most systems (Sommer et al., 1986). In Lake Superior, the coldest of the Laurentian Great Lakes, the phenology of zooplankton community structure is strongly influenced by seasonal variability in thermal structure (Pawlowski et al., 2018). In this case, the spring zooplankton community is dominated by cyclopoid copepods including *Diacyclops thomasi*, calanoid copepod species including *Leptodiaptomus sicilis*, *Limnocalanus macrurus* and the macrozooplankton *Mysis diluviana* (Brown and Branstrator, 2004) with cladocerans becoming more important as summer progresses (Watson and Wilson, 1978; Pawlowski et al., 2018). Breakdown or onset of thermal stratification provides an opportunity to examine the influence of stratification in changing the spatial distributions of zooplankton populations.

Advances in hydroacoustic technology are facilitating measurement of zooplankton distribution at increasingly higher spatial and temporal resolution, which has been important for addressing new questions in large freshwater ecosystems (Meadows, 2013). Applications include mobile down looking surveys measuring *Mysis diluviana* and other zooplankton species in the Laurentian Great Lakes (Holbrook et al., 2006; Rudstam et al., 2008) and mobile survey data have been used to address spatial patterning in other freshwater systems (Heald et al., 2017; Warren et al., 2016). Acoustic Doppler Current Profilers (ADCPs), both shipboard and moored, have also been used extensively in marine environments to describe biological fields (Deines, 1999; Wallace et al., 2010), and to a lesser extent in freshwater lakes (Lorke et al., 2004; Huber et al., 2011). However, application in the Laurentian Great Lakes has been extremely limited. An exception is Miller (2003), who used an ADCP to track patterns in diel vertical migration of *Mysis diluviana* in Grand Traverse Bay, Lake Michigan.

In spring 2019, a large array of moored equipment, including an ADCP, was deployed in western Lake Superior to study convection driven by incident solar radiation prior to the onset of positive stratification. In a process called radiatively driven convection (hereafter RDC; Austin, 2019), sunlight warms surface water prior to reaching the temperature of maximum density (hereafter T_{MD}, approximately 3.98 °C in fresh water at the surface), making it denser and driving convective circulation. During neutrally stratified

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* Corresponding author.
E-mail address: jaustin@d.umn.edu (J.A. Austin).

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conditions, water warmed at the surface is observed to reach the bottom of Lake Superior (180 m in the case of this field site) less than six hours after sunup (Austin, 2019), suggesting that the entire water column is being mixed relatively rapidly. In this particular deployment, the equipment was deployed while the lake was still negatively stratified (cold water on top of warmer water, all below T_{MD}), during which convection occurred over only the epilimnion, which was roughly 80–100 m thick. Roughly a month after deployment, the epilimnion reached the temperature of the hypolimnion, at which point convection took place over the entire water column. The focus of this short note is to document an abrupt change in zooplankton vertical migration behavior coincident with this transition. Given that these observations were opportunistic with regards to zooplankton migration, we do not have corroborating observations that would give us insight into the species involved, but future deployments should include more traditional observations to strengthen this work.

Methods

From 7 May to 16 July 2019, an array of equipment was deployed in 180 m of water in the open waters of the western arm of Lake Superior (47° 26′N, 89° 43′W) (Fig. 1A) to characterize the physical characteristics of radiatively driven convection. The moorings (Fig. 1B) consisted of a large 2-dimensional thermistor array, a spar buoy to make measurements of temperature close to the surface, a meteorology buoy, and an ADCP mooring, all within a kilometer of each other. The ADCP mooring consisted of an upward-looking, 500 kHz Nortek Signature 500 ADCP at approximately 55 m depth, and thermistors spaced every 20 m below the ADCP. The ADCP collected a 7-minute long burst of 4 Hz data every 53 min in 4 m bins spanning from the surface to 52 m depth. The ADCP had five beams, four in a classic Janus configuration and a fifth beam oriented directly upwards. Pitch and roll varied by less than 1^{0} over the course of the deployment. In order to avoid side-lobe interference close to the surface, we used only the upward looking beam. In addition, temperature was measured with RBR SOLO-T thermistors sampling continuously at 2 Hz at a range of depths on the different moorings. In this manuscript, we use thermistors from the spar buoy at 1 m and 20 m depth, and from the ADCP mooring at 140 m and 160 m depth.

In order to estimate the relative scattering intensity of the migrating zooplankton, the linear signal intensity *S(t)* is derived from the recorded returned signal strength intensity (hereafter RSSI), reported in decibels, using.

$$S(t) = S_0 10^{RSSI/20}$$

where S_0 is an arbitrary reference intensity. We model the returned signal *S(t)* as.

$$S(t) = S_0(Z(t) + B(t))R^{-2}\exp(\alpha R)$$

which is a modification of the classic sonar equation (e.g. Deines, 1999), in which R is the range to the cell in question, α is the coefficient of acoustic absorption at 500 kHz for freshwater, taken here to be -0.023 m^{-1} (equivalent to -100 dB/km, Francois and Garrison, 1982), *B(t)* is the slowly varying background scattering due to suspended solids and other constituents that do not change on a diurnal basis, and *Z(t)* is the scattering due to diurnally migrating zooplankton. The two range-dependent terms, which account for beam-spreading and absorption, respectively, do not change over time. The background scattering term *B(t)* is determined by low-pass filtering the data by taking a 24-hour moving mean of the data, excluding the period from two hours before midnight to four hours after midnight each night during which the signal is dominated by migrators. The term of interest is the difference between the raw data and the low-pass filtered data $Z(t) = S(t)-B(t)$, which is a relative measure of backscattering due to diurnal migrators. The relationship between this measure and biomass is complex, dependent on scatterer size, shape, and orientation, and given that we do not have ground-truthing data available, we make no attempt to estimate biomass from the given data. We will therefore use this estimate of scattering qualitatively only, rather than quantitatively, investigating its variability over space and time,

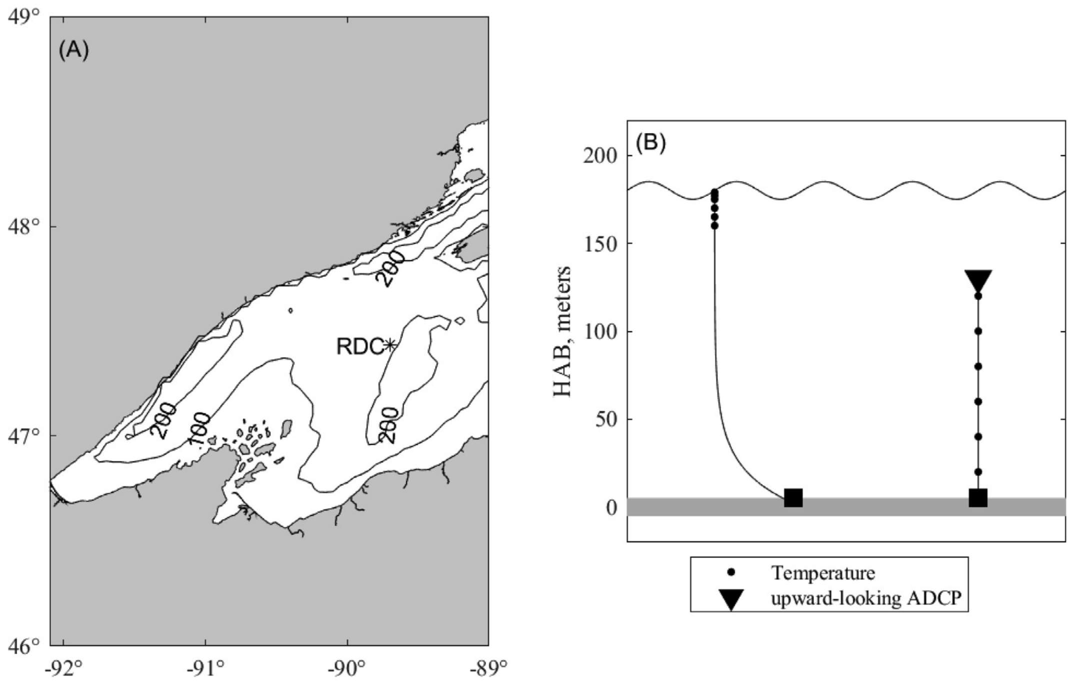

Fig. 1. (A) Map of study site. Depth contours are in meters. Deployment site is marked with an asterisk. (B) Schematic of moored instrumentation used in this manuscript. Spar mooring (left) and ADCP mooring (right).

under the assumption that the scattering intensity $Z(t)$ is proportional to biomass.

In addition to the moored array, conductivity-temperature-depth (CTD) profiles were taken during the deployment cruise on 7 May and again on a mid-experiment surveying cruise on 12–13 June. The SBE9-11 CTD was equipped with a WETLabs WETStar chlorophyll-*a* fluorometer and a WETLabs 650 nm CStar transmissometer with a 25 cm path length, as well as other sensors not used here.

Results

At the time of deployment, the water column was inversely stratified with respect to temperature (Fig. 2, Fig. 3A). At this stage, radiatively driven convection keeps the epilimnion well mixed, and the thermocline at 80–100 m isolates hypolimnetic water from the surface. By 10 June, the epilimnion warmed to the temperature of the hypolimnion, after which convection mixed the entire water column daily as the water column slowly warmed. On 6 July, the water column reaches T_{MD} for 180 m depth ($\sim$3.6 °C), and full water column convection ends. On 12 July, the water temperature reached T_{MD} at the surface and began to form positive stratification.

The vertically averaged scattering intensity (Fig. 4A) increased steadily over the course of the deployment. The source of this increase is not well understood but may reflect a gradual increase in sediment concentration due to mesoscale circulation. The signal associated with scatterers $Z(t)$ (Fig. 4B) emphasizes the diurnal signal present in the data, which we hypothesize is due to zooplankton migrating into the upper 50 m of the water column to feed at night. The average scattering intensity in a four-hour window around local midnight is shown as dots (Fig. 4B), and solid lines show the average backscatter from 7 May to 10 June and from 10 June to the onset of stratification on 6 July. The average magnitude of scattering due to the nocturnal migration drops abruptly by about 40% on 10 June. A two-sample t-test indicates that the mean scattering value before and after the transition differ with a p-value of less than 0.01. This abrupt shift corresponds exactly to the end of the negatively stratified period. Compositing the high-passed data as a function of time of day and depth for days prior to 10 June and for days after 10 June (Fig. 5) shows that the signal peaks in a roughly 4-hour window from roughly an hour before midnight to four hours after midnight, with a remarkably abrupt ending. Sunset and sunrise times are also shown as small black bars at the surface, demonstrating that the migrators arrive at the surface $\sim$ 1.5 h after sundown and return to the depths 0.5 h before sunup.

Discussion

We used an acoustic Doppler current profiler to document an abrupt shift in the spatial extent of upward zooplankton vertical migration at night coincident with the onset of springtime water column mixing in Lake Superior. It is unlikely that the shift in migration behavior is due to changes in water temperature, because the differences in temperature during the transition from negatively to neutrally stratified periods are very small (Fig. 2). Likewise, the light environment and predator abundance does not change appreciably during the transition and is unlikely to be the driver of the change (Fig. 3C). Rather, we hypothesize that the zooplankton which are exhibiting this shift in migration behavior are cuing on the sudden availability of food at depth, as full water column convection distributes phytoplankton over the entire water column, lessening the need for vertical migration. Food availability is widely accepted as one of multiple factors driving vertical migration in zooplankton (Lampert, 1989). Studies have shown that under certain conditions vertical migration may not occur when there is not a food-based advantage to relocation (Pijanowska and Dawidowicz, 1987; Gliwicz and Pijanowska, 1988).

The change in stratification, from negatively to neutrally stratified, is binary in nature; even a small amount of stratification will keep the water column from mixing completely, but once the stratification is removed, the water column mixes thoroughly. This is consistent with the abrupt nature of the change in scattering intensity. Interestingly, the availability of food throughout the water column only dampens vertical migratory behavior, rather than

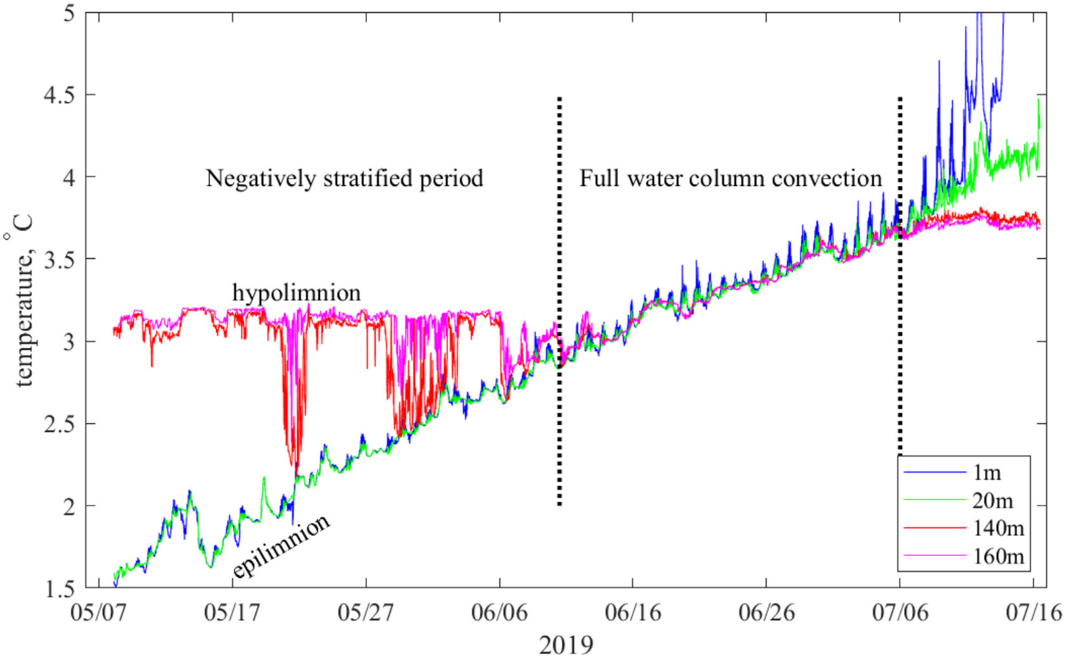

Fig. 2. Temperature at the mooring site at 1 m, 20 m, 140 m, and 160 m depth.

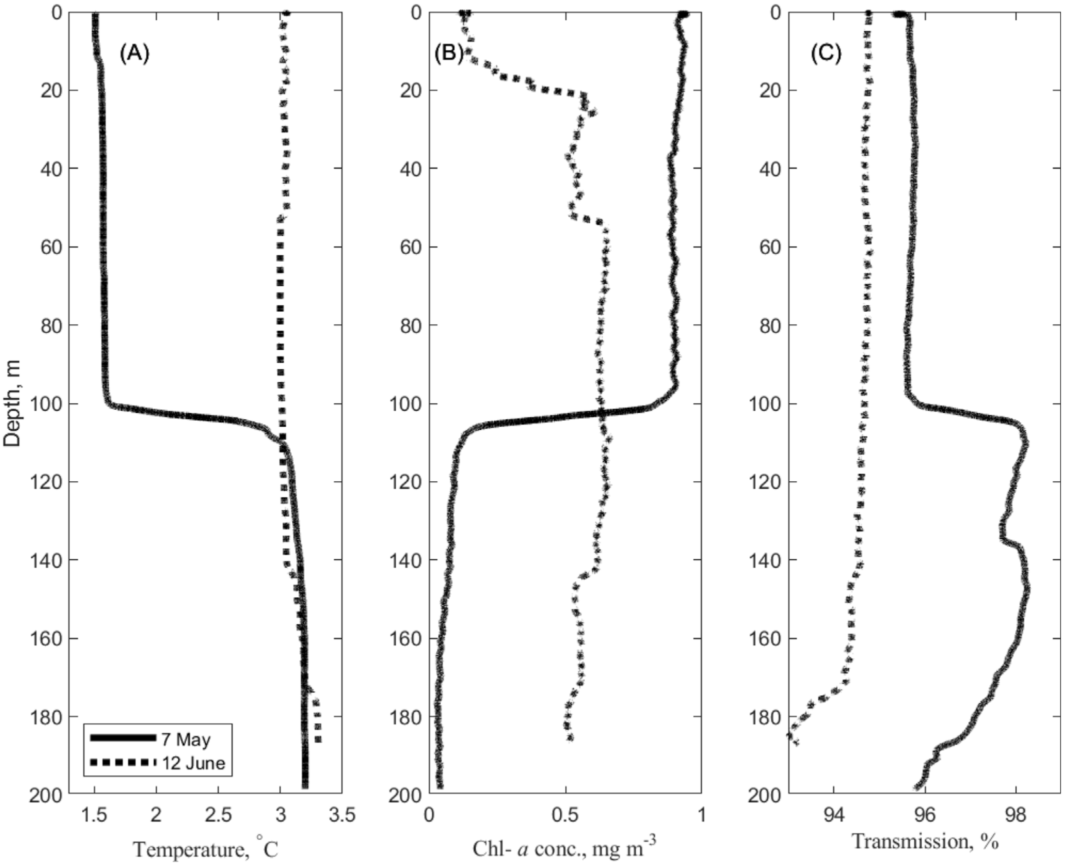

Fig. 3. (A) Temperature, (B) chl-*a* fluorescence, and (C) beam transmission from CTD casts during negative stratification (solid 7 May) and unstratified conditions (dashed 1 June).

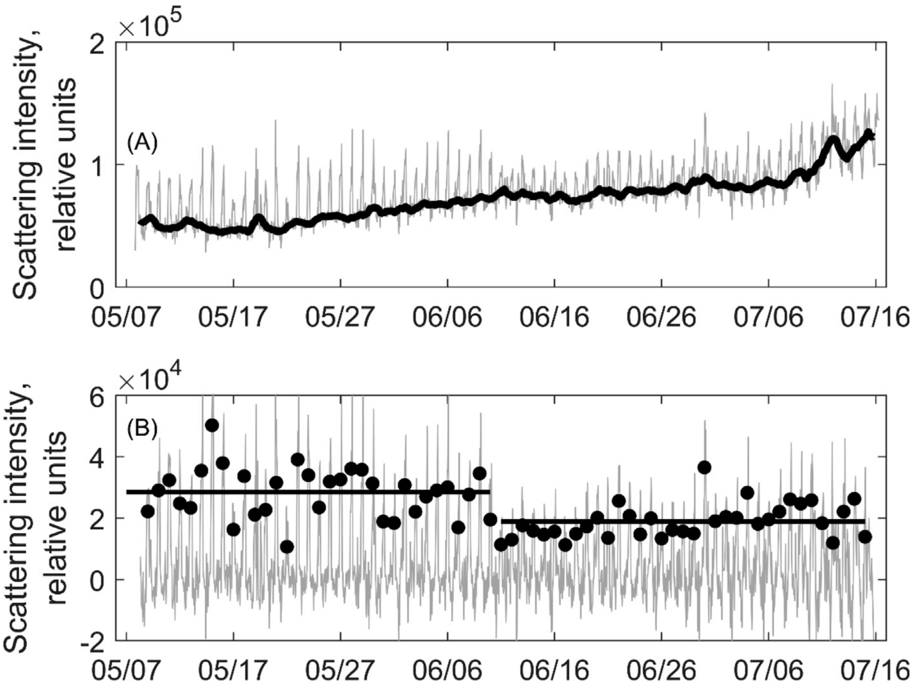

Fig. 4. (A) Raw vertically averaged, range corrected scattering data (*S(t)*, grey) and low-passed data (*B(t)*, black). (B) High passed range-corrected scattering intensity (*Z(t)*, grey). Circles represent mean scattering intensity in a 4-hour window around each midnight. Solid lines represent pre- and post- transition average scattering intensity.

eliminating it. This suggests that either a single species has a range of behaviors, with some individuals ending their migratory behavior and others not, or, more likely, an assemblage of multiple species, some of which continue to find it energetically advantageous

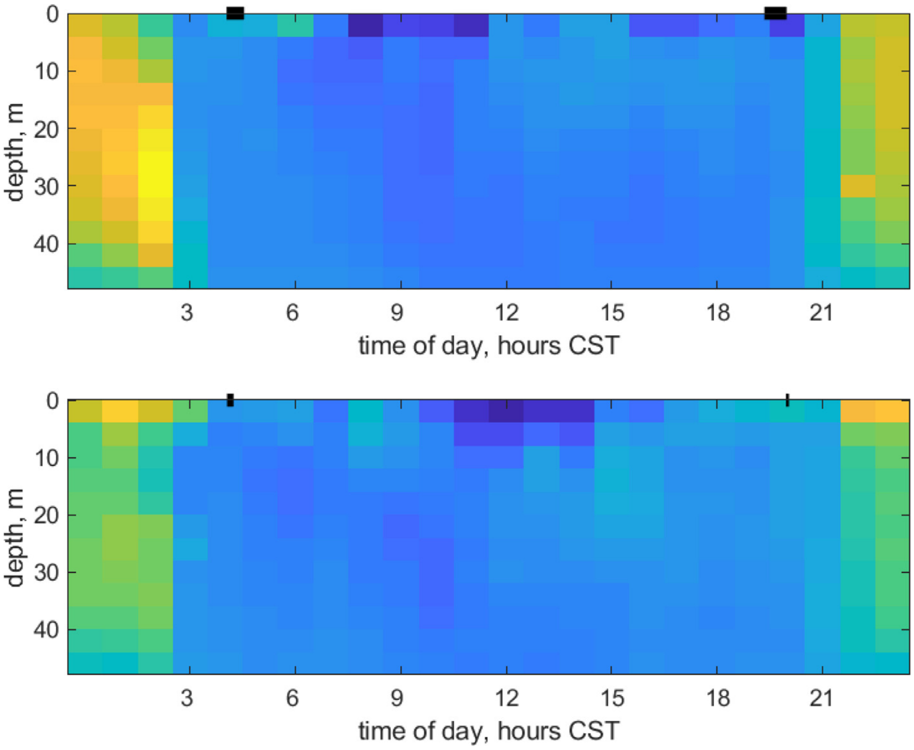

Fig. 5. Relative backscatter intensity as a function of time of day (local) and depth, averaged over (A) all days prior to stratification transition (10 June) and (B) all days following stratification transition. Small black bars at top of plots indicate approximate timing of sunrise/sunset. Colorbar is the same for both figures. More yellow/orange indicates more relative backscatter. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to continue migratory behavior. In either case, our results suggest that a quick transition from migratory to reduced migratory behavior in Lake Superior zooplankton occurs in response to uniformity in food availability across the water column as caused by the collapse of stratification.

The shift in food distribution is clear from the CTD data as well. During negative stratification, there is higher Chl-*a* concentration (~1 mg m^{-3}) in the epilimnion (Fig. 3B) when compared to much lower levels in the hypolimnion (close to 0 mg m^{-3}). This is because the euphotic zone is contained entirely in the epilimnion; a transmission value of roughly 95% over 25 cm light in the epilimnion (Fig. 3C) corresponds to a 1% light level of about 23 m. Radiatively-driven convection keeps phytoplankton evenly distributed over the epilimnion, and the thermocline prevents phytoplankton from being mixed to the bottom. However, once the thermocline is removed, convection mixes heat and constituents over the entire water column, distributing phytoplankton evenly over the water column, with uniform concentration of roughly 0.5 mg m^{-3} (low values of chlorophyll fluorescence in the top 20 m of this cast are due to photoquenching rather than low biomass). Phytoplankton will, in this case, spend less time per day in the euphotic zone than before, but are roughly evenly distributed over the water column. We hypothesize that herbivorous zooplankton would respond directly to this shift in food distribution. Movement by omnivorous taxa (e.g. mysids) likely follows smaller zooplankton because they are an important food resource.

Shipboard methods of determining zooplankton distributions suffer from the fact that shipboard surveying is typically limited in temporal scope because it is resource intensive and weather dependent. This makes consistent observations of change over seasonal to annual time scales difficult at best. In this specific case, the conclusions we draw here would be difficult to draw from a small number of shipboard observations, even if they bracketed the transition in stratification. In contrast, measurements made using a moored ADCP provide a long time series of scattering intensity at relatively high temporal frequency, over a long period, and at multiple depths. That said, the obvious drawback of using an ADCP to measure zooplankton concentration is the lack of species identification. While bounds can be put on the size of the scatterers (Stanton et al., 1993; Stanton et al., 1996; Gal et al., 1999), without ground truthing ADCP data only provides information about the amount of scattering, not about what is causing the scattering. Nonetheless, inferences can be made with this limited data that cannot be made, at present, with other methods, and helps to place more thorough shipboard measurements in a broader temporal context. Moored equipment provides a persistent presence in a lake that shipboard sampling cannot attain.

Approaches using long-term moored ADCPs and other moored acoustic instruments hold the potential to study a variety of other problems in zooplankton ecology. A recent review has highlighted the long-standing observation of a stark disparity in estimated zooplankton abundance between daytime and nighttime collections using traditional net tows (Doubek et al., 2020). Explanations for the pattern, including net avoidance and migration (vertical and horizontal), could be explored through coupled ADCP and net tow sampling programs. Another problem in zooplankton ecology is the inability to finely resolve spatial and temporal patterns in population patchiness in relation to physical and chemical gradients (e.g., in dissolved oxygen concentration). These could be better described by this approach, as one acoustic study has done (Hembre and Megard, 2003). A third, and more vexing set of problems in zooplankton ecology concerns the characterization of under-ice patterns in organism movement and aggregation. These could be explored more thoroughly, and potentially less invasively, with moored instrumentation than by traditional net tows which generally require open holes in the ice (and modified underwater light environments) at the time of sample collection (Block et al., 2018).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

JA collected the data, performed the analysis and initial interpretation, and wrote the bulk of the manuscript. TH contributed to concepts, interpretation of data and sections of writing. DB contributed to interpretation of data, writing, and editing. The authors would like to thank two anonymous reviewers for constructive criticism of our first draft.

Statement of data availability

All data and code necessary to recreate results in this manuscript are available at the Data Repository at the University of Minnesota (DRUM) at https://doi.org/10.13020/eqra-hp74

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