Research Brief

Do *Daphnia* use metalimnetic organic matter in a north temperate lake? An analysis of vertical migration

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Abstract

Diel vertical migration of zooplankton is influenced by a variety of factors including predation, food, and temperature. Research has recently shifted from a focus on factors influencing migration to how migration affects nutrient cycling and habitat coupling. Here we evaluate the potential for *Daphnia* migrations to incorporate metalimnetic productivity in a well-studied northern Wisconsin lake. We use prior studies conducted between 1985 and 1990 and current diel migration data (2008) to compare day and night *Daphnia* vertical distributions with the depth of the metalimnion (between the thermocline and 1% light depth). *Daphnia* migrate from a daytime mean residence depth of between about 1.7 and 2.5 m to a nighttime mean residence depth of between 0 and 2.0 m. These migrations are consistent between the prior period and current measurements. Daytime residence depths of *Daphnia* are rarely deep enough to reach the metalimnion; hence, metalimnetic primary production is unlikely to be an important resource for *Daphnia* in this system.

Introduction

Diel vertical migration (DVM) in zooplankton has a long history of study in limnology (Juday 1904, McLaren 1963, Lampert 1989), and research has traditionally focused on the mechanisms driving this behavior (Stich and Lampert 1981). Commonly cited drivers of DVM are migration to dark waters during the day to avoid visual predators, and returning to warm, food-rich epilimnetic waters by night for access to phytoplankton (Zaret and Suffern 1976, Carpenter and Kitchell 1993). Other factors such as light, ultraviolet radiation, and temperature have also been shown to be strong drivers of DVM in some systems (Dini and Carpenter 1991, Williamson et al. 2011). In freshwater systems, the behaviors of the crustacean zooplankter *Daphnia* are of special importance because their populations have a strong top-down effect on primary production and are a critical food source supporting higher trophic levels (Carpenter et al. 2001, Pace et al. 2004).

Recently, research has shifted from asking what drives DVM to how migrations influence energy dynamics and biogeochemical cycling. Haupt et al. (2009) investigated the consequences of DVM on nutrient transport and algal community composition in mesocosm experiments. Additionally, several studies have evaluated the role of DVM in ocean ecosystems as it influences biogeochemical cycles, and more specifically, carbon uptake dynamics (Steinberg et al. 2000, Berge et al. 2009). Understanding zooplankton behavioral dynamics can provide mechanistic explanations for observed energy dynamics and nutrient flow within and between habitats and ecosystems.

Studies in a series of lakes along the border of northern

Wisconsin and Michigan's Upper Peninsula have greatly added to our understanding of how grazing zooplankton such as *Daphnia* can influence food web structure. These systems, often referred to as "Cascade Lakes," have demonstrated how changes to the upper trophic level of a food web cascade down and influence the abundance of zooplanktivorous fish, grazing zooplankton, and ultimately primary productivity (Carpenter et al. 2001). *Daphnia* migrations in these systems provided strong evidence supporting predation risk as a driver of DVM (Dini and Carpenter 1991). More recently these systems were used in a series of ^{13}C enrichment experiments that identified the importance of terrestrial carbon in supporting microbial, invertebrate, and fish consumers in these lakes (Cole et al. 2002, 2006, Pace et al. 2004, Carpenter et al. 2005). Results from these studies indicate that significant support of the food web derives from terrestrial organic matter, a finding that challenges the often-held assumption that in-lake algal production entirely supports zooplankton grazers and higher trophic levels (Reynolds 2008).

The results of the whole lake ^{13}C additions have been criticized for possibly overestimating allochthonous support of zooplankton. In these studies only the upper mixed layer of the lake was labeled with ^{13}C. If migrating zooplankton were to feed significantly below the mixed layer in the metalimnion where the phytoplankton were not labeled, this consumption of unlabeled organic carbon could potentially be confused with the consumption of allochthonous organic matter (Brett et al. 2009, Cole et al. 2011, Francis et al. 2011, Solomon et al. 2011).

In this study, we compare historical and current DVM in Paul Lake, one of the Cascade Lakes for which we have multiple estimates of allochthonous support of zooplankton, including those from ^{13}C additions. We quantify mean *Daphnia* residence depth and intensity and measure metalimnion depth from the thermocline to the 1% light level where Paul Lake has high metalimnetic chlorophyll concentrations associated with a persistent dissolved oxygen maxima (Carpenter and Kitchell 1993). We evaluate the hypothesis that *Daphnia* are consuming metalimnetic production in this lake. These comparisons refute the hypothesis that *Daphnia* are consuming significant metalimnetic production in this lake because migrations in Paul Lake do not often reach the metalimnion.

Methods

Study site

Paul Lake, located on the University of Notre Dame Environmental Research Center (46º15′09.54″N; 89º30′14.56″W), is a small (1.2 ha), deep (max. depth 12.2 m), humic kettle lake that has been unexploited and unmanipulated since 1971 with the exception of a ^{13}C addition experiment in 2001. Paul Lake has served as a reference system for several whole-lake manipulations (Carpenter et al. 2001, 2011). It is fed almost exclusively by groundwater, has no surface inflow, and drains into adjacent Peter Lake. The fish community is dominated by largemouth bass (*Micropterus salmoides*) with a few pumpkinseed (*Lepomis gibbosus*). The zooplankton community is dominated by large *Daphnia* (i.e., *D. pulex* and *D. rosea*), *Holopedium gibberum*, and several copepod species. In addition, the invertebrate mesopredator *Chaoborus* is abundant. A more complete description and history of this lake can be found in Leavitt et al. (1989) and Carpenter and Kitchell (1993).

Zooplankton sampling

Weekly zooplankton samples were collected from early May to late August 2008. We used an electric diaphragm pump to sample discrete water depths (1, 3, 5, and 7 m) from 10:00 to 11:00 h and 22:00 to 23:00 h in the deepest portion of Paul Lake. Water was pumped for approximately 15 s to clear the pump and line, then water was collected for 60 s, resulting in 31 L of filtered water. The end of the pump was affixed between a pair of circular plates (diameter ~200 mm) mounted parallel, approximately 200 mm apart to prevent water below the intended depth from being drawn into the sampling tube. Pumped water was filtered through an 80 μm mesh-lined concentrating cup. Zooplankton samples were preserved in 95% ethanol, identified to genus, and enumerated. Only data for *Daphnia* spp. DVM are reported here.

Limnological profiles

We used a LiCor submersible light meter and deck light meter to measure light extinction. We lowered the submersible sensor into the water on the sunny side of the boat. Readings were taken at 0.25 m intervals to 1.0 m, then at 0.5 m intervals to 1% of surface irradiance. The 6 depths where light was 100, 50, 25, 10, 5, and 1% of the surface irradiance were calculated from the irradiance curve. The depth where light penetration is 1% of surface irradiance is the compensation depth (Wetzel 2001).

Temperature readings were taken using a YSI oxygen/temperature meter at 0.5 m intervals from 0 to 7 m then at 1 m intervals down to 12 m. Temperatures were recorded to the nearest 0.1ºC and dissolved oxygen to the nearest 0.1 mg/L. We used the temperature profile to determine the thermocline, defined as the depth where water temperature changes most rapidly. We define the metalimnion and region of deep metalimnetic productivity as the layer of water between the top of the thermocline and the compensation depth (Wetzel 2001).

Chlorophyll *a* concentrations were measured at depths related to the above light profile (100, 50, 25, 10, 5, and 1% of surface irradiance). Water was collected from each depth using a Van Dorn bottle. In the lab, 2 replicate 200 mL samples were filtered onto GF/F filters, frozen, and extracted in methanol. Chlorophyll *a* was measured using standard fluorometric techniques (Holm-Hansen and Riemann 1978).

Historical data

We obtained historic *Daphnia* DVM data for Paul Lake from Dini and Carpenter (1991) and Carpenter and Kitchell (1993). In these studies, *Daphnia* migrations were measured using duplicate hauls casting a 12 L Schindler-Patalas trap over 5–6 depths at each of 2–5 horizontal stations across a pelagic transect. Samples were taken at midday and midnight of each sampling day (Dini and Carpenter 1991). Light, temperature, and dissolved oxygen vertical profiles coincident with the vertical migration measurements were retrieved from archived databases available through NTL-LTER (http://lter.limnology.wisc.edu/). These profiles were conducted in accordance with the methods described above.

Data analysis

Mean daytime and nighttime *Daphnia* residence depths were computed using the following weighted equation:

$$Mean\ Depth = \sum X_i Z_i / \sum X_i, \qquad (1)$$

where Xi is the number of *Daphnia* and Zi is the depth of sample *i*.

Routine limnological measurements were taken weekly throughout all sampling periods. Daily profiles were estimated by linear interpolation between the thermocline depths and compensation depths of the weekly profile measurements.

Results

Typical midsummer light, temperature, and dissolved oxygen profiles are consistent with lakes in this region (Fig. 1). The upper mixed layer extended from the surface to a depth of about 3 m and had a relatively uniform temperature of 20–22 °C. Temperature changed most rapidly between 3 and 5.5 m from 20 °C to about 5 °C. Below 5.5 m, cold, anoxic hypolimnetic waters were inhospitable to zooplankton or fish. Dissolved oxygen in the upper mixed layer was relatively constant at 7.5 mg/L. A dissolved oxygen maximum occurred just below the thermocline at about 3.75 m. Light intensity declined

rapidly through the upper mixed layer and reached 1% at approximately 5 m. Chlorophyll *a* concentrations in the upper mixed layer average about 5 mg/L (Fig. 1). The maximum chlorophyll concentration occurred at the 1% light depth with a concentration about 3 times greater than the average in the upper mixed layer (Fig. 1).

The position of the metalimnion between 1985 and 1990 and in 2008 was relatively consistent for all 7 years, spanning from about 3 to 6 m depth (Fig. 2). The thermocline tended to deepen from 2 to 3.5 m as each year progressed. The magnitude (i.e., depth range) of DVM by *Daphnia* in Paul Lake remained stable from 1985 to 1990 and in 2008 (Fig. 2). Mean daytime residence depth was 2.53 m (range 1.28–4 m). Mean nighttime residence depth was 1.73 m (range 0.89–3.65 m). In 2008, only 3.4% of *Daphnia* sampled had daytime residence depths below 3 m. There were 4 instances of reverse migration occurring in 2008 alone. In 3 of 36 samples taken over the 7 years, *Daphnia* mean residence depth was found in the metalimnion (Fig. 2). The 2 instances that occurred in the historical period (1986 and 1990) were both early in the year before a strong oxygen maximum had set up.
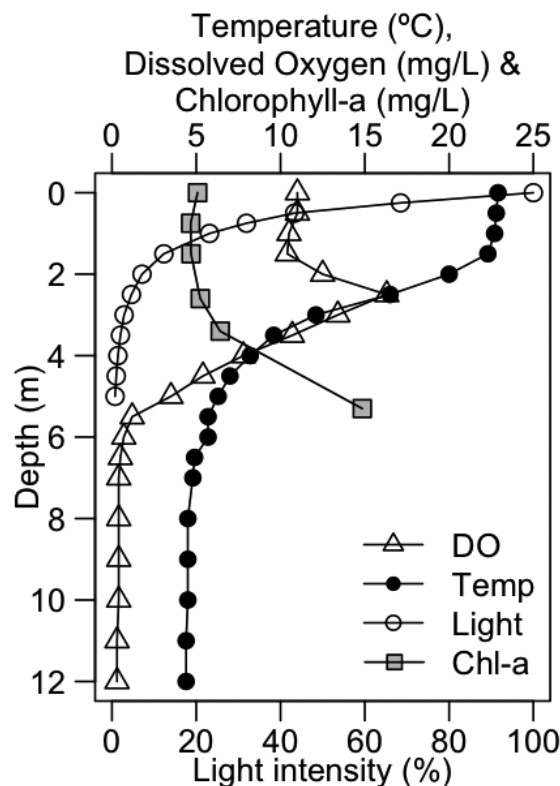
Fig. 1. Typical midsummer stratified temperature, dissolved oxygen, chlorophyll concentration, and light profiles in Paul Lake (actual sampling date 12 Aug 2008). Light intensity is measured as the percentage of surface irradiance (photosynthetically active radiation) at each depth.
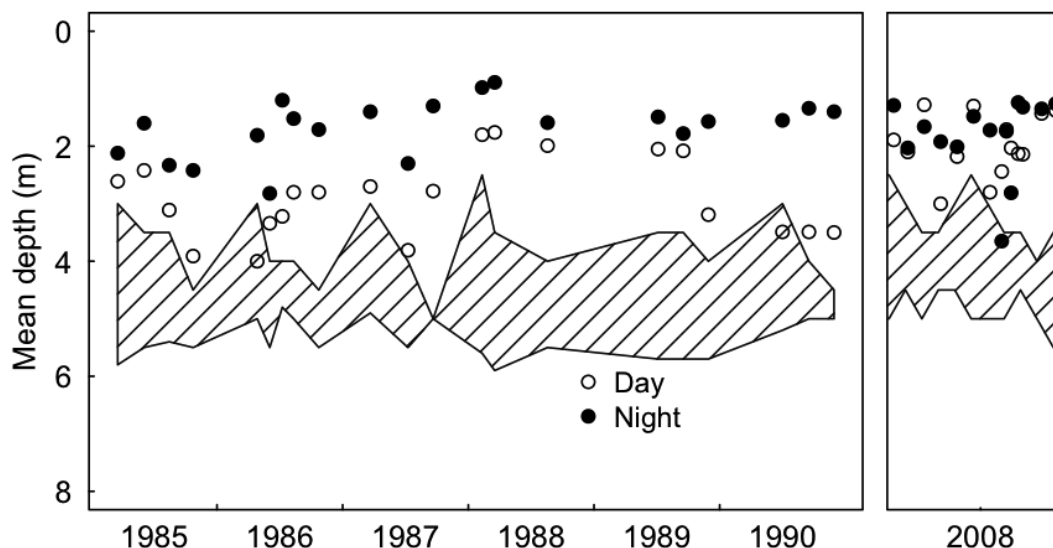
Fig. 2. Daytime (white dots) and nighttime (black dots) mean residence depth distributions of *Daphnia* spp. in Paul Lake. The crosshatched polygon represents the metalimnetic water between the thermocline and the compensation depth.

Discussion

Paul Lake is dominated by large *Daphnia* (>1.0 mm) susceptible to visual predation (Carpenter and Kitchell 1993). In most systems, adult largemouth bass are not known to be effective zooplanktivores; however, in Paul Lake adult largemouth bass do forage on *Daphnia* (Hodgson and Kitchell 1987). Additionally, young-of-the-year largemouth bass are voracious plankton predators and spend up to a month in the epipelagic region of Paul Lake (Post et al. 1997). *Chaoborus* spp. present in Paul Lake serve as tactile predators, and they generally forage on smaller-bodied zooplankton. The low amplitude of *Daphnia* migration (mean 0.8 m) is consistent with avoiding visual predators (e.g., fish) in this system where light does not penetrate deep into the water column. This is in strong contrast to very clear lakes where DVM amplitudes are of much higher magnitude (Francis et al. 2011). Therefore, *Daphnia* in Paul Lake have 2 main concerns for survival: avoiding predation and maximizing food consumption. The vertical migrations of these *Daphnia* reflect a trade-off between avoiding predation and maximizing food consumption (Johnsen and Jakobsen 1987), which has implications for energy dynamics.

Paul Lake is a humic lake receiving significant dissolved organic carbon from the surrounding landscape. This material is an abundant potential carbon source but also strongly influences light dynamics through the water column. Several studies have evaluated the effects of ultraviolet radiation and found it to be a strong driver of DVM in some systems (Williamson et al. 2011). However, Huovinen et al. (2003) found that 99% of UV radiation is absorbed in the first half meter of the water column in several lakes with lower dissolved organic carbon and chlorophyll concentrations than Paul Lake. Therefore, UV radiation is probably not a strong factor influencing *Daphnia* DVM in this system.

Terrestrial resource use by zooplankton in Paul Lake has been estimated 5 different times using both ^{13}C enrichment experiments and ambient isotope measurements (Table 1). Epilimnetic ^{13}C enrichment of Paul Lake showed that zooplankton in this system derive 65–85% of their carbon from epilimnetic primary productivity, labeled with ^{13}C, and 15–35% from an unlabeled source (Pace et al. 2004, Carpenter et al. 2005, Cole et al. 2006). This unlabeled carbon has 3 potential sources: terrestrial organic matter, metalimnetic production, or detritus of algal origin produced prior to the labeling (Cole et al. 2011). The DVM study presented here suggests it is unlikely that *Daphnia* in this system are incorporating significant portions of metal-imnetic production given that their daytime migrations rarely extend below the thermocline. This result agrees with those from 2 studies using ambient stable isotopes in Paul Lake, that consumption of allochthonous organic matter by *Daphnia* is significant (Table 1), and gives greater credence to the estimates from the ^{13}C additions as well (Table 1). The 2 studies using ambient isotopes estimate that allochthonous sources provide *Daphnia* with 22–50% of its food resources (Table 1).

The zooplankton community in Paul Lake is generally dominated by large-bodied cladocerans; however, a range of sizes exist within the *Daphnia* community. Larger bodied daphnids have been shown to migrate to deeper depths to avoid predation (Carpenter and Kitchell 1993). These large zooplankters have high food intake and processing capabilities, and if enough individuals migrate

Table 1. Literature review of estimates of terrestrial organic matter resource use for crustacean zooplankton in Paul Lake. Terrestrial resource use in these studies were either estimated by whole lake ^{13}C addition or by ambient isotope mixing models.

Source publication	Fraction terrestrial	Method
Pace et al. 2004, *Nature*	17.5–26.5%	^{13}C addition
Carpenter et al. 2005, *Ecology*	17–37%	^{13}C addition
Cole et al. 2006, *Ecol Lett*	35%	^{13}C addition
Cole et al. 2011, P *Natl Acad Sci USA*	22–39%	ambient ^{13}C, ^{15}N, ^{2}H
Solomon et al. 2011, *Ecology*	~50%	ambient ^{13}C, ^{15}N, ^{2}H

to the metalimnion, these large-bodied daphnids could accumulate metalimnetic production via grazing and translocate a large proportion of organic matter from the metalimnion into the water column. Conversely, in this study only 3.4% of all daphnids sampled were found below 3 m in the water column; therefore, even if large-bodied *Daphnia* are migrating to the metalimnion, these animals represent only a small fraction of the *Daphnia* community. Hence, sources of organic matter utilized by daphnids in this system are primarily derived from the epilimnion.

Deep layer primary productivity exists mostly in oligotrophic or mesotrophic stratified lakes where adequate light penetration can reach the lower nutrient-rich waters (Lampert and Grey 2003); however, in eutrophic lakes, deep layer primary productivity may occur in particular cases (Matthes 2004). In some of these lakes, zooplankton migrate to the rich food source located in the metalimnion (Jürgens et al. 1994, Gasol et al. 1995, Adrian et al. 2001, Adrian and Schipolowski 2003, Lampert and Grey 2003, Francis et al. 2011). However, there are many tradeoffs that factor into the depth of daytime migrations (Dini and Carpenter 1991, Williamson et al. 2011). While the metalimnion offers a rich phytoplankton food source, energetically it may not be profitable to spend time feeding in cold waters where metabolic activity is constrained (Lampert and Grey 2003). In Paul Lake, the *Daphnia* do not migrate to the metalimnion and therefore are not feeding on metalimnetic carbon, but are probably migrating deep enough during the day to avoid visual predation, which is supported by a previous study by Dini and Carpenter (1991).

While the consumption of metalimnetic material by migrating zooplankton does occur in some lakes (Jürgens et al. 1994, Gasol et al. 1995, Adrian et al. 2001, Adrian and Schipolowski 2003), these results suggest that metalimnetic consumption may not be important to zooplankton in all lakes that contain deep chlorophyll production. Moreover, inputs of carbon from terrestrial sources may be more important to zooplankton in small, oligotrophic, humic lakes where terrestrial organic matter is abundant in the surface waters. Because most of the world's lakes are similar in size to Paul Lake (<2 ha; Downing et al. 2006),

the results of this study may apply to a large number of ecosystems. Many lakes of the North Highland Lake District have similar physical profiles, productivity, and dissolved organic carbon (Hanson et al. 2007). These are likely important factors influencing the food availability and feeding behavior of zooplankton. Small lakes with large perimeter to area ratios and lakes with large watershed to area ratios may have a larger contribution of terrestrial carbon to the zooplankton and upper trophic levels. Two laboratory studies have demonstrated that *Daphnia* can grow and reproduce on terrestrial organic matter. Brett et al. (2009) found that while growth and reproduction of *Daphnia* were poor on diets of 100% terrestrial particles, mixtures of even 20% algal and 80% terrestrial material supported growth and reproduction equal to that attained on a diet dominated by algae. Masclaux et al. (2011) demonstrated that *Daphnia* could grow and reproduce on a diet of terrestrial pollen as long as that pollen had been colonized by fungi. These studies show that zooplankton can consume terrestrial organic matter, and in some systems where it is very abundant, they do. However, we still do not adequately understand the physical, chemical, or biological processes that govern zooplankton resource use in lakes. Future work should focus on using *Daphnia* energetics models and field data to estimate relative use of resources from different habitats. Detailed information on size structure, temperature, and movement will be needed. More broadly, research should develop general patterns that influence zooplankton resource use, such as lake size, productivity, and terrestrial organic matter loading across diverse landscapes, and how these patterns affect carbon and energy cycling in aquatic ecosystems.

Acknowledgements

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