Vertical and temporal distribution of two copepod species, *Cyclops scutifer* and *Diaptomus pribilofensis*, in 24 h arctic daylight

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Factors structuring zooplankton communities in areas with 24 h of sunlight are not well understood. In stratified temperate lakes with fish, zooplankton generally undergo a diel vertical migration (DVM) to avoid predation. Zooplankton abundance may also be linked to the quality and quantity of food. To explore factors that determine vertical structure of zooplankton where DVM does not occur, we obtained time-series data on the vertical distribution of the two dominate copepods, *Cyclops scutifer* and *Diaptomus pribilofensis*, in Toolik Lake, Alaska, a site within the Arctic Long Term Ecological Research area. These two species compose ~80–90% of pelagic mesozooplankton community density. Temperature plays a large role in the vertical distribution of these two species. During the summers of 2002 and 2003, *C. scutifer* underwent a seasonal vertical migration from the epilimnion to the hypolimnion as water temperatures increased. *Diaptomus pribilofensis* exhibited a strong preference for warmer water and were not present in the water column until epilimnetic temperatures reached ~9°C. During both years of this study, *C. scutifer* and *D. pribilofensis* segregated vertically in the water column along thermal gradients when the two species overlapped temporally.

INTRODUCTION

Current understanding of zooplankton vertical distribution in lakes is based on diel vertical migration (DVM) (Lampert, 1993; Loose and Dawidowicz, 1994; Ringelberg, 1999; Kessler and Lampert, 2004). In the context of DVM, zooplankton modify their vertical position as a response to the presence of predators, either migrating deeper in the water column during the day to avoid visually feeding vertebrate predators (Boeing et al., 2006) or moving to shallow depths to avoid tactile invertebrate predators (Dodson, 1988). In lakes too shallow for DVM to occur, zooplankton exhibit diel horizontal migration, using littoral habitat as refuge during the day and migrating to the pelagia at night (Burks et al., 2003; Romare et al, 2003).

Vertical position of zooplankton is also influenced by trade-offs between food resources and abiotic factors such as temperature and dissolved oxygen (Lampert et al., 2003; Liu et al., 2003). Many lakes develop deep chlorophyll maxima (DCM) (Fee, 1976) and have higher metalimnetic food resources (Winder et al., 2003). However, cold water temperatures at deeper depths limit zooplankton growth, reproduction and ingestion rates making epilimnetic waters favorable even if food resources are low (Kessler and Lampert, 2004). The effect of food quality on zooplankton vertical distribution is less clear. Williamson et al. (Williamson et al., 1996) observed higher rates for growth and reproduction when zooplankton were raised in metalimnetic versus epilimnetic water, whereas Cole et al. (Cole et al., 2002)
found the opposite even though concentrations of chlorophyll, particulate carbon and particulate nitrogen were higher in the metalimnion. In addition, cold water can be beneficial to diapausing individuals by reducing respiration through lower metabolic rates and neutral buoyancy (Auel et al., 2005; Lee et al., 2006).

For DVM to occur, zooplankton require a visual stimulus from rapid change in light intensity (Ringelberg, 1999). Consequently, at high latitudes, DVM does not occur during periods of 24-h sunlight (Buchanan and Haney, 1980; Blachowiak-Samolyk et al., 2006). In the absence of DVM, it can be hypothesized that zooplankton will continuously occupy depths that maximize fitness while minimizing vulnerability to predators. However, in arctic lakes during summer periods of continuous sunlight, factors structuring zooplankton vertical distribution are unknown.

Zooplankton sampling has been performed during the ice-free season in the lakes near the Arctic Long Term Ecological Research Station (LTER) since 1975, with much of the research focusing on the role of pelagic zooplankton in trophic interactions and energy flow (O’Brien et al., 1979b; Luecke and O’Brien, 1983; O’Brien and Evans, 1992; Bettez et al., 2002). Nine pelagic species of crustacean zooplankton have been identified from the lakes and ponds in this area (Kling et al., 1992b). The calanoid Diaptomus pribilofensis and the cyclopoid Cyclops scutifer dominate the pelagic zooplankton communities with densities generally an order of magnitude higher than other mesozooplankton species inhabiting these lakes (O’Brien et al., 2004). The two species are similar in size (adult 1–1.8 mm) with nearly ubiquitous distribution in arctic Alaskan lakes (O’Brien et al., 1979a, 1997; Kling et al., 1992b).

Stable isotope analysis has shown that the two copepod species differ trophically (Kling et al. 1992a, Kling 1994). Kling (Kling, 1994) used a $^{15}$N-NH$_4^+$ tracer to label pelagic primary production in an arctic lake and found that D. pribilofensis predominantly used new algal production as a food resource. Isotopic analysis of C. scutifer is less clear indicating an omnivorous diet, potentially comprising of algae, detritus, rotifers or copepod nauplii (Vardapetyn, 1972; Kling et al., 1992b; Kling, 1994). There are no obligate planktivorous fish in lakes near the Arctic LTER, and fish in this area feed primarily on benthic invertebrates (Sierszen et al., 2003). Additionally, stable isotope analysis shows that the dominant invertebrate predator Heterocope septentrionalis does not use C. scutifer or D. pribilofensis as a food resource, indicating relatively little predation on these two species (Kling et al., 1992a; Kling, 1994).

Cyclops scutifer has a highly variable life history. Different populations exhibit 1–3-year life cycles, with both the presence and the absence of diapause (Elgmork, 1985; Elgmork and Eie, 1989). Additionally, there is evidence that C. scutifer prefers relatively cold temperature (<10°C) and has a tendency to occupy the hypolimnion of lakes when sufficient oxygen is available (Elgmork, 1967; Halvorsen and Elgmork, 1976). Comparatively little is known about the life history of D. pribilofensis; however, evidence from congeners has shown Diaptomus spp. to be monocyclic with more rapid growth and reproduction in relatively warm water (Tash and Armitage, 1967; Watras, 1983; Williamson and Butler, 1987).

Much is known about the biogeography and abundance of these two species across lakes in arctic Alaska (O’Brien et al., 2004); however, little is known about their temporal and spatial structure within any given lake. Our goal was to determine what factors influenced the vertical and temporal density distributions of C. scutifer and D. pribilofensis populations in Toolik Lake, Alaska. Thus, we tracked vertical densities of C. scutifer and D. pribilofensis during the summers of 2002 and 2003 to determine where zooplankton species were located in the water column, how the species density distributions changed throughout the summer and what characterized the habitats occupied by the two species.

We used the thermal structure of Toolik Lake to characterize physical habitats. Chlorophyll a (Chl a) and particulate C were used as surrogates of food quantity. We did not look at algal community composition, but O’Brien et al. (O’Brien et al., 1997) found the Toolik Lake phytoplankton community was dominated by edible chrysophytes, dinoflagellates, and cryptophytes. These food sources, in conjunction with D. pribilofensis’ herbivory and C. scutifer’s tendency for omnivory supports our assumption that concentrations of Chl a and particulate carbon are useful indicators food availability. Finally, we used C:N and C:Chl a ratios as surrogates of food quality. Copepods have relatively high biomass N:P ratios indicating a large tissue demand for nitrogen, and likely nitrogen limitation of growth when food resources are nitrogen-deficient (Sterner and Elser, 2002). Phytoplankton production is often nitrogen-limited in arctic lakes (Levine and Whalen, 2001). Thus, seston C:N ratio was used to assess food resource nutritional status, with lower C:N an indication of higher quality food for copepod growth (Jones and Flynn, 2005). Autotrophic productivity is more labile and has lower C:nutrient ratios compared to allochthonous components of particulate organic matter (POM) (Kalff, 2002). We considered seston with a low C:Chl a ratio to be an indication of POM with a higher proportion of algal biomass, and thus a better food source (Davidson et al., 1991). Admittedly, these ratios can be confounded
by other lake processes and can have high covariation in constant light levels (Davidson et al., 1991). In Toolik Lake, the high loading of detrital material from the landscape during snowmelt can lead to departure from Redfield ratio independently of phytoplankton physiological status. In addition, selective grazing of high-quality food could modify the in situ ratios resulting in higher C:Chl a and C:N ratios. However, we felt that if these variables showed consistent vertical patterns their inclusion would offer valuable insight on the role of food quality in structuring zooplankton communities.

METHOD

Site description
This study was conducted at Toolik Lake (68°38′00″N, 149°36′15″W), site of the Arctic LTER, 25 km north of the Brooks Mountains in northern Alaska, USA. Toolik Lake is an oligotrophic multiple basin kettle lake with a maximum depth of 25 m and a mean depth of 7 m (O’Brien et al., 1997). Toolik Lake thermally stratifies shortly after ice-out (generally in late June) and remains stratified with an epilimnetic depth of ~5–7 m until late August with oxygen concentrations near saturation throughout the summer (O’Brien et al., 1997; MacIntyre et al., 2006).

We sampled the vertical temperature structure, food resources and densities of C. scutifer and D. pribilofensis in two locations in Toolik Lake, Toolik Main (TM) Station and South West Basin (SWB) (Fig. 1), approximately weekly from 20 June to 27 July 2002 and 25 June to 25 July 2003. Much of Toolik Lake is shallow (<7 m), and TM and SWB were chosen to provide locations with adequate depth for samples to be taken in the epi, meta and hypolimnion throughout the summer. Weather conditions and complications with sampling equipment prevented us from sampling both basins on each day, and SWB was sampled on 4 days, whereas TM was sampled on 1 day in 2002 and 2003. Due to differences in sampling days between basins, SWB and TM were analyzed separately in 2002 and 2003. Temperature (°C) and fluorescence were measured with a Hydrolab Surveyor 4 with SCUFA submersible fluorometer every 0.5 m from the surface to a depth of 12 m. On each sampling day, discrete quantitative samples of pelagic meso-zooplankton and water for nutrients and Chl a were taken from 0, 1, 3, 5, 8, 10 and 12 m, except for TM 3 July 2002 when equipment failure prevented us from completing a full profile. These depths ensured that samples were taken within the epi, meta and hypolimnion. If a DCM was identified with the fluorescence profile, additional samples were taken within the DCM as well as 1 m above and below the peak, if the depths were not currently being sampled. Chl a and seston samples were collected using a 7 L Van Dorn water sampler, and filtered through 80 μm Nitex netting to remove meso-zooplankton then returned to the lab for further processing. Chl a samples were filtered on Whatman 0.7 μm pore size GF/F filters, extracted for 24 h in acetone with acidification for phaeopigment correction (Wetzel and Likens, 2000) on a Turner Designs 10-AU-005-CE Field Fluorometer. Replicate 300 mL aliquots for particulate carbon and nitrogen were filtered on pre-combusted Whatman 0.7 μm pore size GF/F filters, dried at 55°C for at least 48 h and subsequently analyzed on a Control Equipment Corp. 440HA element analyzer. Ratios of C:N were calculated by dividing the molar concentrations of seston particulate carbon by nitrogen, and ratios of C:Chl a were calculated by weight by dividing micrograms per liter concentrations of seston particulate carbon by Chl a. Any gaps in Chl a, or seston nutrient samples were filled in using data from the Arctic LTER database (http://ecosystems.mbl.edu/ARC/data_doc/lakes/lakedefault.htm).

Early copepodite and nauplii stages of C. scutifer and D. pribilofensis are difficult to differentiate. Thus, we limited our study to late copepodite and adult life stage by straining individuals from all meso-zooplankton water samples using 243 μm Nitex netting, and all zooplankton were considered to be adults for further analysis. In 2002 and 2003, we initially collected
meso-zooplankton by taking triplicate 10 L samples using a 12 L min\(^{-1}\) submersible purging pump. However, due to mechanical failure on 3 July 2002 and again on 11 July 2003, we replaced the sampling device with a 7 L Van Dorn and a 21 L Schindler–Patalas Plankton Sampler in 2002 and 2003, respectively. The equipment malfunction prevented us from comparing the sampling efficiencies of the three devices, and it was assumed that relative densities of zooplankton would be similar even though collection methods differed. Regardless of sampling device, samples were preserved in sugar-buffered Lugol’s solution to stain individuals and make them easier to identify (Steedman, 1976) and identified and enumerated in the laboratory using a Wild M-5 dissecting microscope. After samples were processed, the data were analyzed graphically to look for general patterns in zooplankton depth distribution in relation to water column variables before being quantified statistically. For all analyses, adults of both species were not considered to be present in the water column unless density was >1 individual L\(^{-1}\) in at least 1 depth. Sampled in the vertical profile.

**Statistical analysis**

Spearman’s rank correlation (\(r\)) was used to quantify the covariation between *C. scutifer* and *D. pribilofensis* densities and water column variables on each sampling date (Ludwig and Reynolds, 1988). We used depth on each day as our sampling unit, and *C. scutifer* and *D. pribilofensis* were ranked based on density (individual L\(^{-1}\) ± 1 S.E.). Temperature was ranked to the nearest °C, and Chl \(a\) and particulate carbon concentrations were ranked to the nearest (\(\mu\)g L\(^{-1}\)). Ratios of C:N and C:Chl \(a\) were ranked to the nearest whole number. Statistical analysis was not possible for *D. pribilofensis* when individuals were not present in the water column (NP), or if values for a variable did not change vertically in the water column (NA). Significance testing was done at the \(P < 0.05\) and \(P < 0.01\) level, but should be viewed with caution given the small samples sizes (<10) on each date (Legendre and Legendre, 1998).

**RESULTS**

Ice-out occurred on approximately 10 June 2002 and 25 June 2003 in Toolik Lake. In 2002, a shallow seasonal thermocline had set up by 20 June, and epilimnetic water temperatures were greater than 9°C by 28 June at TM. A storm with winds in excess of 20 m s\(^{-1}\) induced mixing throughout the water column on 1–2 July 2002. The thermocline was deepened and the associated DCM dispersed. The seasonal thermocline was not reestablished until 9 July. Once established, the base of the thermocline did not deepen, and temperatures at its base at 8 m were 8°C (Fig. 2). Hypolimnetic temperatures after 9 July exceeded 6°C and were warmer than in other years with continuous records. In 2003, the thermocline was established by 27 June in SWB but epilimnetic temperatures did not reach 9°C until 4 July. The upper mixed layer warmed over the next 2 weeks. A cold front and strong winds deepened the epilimnion to 8 m by 18 July and reduced temperatures to 9–10°C. The upper water column restratified beginning on 19 July (Fig. 3).

In both years, concentrations of Chl \(a\) and particulate carbon tracked each other on several dates, and Toolik Lake developed a DCM once the lake became thermally stratified indicating higher food quantity at metalimnetic depths. The breadth and amplitude of the chlorophyll maximum varied depending on the sampling day (Figs. 4 and 5). The windstorm in early July 2002 dispersed the DCM such that the subsequent peak had lower algal biomass than in previous years (Miller et al., 1986; MacIntyre et al., 2006). However, the DCM persisted in SWB. In years prior to 2002 and 2003, C:N and C:Chl \(a\) ratios were lowest in the DCM (MacIntyre et al., 2006). During this study, C:N and C:Chl \(a\) did not show consistent vertical patterns, and values of seston nutrient samples showed a high degree of variability depending on depth and day sampled (Figs. 6 and 7). C:N ratios of >8.3 indicate phytoplankton nitrogen deficiency (Guilford and Hecky, 2000), and with the exception of 11 July and 27 July SWB, 2002 values exceeded this threshold throughout the summer. In 2003, C:N ratios were <8.3 on early sampling dates, but were generally higher during later dates (Figs. 6 and 7).

In both 2002 and 2003, *C. scutifer* adults were present in the water column at the beginning of the sampling season, whereas *D. pribilofensis* adults did not appear until epilimnetic temperatures were ~9°C (Figs. 2 and 3). A consistent pattern of vertical separation in the water column developed between *C. scutifer* and *D. pribilofensis* in both 2002 and 2003. In the early season, densities of *C. scutifer* were concentrated in the epilimnion. However, as epilimnetic temperatures increased, coinciding with the appearance of *D. pribilofensis*, the density distribution of *C. scutifer* shifted to depths >3 m. Rarely were high densities of *C. scutifer* and *D. pribilofensis* found in the same strata (Figs. 2 and 3).

*Cyclops scutifer* showed a high negative covariation with water temperature when *D. pribilofensis* was present in the water column and the lake was thermally stratified in both SWB and TM in 2002 and 2003 (Table I). *Cyclops scutifer* had a relatively high positive covariation
with food resources, Chl $a$ and particulate carbon, when *D. pribilofensis* was not present in the water column, and always had a positive covariation with food resources in 2002 SWB and TM. However, the direction of the covariation was not consistent with Chl $a$ and particulate carbon between years. *Cyclops scutifer* had a relatively high negative covariation with Chl $a$ on 18 and 25 July 2003, although the relationship on the prior sampling date was likely due to the storm-driven mixing event. The direction and magnitude of covariation were related to the presence of a DCM in Toolik Lake, and *C. scutifer* consistently had a high positive covariation with Chl $a$ and particulate carbon when a DCM was established (Figs. 4 and 5, Table I).
Covariation between *C. scutifer* and indices of food quality was less consistent with magnitude and direction both within and between sampling basins and years (Table I).

*Diaptomus pribilofensis* had a high positive covariation with temperature when adults were present in relatively high abundances in the water column (Table II). On 18 and 27 July 2002 SWB, high densities of *D. pribilofensis* were found at deeper depths within the DCM even though water temperatures were colder.

**Fig. 3.** 2003 temporal and vertical densities (individuals L$^{-1}$) of *C. scutifer* and *D. pribilofensis* (bottom x-axis) with vertical temperature profile (°C) (top x-axis) in (a) SWB and (b) TM, Toolik Lake, Alaska.
than 9°C. This suggests that *D. pribilofensis* can exploit higher food resources in the DCM even at relatively cold water temperatures. However, high densities were also found above the DCM preventing a large positive covariation with Chl *a*; and on other sampling days, adult *D. pribilofensis* densities were not established in the water column when the DCM was at cold water temperatures (Figs. 4 and 5, Table II).

*Cyclops scutifer* and *D. pribilofensis* always had a relatively high negative covariation when the two species were established in the water column. The covariation between the two species was the lowest on 18 July 2002.

![Fig. 4. 2002 temporal and vertical densities (individuals L⁻¹) of *C. scutifer* and *D. pribilofensis* (same scale as Figs 2 and 3) with vertical food quantity profiles Chl *a* (µg L⁻¹) (bottom x-axis) and particulate carbon (µg L⁻¹) (top x-axis) in (a) SWB and (b) TM, Toolik Lake, Alaska.](image-url)
coinciding with a relatively high density of *D. pribilofensis* located at deeper colder depths (Fig. 2, Tables I and II).

**DISCUSSION**

In both 2002 and 2003, the two dominant zooplankton species in Toolik Lake exhibited a stable pattern of vertical distribution that appeared to be largely driven by the thermal structure of the lake. Storm events in both years of this study provided interesting natural experiments by breaking down the thermal stratification in the water column. When strong winds mixed the water column, densities of both species were nearly uniform in the water column and vertical segregation in the water column was minimal. After the lake

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**Fig. 5.** 2003 temporal and vertical densities (individuals L$^{-1}$) of *C. scutifer* and *D. pribilofensis* (same scale as Figs 2 and 3) with vertical food quantity profiles Chl a (μg L$^{-1}$) (bottom x-axis) and particulate carbon (μg L$^{-1}$) (top x-axis) in (a) SWB and (b) TM, Toolik Lake, Alaska.
restratified, the copepods again were vertically struc-
tured. These changes provided further evidence as to
the importance of lake thermal structure in habitat
selection of the two species.

Along thermal gradients, *C. scutifer* was found in rela-
tively cold water temperatures and demonstrated a
vertical shift in density from the epilimnion to the hypo-
limnion as Toolik Lake warmed and became stratified.

Other studies have observed a tendency for *C. scutifer* as
well as other cyclopoid species to occupy colder hypolim-
nic waters (Elgmork and Eie, 1989; Makino and Ban,
1998; Makino et al., 2003) even though optimal tempera-
tures for growth and reproduction are generally found to
be much higher (Halvorsen and Elgmork, 1976; Makino
et al., 2003). Investigations of *C. scutifer* vertical distribu-
tion have indicated that they are not an obligate cold water

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**Fig. 6.** 2002 temporal and vertical densities (individuals L$^{-1}$) of *C. scutifer* and *D. pribilofensis* (same scale as Figs 2 and 3) with vertical food quality profiles molar C:N (bottom x-axis) and C:Chl a by weight (top x-axis) in (a) SWB and (b) TM, Toolik Lake, Alaska.
species and can occupy warmer epilimnetic waters (Elgmork and Eie, 1989). Schmidt and O’Brien, (Schmidt and O’Brien, 1982) found that *C. scutifer* was more vulnerable to fish predation with increasing light intensity. Attenuation coefficients in Toolik Lake ranged from 0.7 to 0.8 $m^{-1}$ in 2003. Consequently, irradiance near midnight at 12 m depth would range from 0.001 to 0.005 $\mu$mol quanta $m^{-2} s^{-1}$. The onset of feeding of various species of fish occurs for fluxes of $1.5 \times 10^{-2}$ to $1.5 \times 10^{-4} \mu$mol quanta $m^{-2} s^{-1}$. Hence the hypolimnion is unlikely to be a refuge from predation (Kalff, 2002). In addition, *C. scutifer* densities were highest in epilimnetic waters on early sampling dates in both years suggesting that predator avoidance was not the primary mechanism for occupying deeper depths later in the season.

Fig. 7. 2003 temporal and vertical densities (individuals L$^{-1}$) of *C. scutifer* and *D. pribilofensis* (same scale as Figs 2 and 3) with vertical food quality profiles molar C:N (bottom x-axis) and C:Chl a by weight (top x-axis) in (a) SWB and (b) TM, Toolik Lake, Alaska.
Table I: Spearman's rank correlation between *C. scutifer* densities and independent variables sampled in SWB and TM, Toolik Lake 2002 and 2003

<table>
<thead>
<tr>
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<th>SWB</th>
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<th>TM</th>
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<tr>
<td></td>
<td>2002</td>
<td></td>
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<td>2003</td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>28 June</td>
<td>11 July</td>
<td>18 July</td>
<td>27 July</td>
<td>20 June</td>
<td>28 June</td>
<td>3 July</td>
<td>11 July</td>
</tr>
<tr>
<td>Temperature</td>
<td>-0.376</td>
<td>-0.947**</td>
<td>-0.889*</td>
<td>-0.894*</td>
<td>0.612</td>
<td>-0.949*</td>
<td>NA</td>
<td>-1.000**</td>
</tr>
<tr>
<td>Chl a</td>
<td>0.967**</td>
<td>0.546</td>
<td>0.323</td>
<td>0.783</td>
<td>0.542</td>
<td>0.693</td>
<td>NA</td>
<td>0.437</td>
</tr>
<tr>
<td>Particulate carbon</td>
<td>0.783*</td>
<td>0.778*</td>
<td>0.433</td>
<td>0.707</td>
<td>-0.553</td>
<td>0.738</td>
<td>NA</td>
<td>0.169</td>
</tr>
<tr>
<td>C:N</td>
<td>0.000</td>
<td>0.294</td>
<td>-0.457</td>
<td>0.250</td>
<td>-0.167</td>
<td>-0.447</td>
<td>NA</td>
<td>-0.836*</td>
</tr>
<tr>
<td>C:Chl a</td>
<td>-0.706</td>
<td>0.465</td>
<td>-0.627</td>
<td>-0.783</td>
<td>0.152</td>
<td>-0.804</td>
<td>NA</td>
<td>-0.329</td>
</tr>
<tr>
<td><em>D. pribilofensis</em></td>
<td>-0.725</td>
<td>-0.790*</td>
<td>-0.204</td>
<td>-0.707</td>
<td>NP</td>
<td>-1.000*</td>
<td>NA</td>
<td>-0.958**</td>
</tr>
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|                  | SWB          |       |       |       | TM          |       |       |       |
|                  | 2003         |       |       |       |             |       |       |       |
| Temperature      | 0.484        | 0.424  | -0.442 | -0.907** | -0.910**     | 0.440   | -0.907** | -0.632  | -1.000**      |
| Chl a            | 0.703        | 0.898** | 0.490  | -0.471 | 0.615         | 0.845*  | -0.242  | -1.000** | -0.908**      |
| Particulate carbon | 0.491        | 0.955** | 0.213  | -0.500 | 0.574         | 0.885** | -0.167  | -0.200  | -0.529       |
| C:N              | -0.413       | -0.433 | 0.247  | -0.312 | NA            | -0.535  | -0.322  | -0.674  | -0.783*       |
| C:Chl a          | -0.692       | -0.440 | -0.487 | -0.151 | -0.441        | -0.838* | 0.371   | 0.632   | 0.877*       |
| *D. pribilofensis* | NP          | NP     | -0.808* | -0.917** | NP           | NP     | -0.483  | -0.632  | -0.904**      |

NP, individuals not present in the water column; NA, values for a variable did not change vertically in the water column.

* = $P<0.05$, ** = $P<0.01$. 
In contrast, *D. pribilofensis* occupied the relatively warm epilimnetic waters of Toolik Lake with adults only appearing after temperatures were \( \geq 9^\circ C \), and numbers increased at deeper depths as the metalimnion warmed over the summer. *Diaptomus pribilofensis* had relatively high densities in deeper colder water on 18 and 27 July 2002. In both cases, the densities were located within the DCM, suggesting exploitation of greater food resources at deeper depths. However, *D. pribilofensis* did not show a consistent relationship with the DCM on other dates. The epilimnion is generally considered a more favorable habitat for pelagic zooplankton due to higher food quantity and quality (Lampert, 1993; Loose and Dawidowicz, 1994) and warmer temperatures that increase rates of growth and reproduction (Orcutt Jr and Porter, 1983; Loose and Dawidowicz, 1994). *Diaptomus pribilofensis* is exclusively herbivorous (Kling et al., 1992a; Kling, 1994), hence we would expect to find higher densities where primary production or algal biomass is highest. Although we found higher algal concentrations in the metalimnion, primary productivity was highest in the epilimnion during the summers of 2002 and 2003 (M. Evans, University of Michigan Department of Ecology and Evolutionary Biology, personal communication).

Primary productivity is highest after ice-out and decreases in the upper water column as the summer progresses due to nutrient limitation (Miller et al., 1986; MacIntyre et al., 2006). We see evidence for limitation developing in 2002 and 2003 as C:N ratios increase above 8.3 over the summer. Because our particulate C pool is composed not only of phytoplankton but also of detritus and micro-zooplankton, interpretation of increased ratios is made difficult as *C. scutifer* may be selectively grazing on particulates with higher N and P contents. Thus, the increased ratios may be due to changing food quality of the phytoplankton and/or to selective grazing on higher quality food. Regardless, *D. pribilofensis* was found at deeper depths as the summer progresses, and sometimes co-occurred with *C. scutifer* when food resources were high. Vertical mixing supplies inorganic N to phytoplankton within the chlorophyll maximum (MacIntyre et al., 2006), and the downward movement of *D. pribilofensis*, particularly in late July 2002 when nutrient fluxes from hypolimnetic waters were restricted to the chlorophyll maximum (S. MacIntyre, unpublished results), may be due to a search for food of higher nutrient.

*D. pribilofensis* has been shown to be invulnerable to predation by fish or *Heterocope septentrionalis*, a top predator of pelagic zooplankton.

Table II: Spearman’s rank correlation between *D. pribilofensis* densities and independent variables sampled in SWB and TM, Toolik lake 2002 and 2003

<table>
<thead>
<tr>
<th></th>
<th>SWB</th>
<th>TM</th>
<th></th>
<th>SWB</th>
<th>TM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>0.907** 0.791* 0.049 0.527</td>
<td>0.949* NA 0.958** 0.745</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td>-0.725 0.000 0.545 -0.423</td>
<td>-0.683 NA -0.321 -0.227</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Particulate carbon</td>
<td>-0.302 -0.812* 0.000 -0.333</td>
<td>-0.738 NA 0.000 -0.214</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C:N</td>
<td>-0.548 -0.618 0.000 0.707</td>
<td>0.447 NA 0.730* -0.414</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C:Chl a</td>
<td>0.890** -0.757* -0.495 0.422</td>
<td>0.804 NA 0.507 0.471</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. scutifer</td>
<td>-0.725 -0.790* -0.204 -0.707</td>
<td>-1.000** NA -0.958** -0.907**</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

NP, individuals not present in the water column; NA, values for a variable did not change vertically in the water column. * = P < 0.05, ** = P < 0.01.
invertebrate predator in arctic lakes (O'Brien, 1988; O'Brien et al., 2004), indicating relatively little cost of continuously occupying the epilimnion. Moreover, reverse DVM can occur when individuals migrate to the epilimnion during the day if predators occupy deeper layers of the water column (Bayly, 1986; Neill, 1990; Ohman, 1990; Lampert, 1993). Evidence suggests that C. scutifer can be predacious on nauplii and juvenile copepods (Vardapetyan, 1972). Thus, with C. scutifer adults concentrated in the hypolimnion, the use of the epilimnion by D. pribilofensis potentially alleviates predation pressure on their juveniles. However, this study did not look at explicit inter-specific interactions between the two species and more research is needed to explore competition and predation between the two.

We did not directly measure life history characteristics for either species during this study, and results from other studies vary with different populations. It is possible that the seasonal vertical migration of C. scutifer was the result of different biological demands at different life stages or that we measured separate cohorts throughout the autumn. Diaptomus spp. are generally monocyclic and occupying warmer epilimnetic water would benefit rapid reproduction and growth during the short arctic growing season. However, interactions with life stages and cohorts require further investigation for these populations.

Statistical analysis showed that C. scutifer consistently had high covariation with temperature and D. pribilofensis on each sampling day in 2002 and 2003. Cyclops scutifer also had relatively high covariation with food resources, Chl a and particulate carbon. However, this pattern was not consistent, the relatively large values of covariation require further investigation for these populations. More research is needed to explore competition and predation between the two species.

Diaptomus pribilofensis had high covariation with food resources on 28 June 2002 SWB and TM and 18 and 25 July 2003 TM, but the direction of covariation was not consistent. Species density could be positively or negatively related to food resources if populations actively seek depths with more resources or if grazing rates are high enough to reduce concentrations (Pilati and Wurtsbaugh, 2003). Thus, even though the direction of the covariation was not consistent, the relatively large values of covariation suggest that resource availability plays a role in the vertical distribution of D. pribilofensis. The year-to-year differences in depth distribution may depend on the frequency of storm events which affect rates of primary productivity as well as the nutritional status of phytoplankton at different depths in the water column.

In Toolik Lake, the two dominant zooplankton species, C. scutifer and D. pribilofensis, vertically segregated the water column primarily along a thermal gradient and were rarely found in high densities at the same depth when the lake was thermally stratified. An identical pattern of vertical segregation between C. scutifer and D. pribilofensis was also observed in zooplankton samples taken from Toolik Lake during the summers of 1975–77; however, corresponding habitat variables were not collected (W. J. O'Brien, unpublished results). This supports our observation that C. scutifer and D. pribilofensis partition the water column vertically, and this pattern is not isolated to the years of this study. Factors vertically structuring zooplankton populations in the absence of DVM remain largely unresolved in freshwater ecosystems, with this study providing evidence as to the importance of abiotic controls. Food availability determined as Chl a and particulate carbon also had a role in the vertical location of C. scutifer, but did not show a strong relationship with the vertical distribution of D. pribilofensis. Leibold and Tessier (Leibold and Tessier, 1997) suggested that predation and overlap in resource requirements can lead to vertical habitat partitioning in freshwater zooplankton communities; however, aspects of competition and predation between these two species were not directly considered in the present study and still require further investigation. Similarly, differences in growth rates at different temperatures may influence partitioning in the water column. The weaker relationships between independent variables and distribution of D. pribilofensis may indicate that temperature is important, but less important than occupying strata with high primary productivity or where C. scutifer is absent.

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