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Lake depth and light conditions alter *Mysis* vertical distributions

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ABSTRACT

Light regulates the vertical migration of many aquatic organisms. *Mysis* species couple pelagic and benthic habitats in lakes by diel vertical migrations (DVM), transporting energy and nutrients through the water column and food web. Although *Mysis* are generally assumed to remain on the bottom during the day, some have been observed in the pelagic zone during the day, indicating incomplete benthic-pelagic coupling in some systems. The degree to which light attenuation and lake depth interact to affect occurrence of mysids within the water column during the day is understudied. We used standardized *Mysis* net sampling in summers 2020 and 2021 across nine north-temperate lakes to test the hypotheses that 1) *Mysis* remain pelagic during the day at depths with sufficiently low light levels, and 2) pelagic-caught individuals during the day are, on average, smaller than those caught at night. To test these hypotheses, we assessed light, dissolved oxygen (DO), *Mysis* densities, and size distribution between night and day across bathymetric depths. In deep lakes and darkly colored shallow lakes, *Mysis* suspended in the water column during the day where light levels decreased to their light avoidance threshold (~10^{-5} to $10^{-6 \text{ lx}}$). *Mysis* suspended in the water column during the day were smaller than those collected at night. Further, *Mysis* were not captured when DO reached levels < 3 mg/L, regardless of light conditions. Our results suggest that benthic-pelagic coupling by *Mysis* is mediated through light conditions, lake morphometry, and DO conditions, and may include some degree of size-dependent behavior.

1. Introduction

Diel vertical migration (DVM) of zooplankton actively facilitates the transfer of energy and nutrients between benthic and pelagic habitats via respiration, feeding, egestion, and excretion (Baustian et al., 2014; Hays, 2003; Jumars, 2007; Kiljunen et al., 2020). Such behavior contributes to many biogeochemical processes, including the biological carbon pump and the microbial loop (Archibald et al., 2019; Oliveira et al., 2022). DVM behavior also affects trophic interactions and food web structure (Kelly et al., 2019; Pangle et al., 2007; Pangle and Peacor, 2006). Managing systems with DVM can lead to unintended consequences. For example, between 1949 and the 1980 s, freshwater mysids (hereafter *Mysis*) were stocked in lakes and reservoirs in North America and Europe to serve as what was hypothesized to be a better prey source

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for fish than smaller crustacean zooplankton (Fredrickson, 2017; Lasenby et al. 1986). However, DVM behavior enabled *Mysis* to escape predation from visually feeding fishes during the day while simultaneously outcompeting planktivorous fishes for zooplankton prey by feeding in near-surface waters at night, ultimately re-structuring fish communities and causing some fisheries to collapse (e.g., Nesler and Bergersen, 1991; Spencer et al., 1991).

Environmentally induced changes in DVM behavior may have consequences for population, community, and ecosystem-level processes, particularly for organisms that migrate between benthic and pelagic habitats. For example, increasing hypoxic benthic waters in a Finnish lake forced *Mysis* into shallower depths during the day where predatory European smelt (*Osmerus eperlanus*) dramatically reduced the mysid population (Horppila et al., 2003). Similarly, increased nutrients in an Experimental Lakes Area (ELA) lake in Canada due to aquaculture caused hypolimnetic hypoxia, which led to a shift in *Mysis* distribution to shallower waters and a subsequent dramatic decline in mysids (Paterson et al., 2011; Rennie et al., 2019).

Such changes in DVM behavior by *Mysis* can diminish exchange of energy and nutrient cycling between benthic and pelagic habitats (Covich et al., 1999; Van-Duyn Henderson and Lasenby, 1986), thus impacting ecosystem function (Jumars, 2007). In some freshwater ecosystems, *Mysis* can exhibit ‘incomplete’ or ‘partial’ diel vertical migration (pDVM), where a portion of the population does not migrate to the pelagic zone and remains benthic at night (Euclide et al., 2017; Shea and Makarewicz, 1989; Stockwell et al. 2020). In contrast, *Mysis* may also remain in the pelagic zone during the day with a portion of the population not migrating to the benthic zone (Ball et al., 2015; O’Malley et al., 2018; Stockwell et al., 2020). Both behaviors should lead to reduced benthic-pelagic coupling by *Mysis* (compared to lakes with complete benthic-pelagic DVM), including reduced transport of benthic nutrients and energy back into the water column and likewise inhibiting or slowing the transfer of pelagic nutrients and energy to the benthos.

Mysis are sensitive to light and temperature (Gal et al., 1999; Lindström and Nilsson 1988; Lindström et al. 1988), which play key roles in initiating migration (light) and dictating the vertical extent of migration (light and temperature) (Boscarino et al., 2010b). *Mysis* are visual predators (Ramcharan and Sprules, 1986); their eyes represent a relatively large component of biomass, and both light tolerance and spectral sensitivity of their vision respond to the light conditions in their habitat in an adaptive manner (Donner et al, 2016; Lindström and Nilsson, 1988).

Mysis are usually absent from littoral zones because temperature and light levels often exceed their avoidance thresholds (Boscarino et al., 2010b; Gal et al., 1999). In the laboratory and field, *Mysis* avoid waters with temperatures > 12 °C (Boscarino et al. 2007; Paterson et al. 2011). In the laboratory, mysids generally preferred light levels around 10^{-5} to $10^{-6\ \mathrm{lx}}$. Light avoidance levels were size dependent; adult mysids completely avoided light levels around 0.1 lx whereas juvenile avoidance extended up to 44 lx (Boscarino et al., 2010a). Mysid consumption by alewife (*Alosa pseudoharengus*) declined at light levels below $10^{-5\ \mathrm{lx}}$, suggesting that the preferred light levels of mysids may be a response to predation risk (Boscarino et al., 2010). Light levels above $10^{-5\ \mathrm{lx}}$ may therefore limit the distribution of mysids in the field when fish are present. *Mysis* have also been observed to avoid areas of lakes with anoxic conditions, which are often the deepest areas of lakes (Nero and Davies, 1982; Paterson et al. 2011). In these instances, *Mysis* abundances increase with distance from the lake center, resulting in a donut-shaped spatial *Mysis* distribution during low-oxygen conditions (Nero and Davies, 1982).

Mysis have also been observed to suspend in the pelagic zone during the day, and those individuals tend to be smaller compared to *Mysis* that migrate completely to the benthos (Ball et al., 2015; McWilliam, 1970; O’Malley et al., 2018; Possamai et al., 2025). Such behavior could be due to higher light tolerances of juveniles compared to adults (Boscarino et al., 2010b, 2012), inefficient energetic costs for migrating to the bottom for smaller *Mysis* in deep lakes (Hays, 1995), or size-based intraspecific interactions (e.g., cannibalism) that make benthic habitats riskier for juveniles than pelagic habitats (Nordin et al., 2008; Quirt and Lasenby, 2002). The interaction of light attenuation and lake depth likely influences *Mysis* distribution during the day and thus may affect transport of nutrients between benthic and pelagic habitats and predator–prey interactions depending on inter- and intra-lake variation in these characteristics. However, mysids are typically sampled at night in the pelagia (Stockwell et al., 2020), and little is known about how depth and light regime affect the proportion and size distribution of *Mysis* that remain pelagic during the day compared to the animals that migrate to the bottom.

We hypothesized that (1) *Mysis* suspend in the pelagic zone during the day where light levels less than $10^{-5\ \mathrm{lx}}$ are available in the water column (Boscarino et al., 2009), and (2) pelagic-caught individuals during the day are smaller on average than pelagic-caught individuals at night. We evaluated our hypotheses by sampling *Mysis* across nine lakes in North America and Europe that represented a gradient in both depth and water clarity. We tested whether light attenuation, bathymetric depth, dissolved oxygen (DO), and their interactions were associated with *Mysis* pelagic distribution during the day. We also compared size structure (average body length) and demographics (sex, lifestage) of pelagic-caught *Mysis* during the day and night, across depth and light gradients.

2. Methods

2.1. Field collections

We sampled *Mysis* during consecutive days and nights in each of nine lakes across North America and Europe during the summers of 2020 and 2021 (Table 1). Sampling occurred in the pelagic zone across at least four bathymetric depths (i.e., four different sites) per lake, for both day and night. We used the depth of each sample as a continuous variable in our analyses. Sampling depths spanned the shallowest depths where *Mysis* were expected to occur (based on light tolerance thresholds and bottom daytime light levels) to the maximum depth in each lake. Samples were collected with a vertically towed net during a consecutive day/night period without storms and within ± 7 days of a new moon to standardize for moonlight, which can influence DVM behavior (Alldredge and King, 1980; Beeton and Bowers, 1982; Boscarino et al. 2010b). Three replicate vertical net tows were collected at each station from 2 m above the bottom to the surface, day and night, in all lakes. The deepest site in Lake 224 (25 m) was not sampled at night because of thunderstorms.

All night sampling was conducted at least an hour after sunset and an hour before sunrise, using red lights to avoid influencing *Mysis* behavior. *Mysis* were narcotized with Alka-Seltzer or Paracetamol tablets upon collection and then preserved in > 90 % ethanol. *Mysis* collected by the National Oceanic and Atmospheric Administration (NOAA) were preserved in 8 % formalin. Water temperature, DO, and light profiles were taken with site-specific sondes and photosynthetically active radiation (PAR) sensors at each station before each sampling event during the day, with the following exceptions: PAR data were only collected from surface to 20-m depth at each station in Donner Lake; water temperature and DO data were only recorded from surface to 40-m depth at each station in Donner Lake; and PAR, DO, and temperature profiles were only collected at one site in each of the International Institute for Sustainable Development Experimental Lakes Area (IISD ELA) lakes (Fig. 1, Fig. 2, Fig. 3). The IISD ELA lakes are relatively shallow (< 28 m maximum depth), well-mixed, and have a small surface area (< 30 ha). Thus, a single sampling site (Lake 224 = 17 m; Lake 373 = 19 m) is sufficient to characterize temperature and light profiles for all sampling sites in these small lakes. For Donner Lake, we were not able to record temperature and light profiles for the 50-m and 70-m site.

DO was not recorded in Lake Pääjärvi or in Lake Michigan because of

Table 1
Location, coordinates, and depths of lakes sampled in summers of 2020 and 2021. Institutional abbreviations: IISD-ELA = International Institute for Sustainable Development Experimental Lakes Area, IGB = Leibniz Institute of Freshwater Ecology and Inland Fisheries, USGS LOBS = U.S Geological Survey Lake Ontario Biological Station, NOAA GLERL = National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, USGS LSBS = U.S Geological Survey Lake Superior Biological Station, * Breiter Luzin was sampled late summer.

Lake	Institution	Year	Site depths (m)	Max depth (m)	Species	Country	Latitude	Longitude	Net mouth area (m^2)	Upper mesh (μm)	Lower mesh (μm)	Bucket mesh (μm)
ELA 373	IISD – ELA	2021	8,12,14,19	21	*M. diluviana*	CA	49.745°	−93.799°	0.44	500	500	500
ELA 224	IISD – ELA	2021	11,15,22,25	28	*M. diluviana*	CA	49.690°	−93.717°	0.44	500	500	500
Breiter Luzin	IGB	2021*	21,33,44,57	58.5	*M. relicta*	DE	53.353°	13.463°	0.12	500	500	500
Pääjärvi	University of Helsinki	2021	19,36,58,73	87	*M. relicta*	FI	61.067°	25.128°	1.00	500	500	500
Donner	University of Nevada, Reno	2020	20,40,50,70	100	*M. diluviana*	US	39.321°	−120.26°	1.00	500	500	500
Champlain	University of Vermont	2020, 2021	40,60,80,100	122	*M. diluviana*	US	44.586°	−73.380°	1.00	1000	1000	250
Ontario	USGS LOBS	2021	70,105,137,155,177,196	244	*M. diluviana*	US	43.633°	−77.827°	0.78	1000	1000	250
Michigan	NOAA GLERL	2021	45, 67, 87, 110	281	*M. diluviana*	US	43.450°	−87.222°	0.78	1000	1000	1000
Superior	USGS LSBS	2021	50,100,150,250	406	*M. diluviana*	US	47.723°	−86.940°	1.00	1000	250	500

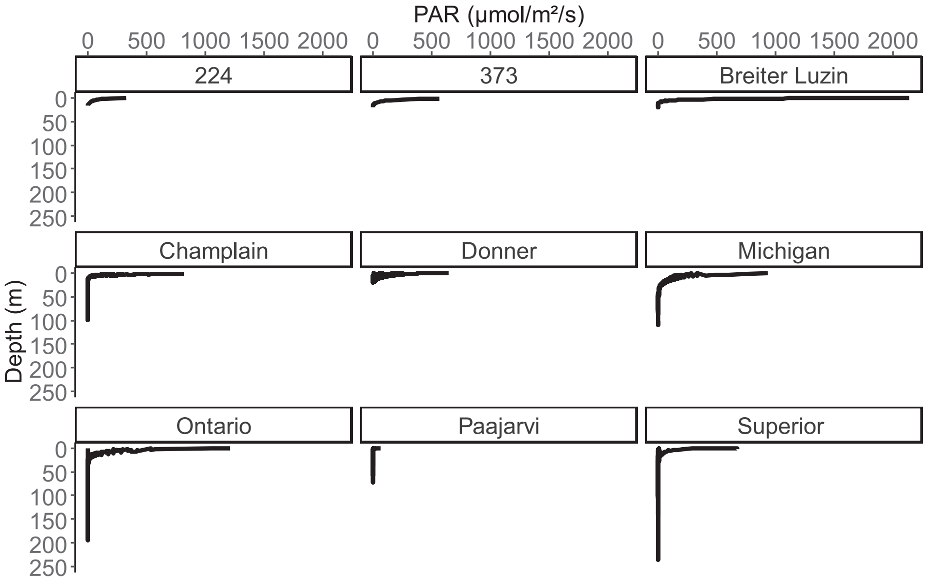

Fig. 1. Light profiles for lakes 224, 373, Breiter Luzin, Champlain, Donner, Michigan, Ontario, Pääjärvi, and Superior.

time constraints. However, DO levels in Lake Michigan are consistently high throughout the water column (Scofield et al. 2020), including in the years 2020–2021 sampled here (LGR, JMW, pers. obs.).

2.2. Sample processing

Sampled *Mysis* were counted and measured for length, density, and sex. Samples from Lake Ontario were processed at the U.S. Geological Survey Lake Ontario Biological Station, samples from Lake Michigan were processed at the NOAA Great Lakes Environmental Research Laboratory, and samples from Donner Lake were processed at the University of Nevada, Reno. The remaining samples were processed at the University of Vermont (UVM). All *Mysis* were measured from the tip of the rostrum to the end of the abdomen. At UVM, *Mysis* were identified for sex, counted, and measured for length using an Olympus SZX dissecting microscope (10 ×) equipped with a digitizing tablet (O'Malley et al., 2018). *Mysis* $<$ 10 mm were considered juveniles, and sex was only determined on adult *Mysis* $>$ 10 mm (O'Malley et al., 2018). We aimed to measure 200 *Mysis* per sample, but samples usually had $<$ 200 individuals. When samples had more than 200 individuals, length measurements were recorded for a random subsample of 200 *Mysis*. Areal densities (individuals/m^2) were calculated by dividing total counts in each sample by the mouth area of the net (Table 1). *Mysis* densities are not greatly impacted by mouth area or mesh size (Silver et al., 2016). We assumed 100 % net efficiency because of the relatively large mesh size of the nets used for sampling (Table 1). Our observational unit for reporting density was the average from all replicates at each station and time of day in each lake. We calculated the average length of all individuals measured for each replicate sample taken at each site and time of day and used the mean of replicates as our observational unit for length at each site and time of day.

Light (in lux) at depth was estimated using PAR (μmol m^{-2} s^{-1}) profiles obtained during the day at the same time as the net samples. Because light levels at depths were often below the detection limit of the instruments, we first calculated the light attenuation coefficients (k_{PAR}) for each site based on the top 20 m of the light profile using the Beer – Lambert Law (Kirk, 1994). We then applied wavelength specific attenuation coefficients derived for a range of k_{PAR} values by Jerome et al.

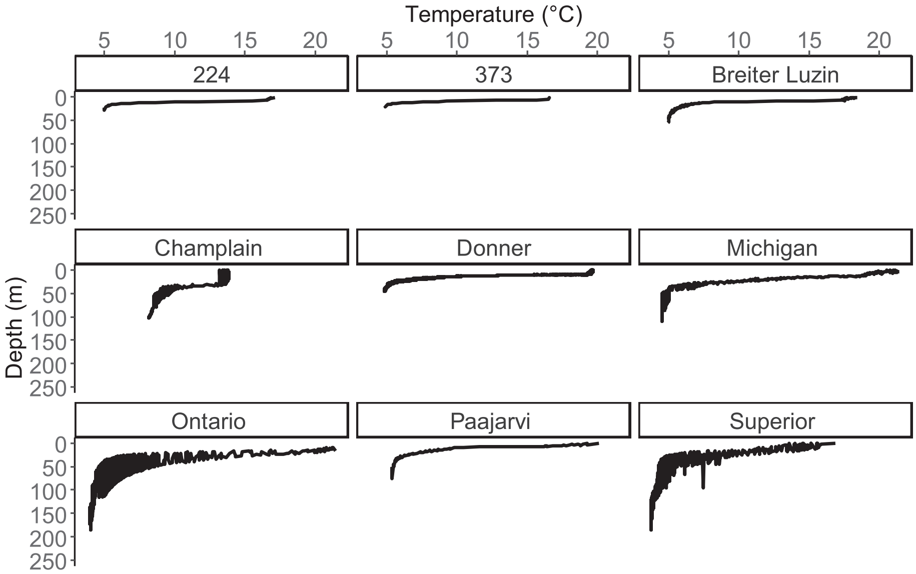

Fig. 2. Temperature profiles for lakes 224, 373, Breiter Luzin, Champlain, Donner, Michigan, Ontario, Pääjärvi, and Superior.

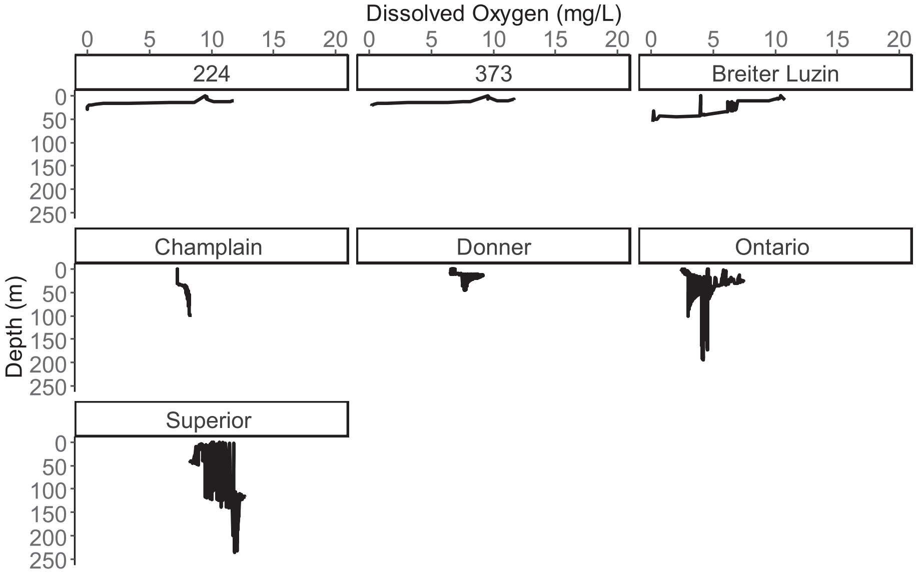

Fig. 3. Dissolved oxygen (DO) profiles for lakes 224, 373, Breiter Luzin, Champlain, Donner, Ontario, and Superior.

(1983) and calculated light intensity by wavelength at each depth. These values were then converted to lux using the standard scotopic (dark-condition) luminosity function. Scotopic lux is a unit that better reflects light perception of mysids than PAR (Gal et al. 1999). For more details on mysid visual sensitivity, see Gal et al. (1999) or Lindström et al. (1990), and for an application to predict mysid vertical distribution, see Boscarino et al. (2009).

We used a logistic regression model to test our hypothesis that site depth, bottom light levels (lux), DO, or their interactions influenced the presence or absence of *Mysis* in the pelagic habitat during the day. *Mysis* behavior (i.e., whether *Mysis* suspend in pelagic habitats during the day) was expressed as a categorical presence/absence variable. Logistic regression allowed us to model the response of a discrete variable with a binomial distribution from continuous and categorical predictor variables. We did not use light or DO as continuous variables because we were not certain where in the water column *Mysis* remained suspended based on our lack of vertical sampling resolution; we took full water column *Mysis* tows and did not use closing nets. Light and DO levels were used as separate categorical variables for statistical analyses. The DO threshold for *Mysis* is $\geq$ 3 mg/L (Sandeman and Lasenby, 1980), so we used this as an acceptable/unacceptable threshold. Light and DO were assigned a value of 1 if their respective levels anywhere in the water column were $< 10^{-5}$ lx and $>$ 3 mg/L at each site and time of day. Otherwise, a value of 0 was assigned. For the logistic model, data were available for light (n = 29) and DO (n = 25).

We used a *t*-test to evaluate *Mysis* length differences between night and day. Only sites where *Mysis* were captured during the day were used in the analysis. We used the average length of the replicates for each event (lake, site, and time of day) as the observation. We conducted a two-sample *t*-test to compare *Mysis* densities between day and night across lakes. All statistical analyses were conducted in R v.4.2.0 (R Core Team, 2017).

3. Results

Mysis were captured in the pelagic habitat during the day at all sites where light levels were $< 10^{-5\ \text{lx}}$ in at least part of the water column (Fig. 4, Table 2), except for the 100-m site on Lake Superior where 2 % of the water column (the bottom 2 m) was below the light tolerance threshold but *Mysis* were exceedingly rare. Site depths, where suspended *Mysis* were captured during the day, ranged from 19 to 250 m with the percentage of the water column with suitable light habitat (i.e., $< 10^{-5\ \text{lx}}$) ranging from 1 % to 89 % (Table 2, Fig. 2).

The percent of suitable light habitat tended to increase with the depth of the sampling site in all lakes, except in Lake Pääjärvi where suitable light habitat exceeded 70 % of the water column at all sites sampled (19- to 73-m depth; Table 2, Fig. 4). Of the remaining lakes with measured light data, suitable light conditions during the day were not present at stations shallower than 80 m and suitable light conditions did not exceed 60 % of the water column (Table 2).

In lakes with some dark daytime habitat, *Mysis* remained suspended in the pelagic habitat regardless of bottom depth both day and night, except where DO levels were below the *Mysis* tolerance threshold in the deeper part of the water column (< 3 mg/L). DO levels were below 3 mg/L at only three stations, while 22 stations had DO levels above this threshold. At night, *Mysis* were collected at all sites in all lakes except the 19-m site in ELA Lake 373, the 25-m site in ELA Lake 224, and the 57-m site in Lake Breiter Luzin. In all three instances, the DO levels were below the *Mysis* tolerance threshold (< 3 mg/L) for the bottom 20–40 % of the water column.

Our logistic model evaluating *Mysis* presence/absence showed that interactions between DO, light, and depth were not significant ($P > 0.05$). However, the main effects of depth (df = 29; $P < 0.001$) and light (df = 28; $P = 0.001$) were strong drivers of *Mysis* daytime pelagic behavior. DO was not significant (df = 27; $P > 0.05$).

The interaction between lakes and time of day collected was not significant in relation to *Mysis* size (ANOVA: $F_{(3,23)} = 1.13$, $P = 0.35$). Overall, pelagic-caught *Mysis* during the day were smaller than pelagic-caught *Mysis* at night (ANOVA: $F_{(1,23)} = 8.89$, $P = 0.006$; Table 3), though in Lake Pääjärvi, average lengths were identical between day and night (Fig. 4). Mean lengths of *Mysis* were also significantly different among lakes (ANOVA: $F_{(6,23)} = 15.32$, $P < 0.001$; Table 3). For lakes where *Mysis* were captured during the day, the proportion of *Mysis* averaged (± SE) 46 ± 14 % juveniles and 54 ± 15 % adults during the day. By comparison, at night, the proportion of juveniles dropped to 28 % (± 15 %) and adults increased to 72 % (± 14 %). Sixty-one percent (± 7 %) of adults were females, and 39 % (± 7 %) were males at night.

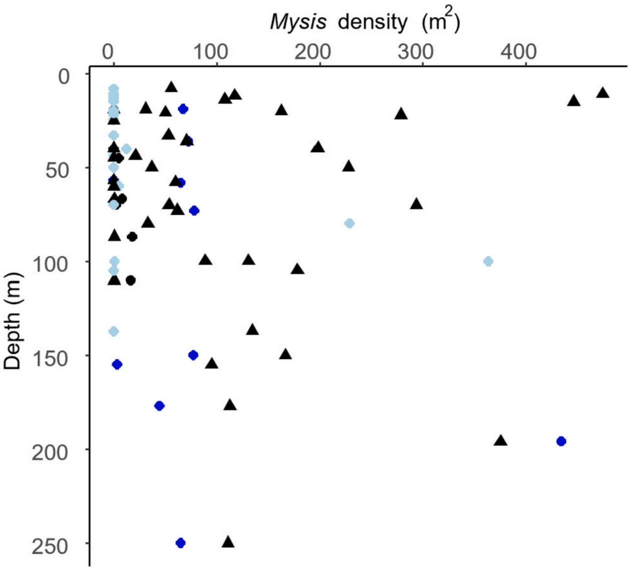

Fig. 4. *Mysis* density (ind m^{-2}) sampled at different bathymetric depths across nine lakes both day and night. *Mysis* estimates during the day at sites with unsuitable light levels ($>10^{-5\ \text{lx}}$) are represented by light blue circles, and *Mysis* estimates during the day at sites with suitable light levels ($< 10^{-5\ \text{lx}}$) are represented by dark blue circles. *Mysis* collected during the day at sites with no available light data are represented by black circles. *Mysis* collected at night are represented by black triangles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Percent of water column with suitable light habitat ($< 10^{-5\ \text{lx}}$) at each site in each lake where *Mysis* were captured in the pelagic habitat during the day. *Mysis* were captured in the pelagic habitat at night in all sites in each lake. Lakes where *Mysis* were not captured during the day had no suitable light habitat during the day at any depth. *Mysis* densities (individuals/m^2) are also presented. A dash (–) indicates no data were available.

Lake	Site depth (m)	% Suitable light habitat	Suitable DO habitat (< 3 mg/L)	Day density (ind. m^{-2})	Night density (ind. m^{-2})
ELA 373	8	–	–	0	56
	12	–	–	0	118
	14	–	–	0	108
	19	0	No	0	0
ELA 224	11	–	–	0	475
	15	–	–	0	447
	22	–	–	0	279
	25	0	No	0	0
Donner	20	0	Yes	0	163
	40	–	–	0	198
	50	–	–	0	228
	70	–	–	2.6	294
Breiter Luzin	21	0	Yes	0	50
	33	0	Yes	0	53
	44	0	Yes	0	21
	57	0	No	0	0
Pääjärvi	19	70	–	67	31
	36	83	–	72	71
	58	87	–	65	60
	73	89	–	78	62
Champlain	40	0	Yes	0	12
	60	0	Yes	0	5
	80	5	Yes	33	229
	100	25	Yes	89	364
Michigan	45	–	–	4.7	0
	67	–	–	8.5	0.4
	87	–	–	18.3	0.8
	110	–	–	16.2	0.4
Ontario	70	0	Yes	0	54
	105	0	Yes	0	179
	137	0	Yes	0	135
	155	1	Yes	3	95
	177	45	Yes	44	113
	196	55	Yes	435	376
Superior	50	0	Yes	0	37
	100	2	Yes	1	131
	150	30	Yes	77	167
	250	60	Yes	65	111

Table 3
Average (±SE) lengths (mm) of *Mysis* collected during the day and at night. *Mysis* were not captured during day sampling in Lake 373, Lake 224 and Breiter Luzin. *Mysis* were collected in one sample in Donner Lake during the day; n = individuals measured.

Lake	Day	Night
Pääjärvi	9.9 (± 0.5) n = 727	9.9 (± 0.4) n = 797
Donner	10.6n = 8	12.5 (± 1.3) n = 1833
Champlain	7.9 (± 2.5) n = 664	9.3 (± 0.9) n = 2328
Ontario	8.3 (± 0.1) n = 703	10.3 (± 0.5) n = 1965
Michigan	4.1 (± 0.2) n = 12	8.6 (± 0.5) n = 105
Superior	7.7 (± 0.7) n = 863	9.7 (± 0.5) n = 1910

Overall, *Mysis* densities were higher at night than during the day across all lakes (Welch two-sample *t*-test: $t_{59} = -4.63$, $P < 0.05$; Fig. 4). Mean (± SE) density during the day was 27.8 ± 73.2 individuals m^{-2}, and mean densities at night averaged 139.7 ± 131.8 individuals m^{-2}. Though we expected *Mysis* densities to be lowest at the shallowest sites sampled and highest at the deepest sites sampled in each lake, our findings were not consistent with this expectation across all lakes. For example, *Mysis* were not captured day or night at the deepest sites sampled in Lake Breiter Luzin (57 m), ELA Lake 373 (19 m), and ELA Lake 224 (25 m) where DO levels were < 3 mg/L, but *Mysis* were captured at all of the other shallower sites sampled at night in these three lakes where DO was > 3 mg/L throughout the water column. In these three lakes, overall *Mysis* densities at night seem to be highest at shallower site depths (Fig. 5).

4. Discussion

We expected *Mysis* to suspend in the pelagic habitat during the day when light levels did not exceed their preference threshold of 10^{-5} $^{\text{lx}}$ (Boscarino et al., 2009) in the water column. Our results were consistent with this expectation. Typically, the bathymetric depths at which we found pelagic *Mysis* during the day were at the deeper sites in each lake ($>$ 80 m). However, *Mysis* were also suspended during the day at shallow depths (19 m) in Lake Pääjärvi, as the extremely low light penetration in this brown-water lake (Lindström and Nilsson, 1988) makes the pelagic habitat suitable for *Mysis* also during the day. *Mysis* have also been found suspended during the day in several lakes with day-time occupied depth depending on light penetration (Ball et al., 2015; Carpenter et al., 1974; Griffiths, 2007; O'Malley et al., 2018; Penk, 2011). For example, in mesotrophic Lake Champlain, *Mysis* have been detected in the water column during the day at 60-m sites (Ball et al., 2015; Gutowski, 1978; O'Malley et al., 2018), whereas in lakes Ontario, Michigan, and Superior, *Mysis* have been observed suspended mainly at sites deeper than 100 m (Bowers 1988; LGR, pers. obs.). Another example of daytime pelagic occupancy by *Mysis* in a high-DOC lake is Buck Lake, where *Mysis* were found suspended during the day (Nordin et al., 2008). Our results suggest that light is the leading factor of *Mysis* vertical distribution during the day because when light levels below their threshold were available in the water column, at least some *Mysis* were suspended regardless of depth.

We did not capture *Mysis* at the deepest site either day or night in three of the lakes. In each of these lakes (ELA Lakes 224 and 373 and Lake Breiter Luzin), DO levels in the deepest parts of the hypolimnion were below the *Mysis* avoidance threshold ($<$ 3 mg/L), thus making the benthic habitat at these sites uninhabitable. Avoidance of deep hypoxic waters by mysids has been previously observed in the ELA lakes and Lake Breiter Luzin (Nero and Davies, 1982; Paterson et al., 2011; Scharf and Koschel, 2004). In lakes Champlain, Ontario, and Superior, where highest densities were at the deepest sites, DO levels were sufficient ($>$ 3 mg/L) throughout the hypolimnion. Low DO can be problematic for *Mysis*. For example, in Crystal Lake (Michigan, USA) and Lake Hiidenvesi (Finland), both eutrophic lakes, *Mysis* avoided hypoxic zones by moving upward in the water column (Horppila et al., 2003; Sherman et al., 1987). Also in the mesotrophic Lake Breiter Luzin (Germany), the *Mysis* populations moved upward and away from the deepest part of the lake as the hypoxic zone seasonally expanded (Waterstraat et al., 2005). In Lake Hiidenvesi, a shift to pelagic habitat during the day by *Mysis* caused the population to collapse because of intense predation by fish (Horppila et al., 2003). Similarly, in small boreal lakes, *Mysis* avoided deep benthic habitat and moved to shallower regions when oxygen decreased below 3 mg/L (Sellers, 1995; Paterson et al., 2011). Collectively, these observations emphasize the importance of hypolimnetic DO for shaping mysid distribution.

The average length of pelagic-caught *Mysis* during the day was smaller than pelagic-caught *Mysis* at night across lakes, probably because juvenile *Mysis* have higher tolerance to higher light and temperatures compared to adult *Mysis* (Boscarino et al., 2010a; Gal et al., 1999). In addition to physiological explanations, the predator-avoidance hypothesis posits that adult *Mysis* are more likely to avoid pelagic habitat due to increased detectability by visual predators compared to juveniles (Beeton, 1960; Boscarino et al., 2009, 2010b).

Size- or lifestage-dependent habitat selection may also be influenced by predator avoidance. Juveniles may avoid benthic habitat to reduce cannibalism by larger *Mysis* (Fraser et al., 2005; Quirt and Lasenby, 2002). *Mysis* are opportunistic feeders and feed on detritus (Lasenby and Langford, 1973; Lasenby and Shi, 2004; Sierszen et al., 2011); large *Mysis* could prefer to feed on detritus in the benthic habitat while avoiding predators in the pelagic zone (Possamai et al., 2025).

Our study had several limitations, including the absence of light and DO data in certain cases. For example, light measurements were only recorded at one site (20 m) in Donner Lake, and DO data were unavailable for Lake Pääjärvi and Lake Michigan. Nevertheless, Lake Michigan is not known to experience low DO levels in its deep waters (Rowe et al.,

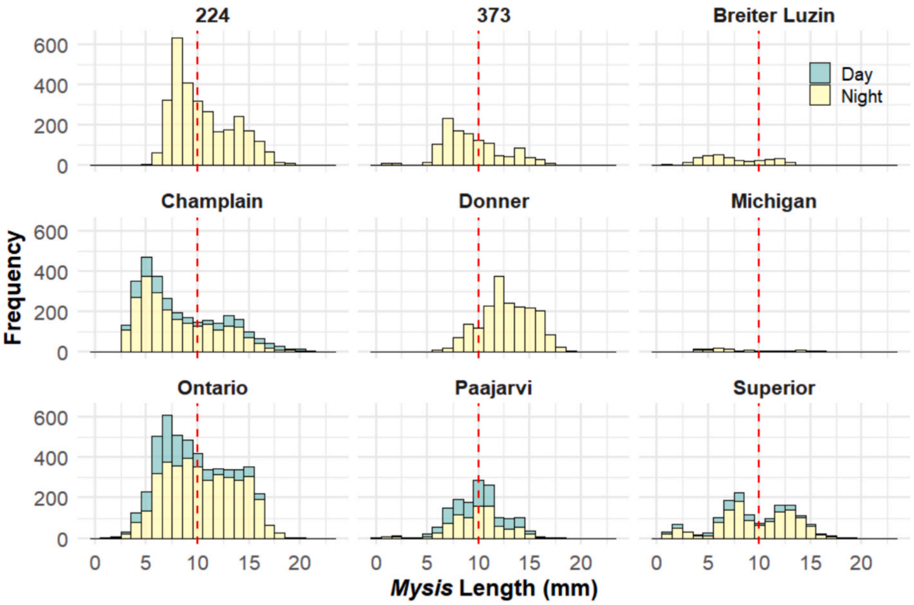

Fig. 5. Distribution of *Mysis* lengths across different lakes during day and night sampling. The red dashed line represents the threshold separating juveniles from adults. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2015). Different *Mysis* species and populations may exhibit variations in spectral sensitivity. For example, *Mysis relicta* from lakes Vuohijärvi and Pääjärvi had different sensitivities to light (Audzijonyte et al., 2005). Lake Vuohijärvi is characterized by clear water with mysid sensitivity similar to Lake Ontario, whereas Lake Pääjärvi is a dark-water lake with light sensitivity shifted towards longer wavelengths (Audzijonyte et al., 2005; see also Lindström and Nilsson 1988). Despite these limitations, our study assessed the influence of light on *Mysis* daytime vertical distribution across a suite of lakes with varying light and DO levels and depths. Our results were consistent with expectations of *Mysis* responses to light and DO levels. In the future, adding systems that experience limitations in both light and DO would be valuable to further evaluate the roles of these factors on *Mysis* behavior. Additionally, light and DO availability in lakes varies seasonally. We sampled only during thermal stratification and at the most productive time of the year in pelagic habitat; other seasons may have more or less *Mysis* in the water column during the day.

Mysis are an important component of lake food webs where they occur, and understanding the role that light plays in *Mysis* DVM is important for evaluating benthic-pelagic coupling in lakes. We have shown that small mysids are present in the water column during the day when the light levels are below the light preference of these animals in at least part of the water column, but measured densities are typically lower than during the night. Consequently, light is a critical factor that affects the likelihood that *Mysis* remain suspended in the water column during the day. Furthermore, our observations that *Mysis* were not captured at any site where hypolimnetic DO levels were below the *Mysis* tolerance threshold (< 3 mg/L) suggests that suitable light and DO are necessary environmental conditions for finding *Mysis* in the water column.

CRediT authorship contribution statement

Rosaura J. Chapina: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Brian P. O'Malley:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Kelly Bowen:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Martta L.M. Viljanen:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Zachary A. Bess:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Daniel L. Yule:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization. **Jens C. Nejstgaard:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Stella A. Berger:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Michael D. Rennie:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Michael J. Paterson:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Steve A. Pothoven:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **James M. Watkins:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Lars G. Rudstam:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Sudeep Chandra:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Jason D. Stockwell:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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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Data availability statement

All data necessary to recreate analysis in this manuscript are publicly available on Zenodo (https://doi.org/10.5281/zenodo.12612234).

Author information

All authors contributed to and conceived of the ideas for this study. Authors contributed to the conception and design of the study and to the analysis tasks.

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