

## The effects of temperature and predator–prey interactions on the migration behavior and vertical distribution of *Mysis relicta*

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### Abstract

The extent to which temperature, temperature gradients, predator smell, and prey availability influence the migratory behaviors and vertical distribution of the opossum shrimp, *Mysis relicta*, was explored through controlled laboratory experiments and comparisons with field distributions of mysids in Lake Ontario. By varying environmental conditions in 2-m tall experimental columns in a temperature-controlled room, we determined that mysids prefer temperatures between 6°C and 8°C with limited movement into waters of 12°C or higher. No mysids moved into waters above 16°C in the absence of prey. However, a higher proportion of mysids moved into temperatures of 14°C and 16°C (but not 18°C) when densities of *Daphnia pulicaria* exceeding 120 L<sup>-1</sup> were present at those temperatures. *Mysis* avoided waters with kairomones from a primary mysid predator, the alewife (*Alosa pseudoharengus*). The rate of temperature change with depth did not restrict mysid movements. A temperature preference function based on the experimental data was applied to an existing model of mysid vertical distribution. The modified model predicted the depth of maximum mysid density to within 1 m and yielded high percentage overlap index values when compared with published mysid vertical distributions in Lake Ontario. Our approach may be used to model how diurnal, seasonal, and larger climactic changes can impact both the vertical position and feeding ecology of mysids, a keystone species in many deep-water pelagic food webs.

Modeling how changes in an organism's environment affect the organization and movement of a population through space is an important tool for understanding food web dynamics (Gotelli 2001; Hardiman et al. 2004). The influence of different exogenous factors such as light, temperature, and predator/prey densities on the spatial

distribution and movement patterns of zooplankton during diel vertical migration (DVM) has received considerable research attention (see reviews in Lampert 1989 and Hays 2003); however, much of this DVM research has focused on conditions affecting the movements and spatial distributions of the “average” zooplankton in a migrating population and offers little insight into how these factors are impacting the entire vertical distribution. However, predator–prey interactions likely occur at the edges of a migrating population's distribution, and it is therefore difficult to draw conclusions about a particular environmental factor's impact on aquatic food web dynamics without information on the entire distribution.

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The opossum shrimp, *Mysis relicta*, exhibits dramatic diel vertical migration and is an important component of many deep-water food webs in North America and Eurasia (Lasenby et al. 1986; Beattie and Clancy 1991; Spencer et al. 1999). In the Great Lakes, mysids are predators on zooplankton and therefore competitors with planktivorous fish like alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*). The amount of zooplankton biomass required to sustain the Lake Ontario mysid population is approximately equal to the zooplankton biomass needed to

maintain the entire planktivorous fish population in the lake (Johannsson et al. 2003). Mysids are also an important source of polyunsaturated fatty acids for both alewife and rainbow smelt in Lake Ontario, which may be important in decreasing overwinter mortality of alewife (Snyder and Hennessey 2003). The significance of mysids in food webs other than the Great Lakes is most apparent in systems where mysids were introduced as potential prey for young piscivores (Lasenby et al. 1986). These introductions have resulted in unintended declines of native zooplankton and changes in zooplankton species composition, as well as reduced fish growth rates and elevated levels of toxic accumulation in piscivores (Rieman and Falter 1981; Spencer et al. 1991). Thus, mysids represent a pivotal group in understanding food web dynamics in the Great Lakes and other deep-water ecosystems across North America.

Many of the interactions between mysids and their prey and predators occur at night when mysids ascend from their daytime benthic habitat to the pelagia to feed on zooplankton (*see review by Johannsson et al. 2003*). The current literature suggests that mysid DVM is primarily limited by light and temperature (*see reviews by Beeton and Bowers 1982 and Johannsson et al. 2003*). Light levels of  $10^{-2}$  to  $10^{-4}$  lux (Teraguchi et al. 1975; Moen and Langeland 1989; Rudstam et al. 1989), temperatures above 15°C (Mauchline 1980; Gal et al. 2004), strong thermal gradients (Beeton 1960; Gal et al. 2004), and high epilimnetic predator densities (Gal et al. 2004) have all been implicated as important behavioral modifiers of mysid vertical movements. However, most mysid DVM studies have been limited to examining light and temperature conditions associated with the upper boundaries or density peak of the migratory layer and have not assessed factors influencing their entire vertical distribution.

Preference functions for factors that influence migration patterns, such as light and temperature, are necessary for predictive models of aquatic organisms' vertical distributions (Rudstam and Magnuson 1985). During the thermally stratified fall and summer seasons, both temperature and light preference functions are necessary to construct predictive mysid vertical distribution models (Gal et al. 2004). Gal et al. (2004) derived a mysid light preference function from field observations under isothermal conditions in Lake Ontario and a temperature preference function based on feeding rate experiments of mysids at different temperatures (Rudstam et al. 1999). Peak feeding rates for mysids occur between 10°C and 12°C (Chipps 1998; Rudstam et al. 1999). Gal et al. (2004) combined both the light and temperature preference functions into a mysid vertical distribution model that predicted the diel changes in distribution of mysids throughout the water column. However, this model could not predict mysid distributions in Lake Ontario without the addition of an avoidance function for steep temperature gradients based on observations by Beeton (1960). Neither the temperature preference function nor the temperature gradient function used in Gal et al. (2004) has been evaluated in the laboratory.

Gal et al. (2004) hypothesized that *M. relicta's* avoidance of sharp thermal gradients may represent either a direct

response to the change in temperature near the thermocline or a response to increasing fish kairomones encountered in warmer waters. High predator densities in upper waters have been shown to influence the position of vertically migrating zooplankton in the water column (Loose 1993; De Meester and Cousyn 1997; Peacor et al. 2005). If this leads to movement into lower temperatures, it can result in lower overall growth rates of migratory invertebrates (Moore et al. 1996; Fiksen 1997). Berrill and Lasenby (1983) report lower growth rates for *M. relicta* at 4°C than 8°C. Therefore, if mysids choose to occupy deeper and colder water due to higher kairomone concentrations in shallower waters, their growth may be compromised. In Lake Ontario, mysids would also have less access to zooplankton prey that is more abundant higher in the water column (Gal et al. 2006).

We know of only a few studies involving the influence of kairomones on mysids. Quirt and Lasenby (2002) demonstrated that juvenile and immature mysids responded to the presence of adult mysid kairomones by shifting their position in a choice-test olfactometer. The only studies exploring the effects of fish kairomones on *Mysis* spp. have shown decreased feeding rates of mysids in the presence of predators (Hamrén and Hansson 1999; Lindén et al. 2003; Lehtiniemi and Lindén 2006), but the migratory responses of mysids to fish kairomones have not been investigated.

Prey densities may also affect the migratory movements and average temperature experiences of mysids, since the interaction between prey density and temperature influences *Daphnia* and other smaller zooplankton's vertical migration in both the field and laboratory (Marcogliese and Esch 1992; Han and Straskraba 2001). Huntley and Brooks (1982) reported that calanoid copepods are more likely to undergo DVM if food is abundant in warmer waters but less likely to move if prey densities fall below a certain threshold concentration. Similarly, *Daphnia* responded to changing prey gradients by raising or lowering their depth distributions (Winder et al. 2004). To our knowledge, similar studies exploring links between mysid depth preference and prey density-temperature interactions have not been conducted.

Quantifying the response of mysids to temperature, predators, and prey under controlled conditions is a necessary first step to model the vertical distributions and degree of spatial and temporal overlap of mysids, their prey and their predators. The objectives of this study are threefold: (1) to determine the effects of temperature and rate of temperature change on the migration patterns of *M. relicta* in the laboratory, (2) to assess how kairomones from a primary mysid predator (alewife) and the density of a prey species, *Daphnia pulicaria*, interact with temperature to influence mysid depth distributions, and (3) to use results from our temperature preference experiments to predict vertical distributions of mysids in Lake Ontario during thermal stratification. Our approach was to monitor vertical movement responses of mysids to different manipulations of temperature, predator kairomone concentrations, and prey densities in 2-m tall observation columns in the laboratory. The experiments were designed to test the following hypotheses: (1) mysids select for

temperatures that will maximize consumption rate on zooplankton (10–12°C, Chipps 1998; Rudstam et al. 1999) (2) mysid vertical migration is limited by thermal gradients, (3) mysids will avoid waters with fish kairomones, and (4) mysids will ascend into waters considered thermally suboptimal to seek zooplankton prey. Finally, we use the results of the temperature preference experiments to construct a function describing the probability of observing a mysid at different temperatures. This function was combined with a light preference function created by Gal et al. (2004) to predict published field distributions of mysids in Lake Ontario from the summer and fall of 1995 and 1996 (Johannsson et al. 2003). The ability to predict the vertical distribution of mysids across different seasons will provide important insight into how environmental changes can affect the spatial overlap and trophic interactions between mysids, their prey, and their predators in deep-water, pelagic food webs.

## Materials and methods

We conducted four experiments to determine the effects of temperature and temperature gradients on mysid vertical movement as well as how temperature interacts with predator and prey densities to influence vertical distribution. Each experiment is identified with the following descriptors: (1) temperature, (2) temperature threshold and acclimation, (3) kairomone–temperature interaction, and (4) prey–temperature interaction.

*Collection and maintenance of mysids*—We collected live mysids with vertical net hauls (1-m diameter, 1-mm mesh net) through the mysid layer at night at a 170-m deep site in southeastern Lake Ontario near Oswego, New York, in May, August, and September 2004. Immediately after collection, live mysids were placed into light-proofed coolers filled with hypolimnetic water and transported back to the laboratory where they were stored in 50-liter tanks of 4°C dechlorinated Lake Ontario water. Tanks were cleaned and water was replaced at least once per week. An opaque blind was placed immediately outside the entrance door of the experimental room to prevent fluorescent light from entering. Mysids were fed ad libitum densities of Cyclop-eez (a food source derived from the subclass Copepoda and closely resembling *Artemia* nauplii in nutritional value). All feeding and handling of mysids and cleaning of tanks was done in red or infrared light, since mysids are insensitive to both infrared and light in the far red portion of the visual spectrum (Jokela-Määttä et al. 2005).

Mysids selected for experiments were 12–16 mm long (mean = 15 mm, Table 1) and were starved for approximately 12 h prior to experimental observation. The 12-h starvation period was chosen to ensure that the mysids would be active and not complacent when they entered the experiment. We noticed no differences in vertical movement behaviors of mysids by size. There were also no significant differences found in sex ratios between treatment groups throughout the course of our experiments (binomial chi-square analysis;  $p = 0.78$ ;  $n = 9$ ).

*Experimental setup*—Three 2-m high, 8-liter cylindrical columns were used as observational columns (Fig. 1). These columns were 7.62 cm in diameter, made of clear Plexiglas, and hung approximately 0.5 m away from each other from the ceiling of a temperature-controlled room. Columns were labeled from 0 cm (bottom of the column) to 180 cm (top of the column), in 10-cm increments. Each column was filled to the 180-cm line with dechlorinated Lake Ontario water and allowed to reach ambient room temperatures prior to observations. A behavioral trial was defined as a 45-min period of observing mysid vertical movements within a single column, in which a particular experimental variable was manipulated. Each manipulation of temperature, kairomone concentration, or prey density was considered an experimental treatment. At least three replicate sets of trials (treatment and two control columns) were performed for each treatment condition.

To create a thermal gradient, a heater was lowered down to the 90–110 cm interval of the column and set to a specific temperature. The desired upper column temperature was maintained by a temperature controller (Aqualogic digital temperature controller) connected to the heater. Temperature gradients took between 3–5 min to become established for all treatments. After the gradient had become established, we monitored changes in temperature throughout the column by taking temperature readings at each 10-cm interval over a 45-min time period with a temperature probe (Yellow Springs Instruments, Model 95). Temperatures varied less than 1°C for each depth interval over this 45-min time period for all treatments.

Region 1 (0–70 cm) was kept at the temperature of the room and ranged from 3–4°C in all temperature, kairomone–temperature interaction, and prey–temperature interaction experimental trials (Table 1). Room temperatures and, therefore, region 1 temperatures were held between 10°C and 11°C for the temperature threshold and acclimation experimental trials (Table 1). Region 2 (70–100 cm) began when a 0.05°C cm<sup>-1</sup> change was observed and ended when the set upper column temperature was reached. Region 3 began when the set upper column temperature was stabilized and continued to the top of the column, which corresponded to a column depth of 100–180 cm. Region depth designations remained consistent across all experimental trials (Fig. 2). Temperature gradients will hereafter be expressed as the ratio of the region 1 : region 3 water temperatures (Table 1).

## Experiments

*Behavioral observations and preliminary trials*—Mysid positions were recorded using an infrared, digital video camera recorder at 3-min intervals over a period of 45 min for a total of 15 observations per mysid. We recorded observations of mysids in the columns using an infrared, digital video camera recorder (Sony Digital Handycam, Model TRV18). The experimental room was otherwise kept in complete darkness throughout the behavioral observation period. At the onset of each trial, mysids were placed into the bottom half of the column in all four experiments and restricted from entering the upper column by closing

Table 1. Conditions of the four migration experiments (temperature, temperature threshold and acclimation, kairomone–temperature interaction, prey–temperature interaction) and differences in mean lengths,  $L$  (mm), and sex ratios (% males) between experimental trials. The number of replicates for each trial is denoted by  $n$ . “HC” indicates a high concentration treatment, and “LC” represents a low concentration treatment.

Experiment	Treatment (upper column)	Mean region 1 : region 3 gradient (°C : °C)	$n$	$L$ (mm) ( $\pm 1$ SE)	% males
Temperature	4°C	3.5 : 3.5	63	16.1 (0.27)	36
	6°C	3.3 : 6.1	4	15.6 (0.77)	36
	8°C	3.3 : 8.2	3	15.7 (0.82)	33
	10°C	3.5 : 10.4	7	15.6 (0.75)	43
	12°C	3.4 : 12.3	5	15.5 (0.75)	42
	14°C	3.5 : 14.4	10	16.3 (0.58)	38
	16°C	4.0 : 16.0	3	16.7 (0.53)	43
	18°C	3.8 : 18.2	3	16.1 (0.63)	50
Temperature threshold and acclimation	10°C	10.3 : 10.3	28	16.7 (0.43)	52
	12°C	10.3 : 12.6	6	17.3 (0.76)	40
	14°C	10.4 : 14.3	6	16.3 (0.99)	50
	16°C	10.5 : 15.8	3	16.2 (1.06)	50
	18°C	10.4 : 17.6	3	16.2 (1.06)	50
	20°C	10.8 : 19.9	3	16.2 (0.97)	67
Kairomone–temperature interaction	Control	3.5 : 10.4	11	15.1 (0.38)	56
	HC	3.5 : 10.4	5	14.8 (0.43)	67
	LC	3.5 : 10.4	5	14.4 (0.30)	60
Prey–temperature interaction	Control, 14°C	3.5 : 14.4	10	15.0 (0.55)	44
	HC, 14°C	3.5 : 14.4	4	14.5 (0.35)	47
	LC, 14°C	3.5 : 14.4	4	12.9 (0.47)	33
	Control, 16°C	4.0 : 16.0	6	14.5 (0.64)	44
	HC, 16°C	4.0 : 16.0	5	13.9 (0.47)	33
	LC, 16°C	4.0 : 16.0	4	14.5 (0.47)	25
	Control, 18°C	3.8 : 18.2	6	14.1 (0.60)	44
	HC, 18°C	3.8 : 18.2	4	13.4 (0.29)	33
	LC, 18°C	3.8 : 18.2	4	13.3 (0.51)	25

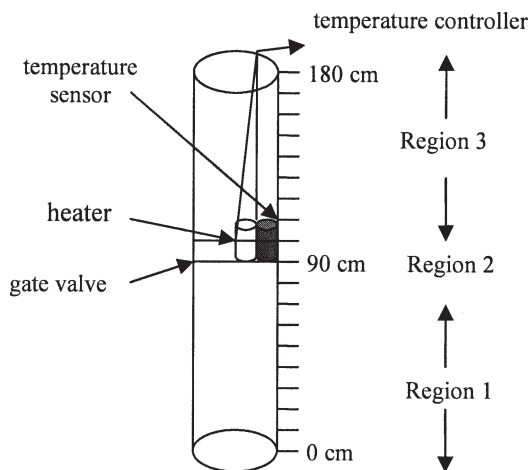


Fig. 1. Schematic of experimental setup. Mysid depths were recorded in units of 10 cm (i.e., 0–10 cm = “10,” 10–20 cm = “20,” etc.) and later related to thermal regions. Region 1 extended from 0 to 70 cm, region 2 from 70 to 100 cm, and region 3 from 100 to 180 cm. A heater and temperature sensor were lowered down to the 90–110 cm interval of the column. Both were connected to a temperature controller outside the column that maintained the region 3 temperature throughout the experiment. A gate valve was also fitted to the column at the 90–100 cm interval. Drawing not to scale.

a gate valve (7.62-cm diameter Valterra gate valve) that was fitted to the middle of the column. Gate valves remained closed until the observation period commenced to ensure that all mysids began the trials in region 1.

Preliminary trials were conducted to monitor mysid movements under isothermal conditions. We found no significant differences between mysid distribution in columns with one versus three mysids (two-tailed  $t$ -test,  $p = 0.245$ ,  $n = 32$ ). Therefore, we used three mysids in all experiments to increase the number of observations per trial. Each column was manually scanned with the infrared camera until the position of each mysid in the column was determined. Mysids quickly moved through the whole column under isothermal conditions and showed no significant preference to a region after 6 min (7 : 3 : 8 multinomial goodness-of-fit chi-square test,  $p > 0.05$ ,  $n = 63$ ). To avoid bias toward region 1, where the mysids were located at the start of the experiments, we did not use observations recorded in the first 6 min of each trial. We chose 3 min as our recording interval since preliminary trials indicated that this amount of time was sufficient for a mysid to move from one end of the column to the other.

*Experiment 1: Temperature*—One 4°C isothermal condition (control) and eight distinct temperature gradients were

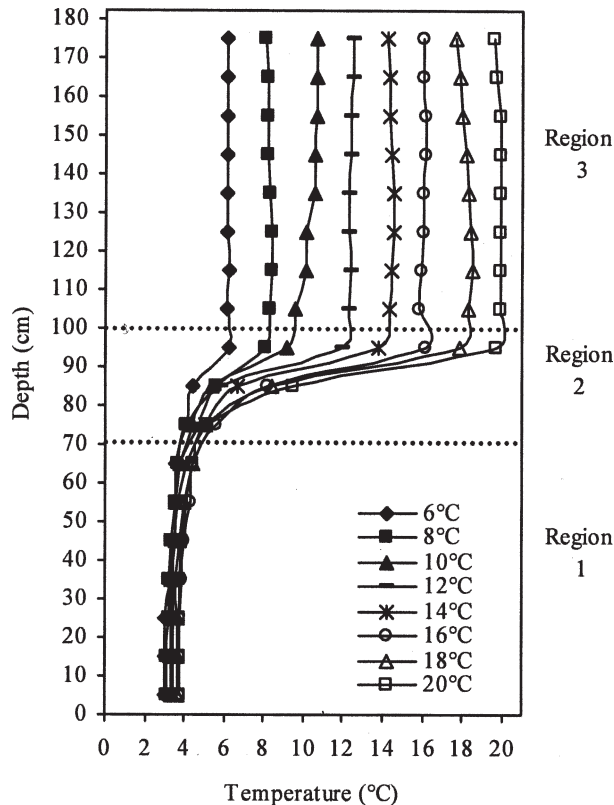


Fig. 2. Thermal gradients established in each temperature experimental treatment. Temperature values represent an average of measurements taken with a temperature probe at 10-cm intervals, starting at 5 cm, to obtain an average temperature value for each 10-cm section of the column. Dotted lines separate each temperature region. The lower region of the column (region 1) ranged from 3°C to 4°C for all treatments. The middle region (region 2) began when a  $0.05^{\circ}\text{C cm}^{-1}$  change was noted and ended when the upper column temperature was reached. Region 3 began where the set upper column temperature was reached and stabilized.

established in the temperature experiments to determine the temperature preferences of mysids relative to 4°C (Fig. 2). Region 3 temperature treatments were varied at 2°C intervals (i.e., Treatment 1 = 4°C:4°C, Treatment 2 = 4°C:6°C, Treatment 3 = 4°C:8°C, etc.) up to a 4°C:20°C gradient (higher temperatures are lethal to mysids, Smith 1970). These temperature ranges are similar to gradients present during stratified conditions in Lake Ontario (Johannsson et al. 2003). Mysids were acclimated to 4°C for at least 1 week prior to experimentation.

Three columns were used to monitor mysid vertical movements. The treatment column housed a heater set to the desired temperature, while the other two columns served as controls. The first control column contained a “dummy” heater, which was suspended at the same depth as the heater in the first column but emitted no heat, as well as a gate valve. The second control column contained neither a heater nor a gate valve. The dummy heater/gate valve control was necessary to demonstrate that the mere physical presence of the heater and gate valve was not influencing vertical movement decisions. Columns were

randomly selected to receive either of the controls or a temperature treatment for each set of trials. Comparisons of mysid distributions between these two controls revealed no significant differences in vertical distribution (two-tailed *t*-test,  $p = 0.36$ ,  $n = 63$ ) and data from these columns were subsequently pooled and treated as controls.

*Experiment 2: Temperature threshold and acclimation*—One 10°C (control) isothermal condition and five distinct temperature gradients were created in the temperature threshold and acclimation experiments (10°C:12°C, 10°C:14°C, 10°C:16°C, 10°C:18°C, 10°C:20°C) (Table 1). Mysids were acclimated to 10°C for at least 1 week prior to experimentation. Observations of mysid position in the water column were compared with those from the temperature experiments to separate the effects of absolute temperature from the effects of acclimation temperature and rate of temperature change with change in depth.

*Experiment 3: Kairomone-temperature interaction*—Alewives collected from Cayuga Lake, New York, were kept in an unfiltered, 500-liter tank to allow a daily buildup of kairomones. Water was exchanged on a daily basis, but prior to the exchange, water was extracted and diluted to a concentration believed to be representative of a low and high alewife density in Lake Ontario ( $0.073 \text{ fish m}^{-3}$  and  $1 \text{ fish m}^{-3}$ , respectively). Low concentration (LC) was calculated as 50% of the estimate of alewife abundance in Lake Ontario of Rand et al. (1995) from the summer of 1991 ( $2.2 \text{ alewife m}^{-2}$  equally distributed in the top 15 m of the water column, or the average depth of the epilimnion in August 1995). High concentration (HC) was set to 14 times higher than low concentrations ( $1 \text{ fish m}^{-3}$ ). Columns were randomly selected to receive high-kairomone, low-kairomone, or kairomone-free water. While it is possible that mysids respond differently to different types of predator kairomones, we chose to use alewife kairomones since alewives are the most abundant of the primary predators of mysids in Lake Ontario and would presumably offer a high probability of eliciting an antipredator response. There is also no evidence to suggest any significant variability in kairomone composition in alewives from different ecosystems.

Predator water was placed into the upper portion of the treatment columns and mysids were closed off from entering the top half by shutting the gate valve. Region 3 of both treatment and control columns was subsequently heated to 10°C. Once the desired upper column temperature had been reached, the gate valve was opened and mysids were provided access to the upper column waters.

A 4°C:10°C thermal gradient was chosen for this experiment to ensure minimal mixing of region 1 and region 3 waters, but not preclude movements of mysids from one region to another (as determined by results from the temperature experiments). We tested the mixing of water by adding a known amount of fluorescent dye (from a fluorescein filter set) to the predator water that was introduced into the top of the column. After 45 min, we sampled water at 10-cm intervals and later ran these samples through a fluorometer (Aminco J4 Fluorometer)

to test how much of the dye breached the thermal gradient. Concentrations of dye were over two orders of magnitude greater in region 3 than in region 1, supporting the assumption of minimal mixing between the two thermal layers.

*Experiment 4: Prey–temperature interaction*—*D. pulicaria* populations used in this experiment were obtained from Oneida Lake, New York, in late spring 2004 and maintained in the laboratory by feeding on *Scenedesmus* algae. *D. pulicaria* (mean length = 0.98 mm;  $n = 482$ ; SD = 0.26) was selected as the prey item because they were readily available and *M. relicta* show strong preference for *Daphnia* spp. over other types of zooplankton prey including bosminids, cyclopoids, and calanoid copepods (Bowers and Vanderploeg 1982; Cooper and Goldman 1982). Johannsson et al. (2003) also demonstrated that *Daphnia* spp. can make up 40–55% of an adult mysid's diet in August in the eastern portion of the lake where our sampling took place. While it is possible that mysid movement responses vary depending on the type of prey or population introduced, we believe that using a preferred *Daphnia* prey is appropriate for determining whether prey availability significantly alters mysid migration decisions.

Prey were introduced into the experimental setting in the same manner as the predator water in the kairomone–temperature interaction experiment. The two treatment concentrations selected for use in this experiment were based on both the highest offshore crustacean zooplankton density ( $127 \text{ L}^{-1}$ ) and the average prey density ( $48 \text{ L}^{-1}$ ) recorded in Lake Ontario in 2003 (Mills et al. 2003). Control columns contained no prey.

Region 3 temperatures were set to  $14^\circ\text{C}$ ,  $16^\circ\text{C}$ , and  $18^\circ\text{C}$  in this experiment since results of the temperature experiments indicated that these temperatures were avoided by mysids in the absence of prey. We assumed that *Daphnia* would stay in region 3, since *Daphnia* spp. often spend most of the night in the epilimnion (Bowers and Vanderploeg 1982; Nero and Sprules 1986). We counted the number of *Daphnia* in the top and bottom half of the columns 45 min after introducing the prey to test how many *Daphnia* had breached the thermal gradient. Mean prey abundance was over 3.5 times higher in the upper column (top column: bottom column abundance ratios ranged from 2.3 to 4.1 across a  $4^\circ\text{C}$ : $14^\circ\text{C}$  and a  $4^\circ\text{C}$ : $18^\circ\text{C}$  gradient for the high concentration treatment;  $n = 4$ ), supporting our assumption that the majority of *Daphnia* would remain in warmer waters.

*Data analyses*—The proportion of all observations (excluding region 2) in a given column that were in region 3 was considered an independent data point for statistical comparisons in the temperature and temperature threshold and acclimation experiments. Proportions were used as data points since individual observations of position within the column at 3-min intervals may not have been independent. Region 2 observations were excluded from the analysis since region 2 temperatures were highly variable between treatments. One-way analysis of variance (ANOVA) and Dunnett's  $t$ -test ( $\alpha = 0.05$ ) were performed

to test for differences in the proportion of observations at different temperatures in both experiments relative to controls.

Average depth in each column over the duration of the experiment (45 min) was considered an independent data point for statistical analyses for the prey–temperature and kairomone–temperature interaction experiments. We chose to compare depths rather than region proportions because we were interested in how prey and predator densities affected depth distributions, not preferences for one temperature region over another. We used a combination of nonparametric Kruskal–Wallis and Wilcoxon rank sum tests as well as one-way ANOVA (with Dunnett's  $t$ -test) to test for differences in mean depth as a function of prey density and predator kairomone concentration.

*Model development*—The temperature preference curve ( $f_{\text{MOD}}(T)$ ) derived from the temperature experiment (see *Results section* for function derivation) was used with a mysid light preference function ( $g(L)$ ) from Gal et al. (2004) to predict vertical distribution patterns of *M. relicta* in Lake Ontario (Table 2). The two preference functions were considered to be independent, and therefore multiplicative (Papoulis 1984; Gal et al. 2004). Following Gal et al. (2004), we consider the probability of finding a mysid at a given depth  $z$  ( $P_z$ ) to be proportional to the product of  $f_{\text{MOD}}(T_z)$  and  $g(L_z)$ —the preference for temperature and light at depth  $z$ . Therefore, the probability of finding a mysid at depth  $z$ , given all available depths (1,  $z_{\text{max}}$ ) equals

$$P_z = \frac{f_{\text{MOD}}(T_z) \times g(L_z)}{\sum_1^{z_{\text{max}}} (f_{\text{MOD}}(T_z) \times g(L_z))} \quad (1)$$

Our predictions based on temperature and light preferences represent a modification of a model created by Gal et al. (2004) to predict mysid vertical distributions in Lake Ontario. The original form of the Gal et al. (2004) model used both temperature preferences based on mysid feeding rates on zooplankton ( $f_{\text{GAL}}(T)$ ) and mysid light preferences ( $g(L)$ ) (Table 2). A second form of the Gal et al. (2004) model added a temperature gradient function ( $h(G)$ ), which accounted for potential limitations imposed by thermal gradients (Beeton 1960) (Table 2). These preference functions were also considered to be independent and multiplicative (Gal et al. 2004). Hereafter, our version of the mysid preferred temperature curve and vertical distribution model will be identified as the “modified curve,” ( $f_{\text{MOD}}(T)$ ), and “modified model,” respectively. The two versions published in Gal et al. (2004) will be referred to as “Gal model I,” which does not include a temperature gradient function, and “Gal model II,” which contains the temperature gradient function,  $h(G)$ .

*Comparison of model predictions with field data*—We compared model predictions of both forms of the Gal model and our modified model with published field distributions from 01 August 1995 at a 130-m station and

Table 2. Model equations. The  $z$  subscript indicates that the function is evaluated at depth,  $z$ , when predicting field distributions of mysids in Lake Ontario.  $L$  indicates light levels in units of mylux, and  $T$  is temperature in degrees Celsius.

Model used in	Function	Model equations	Data source
(a) Gal model I, II	Light function $g(L)$	For $L_z \leq 10^{-8}$ : $f(L_z) = 0.128$ for $L_z > 10^{-8}$ :	Gal et al. (2004)
(b) Modified model		$g(L_z) = e^{-0.5 \left\{ \frac{\log L - (-6.86)}{0.56} \right\}^2}$	
Gal model I, II	Temperature function $f_{\text{GAL}}(T)$	$f_{\text{GAL}}(T_z) = -0.0052 \times T^2 + 0.0929 \times T + 0.5611$	Rudstam et al. (1999)
Modified model	Temperature function $f_{\text{MOD}}(T)$	$f_{\text{MOD}}(T_z) = e^{-0.5 \left\{ \frac{\ln T - (\ln 6.07)}{0.2314} \right\}^2}$	This study
Gal model II	Temperature gradient function $h(G)$	$G_z = T_z - T_{z-1}$ if $G_z = 0$ : $h(G_z) = 1$ , if $G_z \leq 0.7$ : $h(G_z) = G^*(-1.357) + 1$ , if $0.7 < G_z < 1.2$ : $h(G_z) = G^*(-0.1) + 0.12$ , if $G_z \geq 1.2$ : $h(G_z) = 0$	Beeton (1960); Gal et al. (2004)

from 01 October 1996 at an 80-m station (Johannsson et al. 2003). *M. relicta* distributions were measured during the night at both stations with a 420-kHz acoustic system (see Gal 1999). These mysid acoustic estimates were validated with stratified net tows at each sampling site. Both profiles represent sections of the data where there were no obvious fish targets present. Ship lights were turned off during sampling to eliminate the effect of light deterrence on mysid distributions (Gal 1999).

Comparisons were made between differences in predicted versus observed depth of peak mysid densities as well as the percentage overlap between predicted and observed mysid distributions ( $|1 - (0.5 \times \Sigma(\text{observed} - \text{predicted})| \times 100)$ , Czekanowski Index, Feinsinger et al. 1981). A perfect fit of predicted to observed distributions would therefore result in a Czekanowski overlap index score of 100%.

Temperature and light profiles were recorded at both stations using a Hydrolab profiler down to 60-m depth, below which temperature was assumed to remain constant. A calibrated LI-193 (Licor) underwater spherical quantum sensor was used to measure underwater irradiance at 1-m intervals down to the instrument's detection limit. Light values in units relevant to mysid vision were then calculated for each depth given a surface light level and measured extinction coefficients (see Gal et al. 1999). This unit, termed "mylux," was derived by Gal et al. (1999) and is obtained by using a mysid-specific photometer fitted with a filter that approximates the sensitivity of the mysid eye to different wavelengths. Mylux is related to mysid vision in the same way as lux is a measure of brightness relevant to human vision (see Gal et al. 1999).

Results

*Experiment 1: Temperature*—Temperature strongly affected the proportion of mysids observed in region 3 relative to a 3–4°C region 1 (one-way ANOVA,  $F_{8,92}, p < 0.0001, n = 101$ , Dunnett's  $t$ -test) (Fig. 3A). Proportions

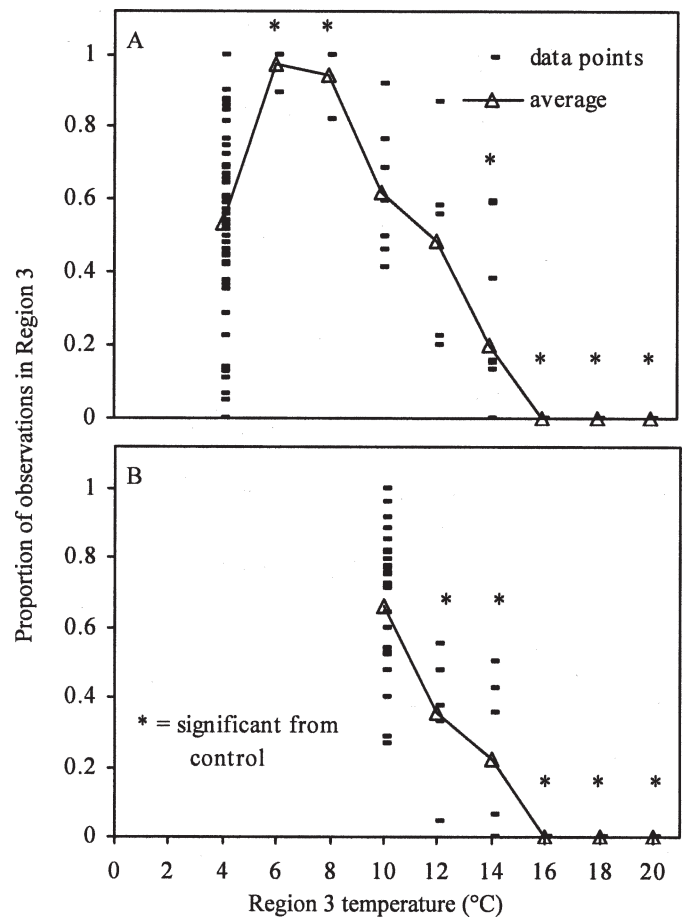


Fig. 3. Proportion of all region 1 and region 3 mysid observations that were recorded in region 3 (upper column region) for the (A) temperature and (B) temperature threshold and acclimation experiments. Treatment comparisons were made relative to control, or isothermal, columns (i.e., 4°C and 10°C in temperature and temperature threshold and acclimation experiments, respectively). Degree of significance was based on one-way ANOVA and Dunnett's  $t$ -test with an experiment-wise error rate of 0.05.

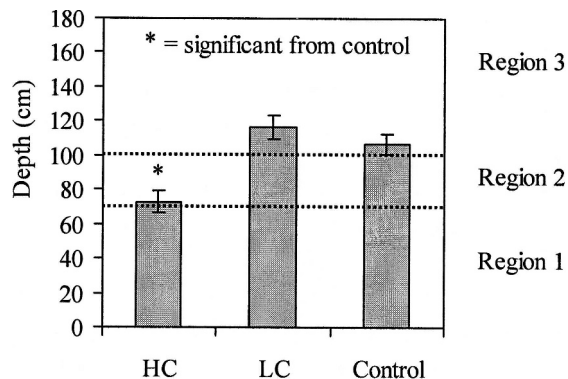


Fig. 4. Effects of different predator kairomone concentrations on mysid vertical distribution. Bars represent average depths ( $\pm 1$  SE) of mysids in columns under each treatment condition. Temperature regions in the column are separated by dotted lines. All trials were run with a 10°C upper column temperature and a 4°C bottom column temperature. Predator smell was most highly concentrated in the upper column (depths >100 cm). “HC” indicates high kairomone concentration treatment (1 fish  $m^{-3}$ ), and “LC” represents the low concentration kairomone treatment (0.073 fish  $m^{-3}$ ). Control indicates no fish kairomones were present. Degree of significance was based on one-way ANOVA and Dunnett’s *t*-test with an experiment-wise error rate of 0.05.

were normally distributed around the means and were not transformed prior to ANOVA. Mysids displayed strong preferences for 6°C and 8°C, strong deterrence to 14°C, and a complete avoidance of 16°C and higher temperatures. No significant attraction or deterrence effects were observed for 10°C and 12°C relative to controls. Given that mysids maximize consumption rate on zooplankton between 10°C and 12°C (Chipps 1998; Rudstam et al. 1999), we therefore reject the first hypothesis that mysids prefer temperatures that maximize consumption rates on zooplankton.

*Experiment 2: Temperature threshold and acclimation*—When mysids were acclimated to 10°C, their avoidance of higher temperatures was similar to the reactions observed for mysids acclimated to 4°C. Ten degrees was preferred to all other region 3 temperatures in this experiment (one-way ANOVA,  $F_{5,43}$ ,  $p < 0.0001$ ,  $n = 49$ , Dunnett’s *t*-test) and no mysids were observed in 16°C and higher temperatures (Fig. 3B).

The rate of temperature change along a thermal gradient does not appear to influence vertical ascent. Mysids moved across a steep 4°C:14°C gradient in the temperature experiments (a 10°C change), but did not move across a 10°C:16°C gradient in this experiment. Thus, mysid migration seems to be limited by absolute temperature rather than rate of temperature change, as 16°C was the upper threshold of mysid ascent in both the temperature and temperature threshold and acclimation experiments (but see results from prey-temperature interaction experiment). We therefore reject our second hypothesis that thermal gradients directly limit mysid ascent through the water column.

*Experiment 3: Kairomone-temperature interaction*—Mysids avoided waters with alewife kairomones. Significant differences in mean column depth were observed between experimental and control conditions in the high concentration (1 fish  $m^{-3}$ ) trials, but no significant differences were observed between control and low-kairomone concentrations (0.073 fish  $m^{-3}$ ) (one-way ANOVA,  $F_{2,18}$ ,  $p = 0.002$ ,  $n = 21$ , Dunnett’s *t*-test; Fig. 4).

*Experiment 4: Prey-temperature interaction*—Mysids will move into warmer temperatures when prey are present versus when prey are absent. Significant differences in average column depth were found for both 14°C and 16°C trials (Kruskal-Wallis test,  $p = 0.03$ ,  $n = 18$  for 14°C and  $p$

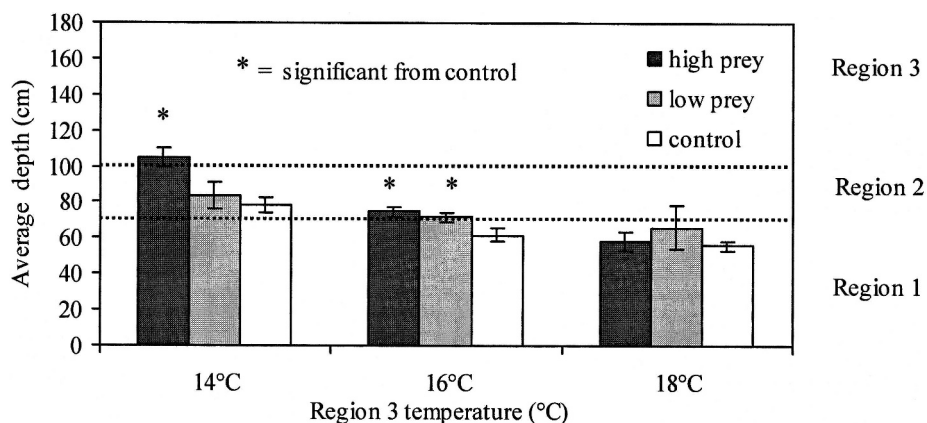


Fig. 5. Effects of different prey densities on mysid vertical distribution. Bars represent average ( $\pm 1$  SE) depths of mysids in columns under each treatment condition. Temperature regions in the column are separated by dotted lines. Trials were run with a 14°C, 16°C, and 18°C region 3 (upper column) temperature. Introduced prey were most highly concentrated in the upper portion of the column (depths >100 cm) in all experimental trials. High prey concentration was set to 127  $L^{-1}$ , and low prey concentration was 48  $L^{-1}$ . Control indicates no prey were present. Degree of significance was based on a combination of Kruskal-Wallis and Wilcoxon rank sum tests with an experiment-wise error rate of 0.05.

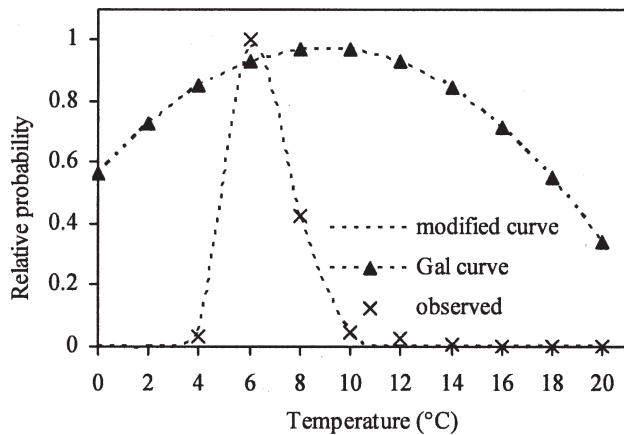


Fig. 6. Comparison of mysid temperature preference curves used in the Gal ( $f_{\text{GAL}}(T)$ ) and the modified ( $f_{\text{MOD}}(T)$ ) models based on results from both the temperature and temperature threshold and acclimation experiments. The modified curve is a Gaussian curve based on the logarithm of temperature (see results) fit to the observed probability of finding a mysid in a particular temperature condition relative to all other available temperatures. The peak of the modified curve occurs at 6.07°C compared with the Gal curve, which peaks between 9°C and 10°C.

< 0.001,  $n = 15$  for 16°C; Fig. 5). Pairwise comparisons revealed significant differences between the high concentration treatment (127 L<sup>-1</sup>) and control for the 14°C trials (Wilcoxon rank sum test,  $p = 0.007$ ,  $n = 14$ ) and for the 16°C trials (Wilcoxon rank sum test,  $p = 0.002$ ,  $n = 11$ ). Higher mean column depths were also observed in the 16°C trials at low prey concentrations (48 L<sup>-1</sup>) relative to controls (Wilcoxon rank sum test,  $p = 0.005$ ,  $n = 10$ ), but not for the 14°C trials (Wilcoxon rank sum test,  $p = 0.42$ ,  $n = 14$ ). No mysids were ever found in 16°C waters under control conditions; however, mysids were observed in 16°C waters in both the low- and high-prey density treatments. No significant differences were found in average column depth in the 18°C trials (Kruskal-Wallis test,  $p = 0.94$ ,  $n = 14$ ). No mysids were ever observed in 18°C waters regardless of prey density.

**Temperature preference function**—A temperature preference curve ( $f_{\text{MOD}}(T)$ ) was generated based on the probability of finding an individual mysid in a particular temperature relative to all other temperatures (Fig. 6). Relative probabilities were calculated as the mean proportion of region 3 observations over the mean proportion of region 1 observations for each treatment in both the temperature and temperature threshold and acclimation experiments. Relative probabilities for each treatment were divided by a correction factor (correction factor = 1.15 in the temperature experiments and 1.97 in the temperature threshold and acclimation experiments). These correction factors account for the 1.15 and 1.97 times as many observations in region 3 as in region 1 under control (isothermal) conditions for the temperature and temperature threshold and acclimation experiments, respectively. This procedure corrects for any preference for the upper region of the columns independent of the temperature gradient.

Table 3. Comparison between Gal et al. (2004) and modified models in predicting *Mysis relicta* vertical distribution. Percentage overlap was calculated using Czekanowski's Index (Feinsinger et al. 1981). Difference from peak values was calculated as the difference, in meters, between model predictions and actual observations of peak mysid densities.

	Gal model I	Gal model II	Modified model
Functions used	$f_{\text{GAL}}(T_z)$ , $g(L_z)$	$f_{\text{GAL}}(T_z)$ , $g(L_z)$ , $h(G_z)$	$f_{\text{MOD}}(T_z)$ , $g(L_z)$
% overlap (August)	71	44	83
% overlap (October)	25	71	77
Difference from peak (August)	0 m	2 m	0 m
Difference from peak (October)	42 m	4 m	1 m

A Gaussian curve based on the logarithm of temperature was fitted to our experimental data for temperatures between 0°C and 20°C, which minimized the sums of squares of differences between observed and predicted region 3:region 1 ratios (nonlinear least-squares regression, SAS statistical package version 9.1,  $a = 0.2314$ ,  $T_{\text{pref}} = 6.07$ ,  $r^2 = 0.99$ ) (Table 2, Fig. 6). The equation for this temperature preference function ( $f_{\text{MOD}}(T)$ ), where  $T$  is equal to temperature, is

$$f_{\text{MOD}}(T) = e^{-0.5 \left\{ \frac{\ln T - \ln T_{\text{pref}}}{a} \right\}^2} \quad (2)$$

The parameter  $a$  is the standard deviation of the fitted curve ( $a = 0.2314$ , SE = 0.0008), and  $T_{\text{pref}}$  represents the preferred temperature of mysids as predicted by the curve ( $T_{\text{pref}} = 6.07^\circ\text{C}$ , SE = 0.01) (Fig. 6). This function was chosen based on the good fit to the observed data.

**Comparison of model predictions to field data**—The new temperature preference function was used in conjunction with the light preference function of Gal et al. (2004) to construct our modified model of mysid vertical distribution in Lake Ontario. Observations of mysid vertical distribution on 01 August 1995 and 01 October 1996 in Lake Ontario were compared with predictions from the modified model and Gal models I and II. The modified model was a better predictor of mysid distribution than both versions of the Gal model (Fig. 7A,B). Not only did the modified model predict the depth of the peak abundance to within 1 m, but the percentage overlap between the predicted and observed distributions was high (83% for August and 77% for October) (Table 3). The Gal model I had overlap values of 71% in August and 25% in October (Table 3). The Gal model II had overlap values of 44% in August and 71% in October (Table 3).

## Discussion

Diel vertical migration has evolved in response to the challenges associated with living in a spatially and

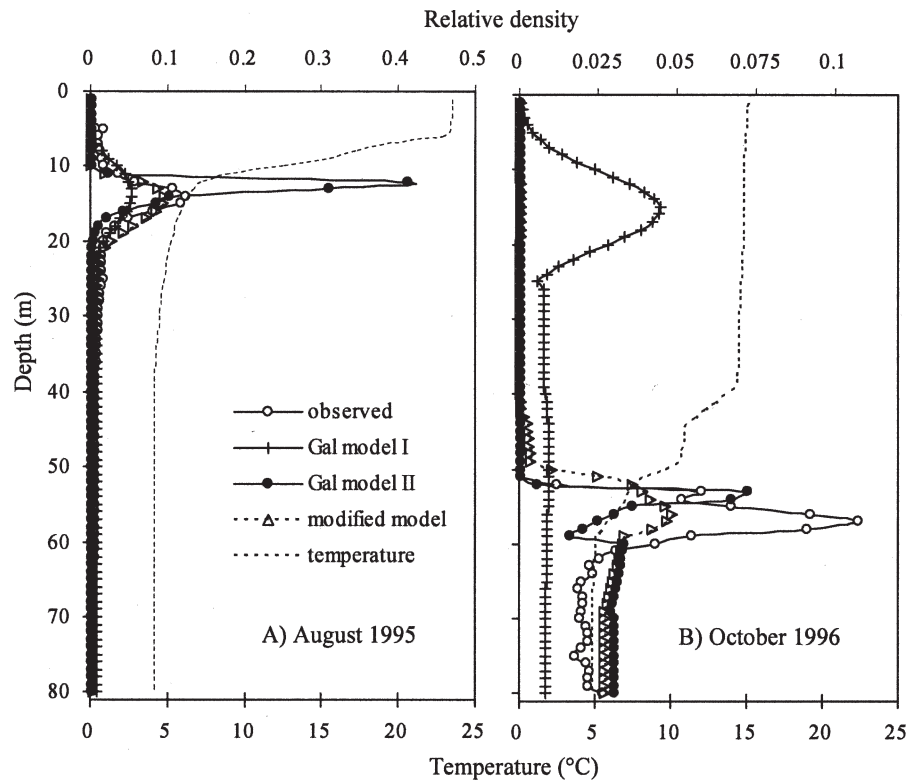


Fig. 7. Comparison of the modified model and Gal model I and II in predicting *M. relicta* vertical distribution over two seasons of thermal stratification in Lake Ontario. Gal model II included a temperature gradient function, while Gal model I did not. Sampling locations and seasons were as follows: (A) summer station with bottom depth of 80 m taken in August 1995 off Oswego, New York, and (B) fall station with bottom depth of 130 m taken in October 1996 at Station 41 (midlake) (Gal 1999; Johannsson et al. 2003). Mysid densities were based on acoustic sampling of the water column. The distributions are given as relative densities and, therefore, the total density for a given profile equals one.

temporally stratified environment (Hardiman et al. 2004). Annual, seasonal, and diurnal changes in exogenous factors such as light, temperature, and prey and predator density gradients can influence the organization and movement of a population through space and, consequently, the degree of spatial overlap with its prey and predators. The ability to quantify and model the response of a migrating population to varying biotic and abiotic factors therefore has important implications for the predator-prey dynamics of a system.

Much of the research done on zooplankton vertical movement has focused on light and chemical cues as the main proximate factors controlling DVM behavior. This study demonstrates that the vertical movements and distribution of *M. relicta* are also strongly influenced by absolute temperature, but that rate of temperature change is less significant. Mysids preferred temperatures between 6°C and 8°C, were deterred by temperatures higher than 12°C, and completely avoided temperatures of 18°C and higher in the laboratory. We were able to successfully predict mysid vertical distribution during stratified conditions in Lake Ontario with a model based on a temperature curve derived from these experiments. We also show that mysid movements are affected by the presence of high predator kairomone concentrations or prey densities in

upper waters. We believe these results can be used to predict how seasonal, temporal, and diurnal changes in a mysid's environment can influence mysid vertical distribution and, consequently, the degree of spatial overlap between mysids, their predators, and prey.

Our laboratory results were based on observations of mysid movements in 2-m tall vertical columns. We believe that the conditions in our experimental columns are comparable to the environmental conditions experienced by mysids in Lake Ontario. For example, upper column temperatures spanned the range of temperatures available to mysids during their migratory ascent in Lake Ontario. Mysids also began each temperature experiment in 4°C waters to mimic their daytime, benthic habitat. Therefore, the physiological status of the mysids should have been similar to field conditions. Given the relatively quick movement responses of mysids from the bottom of the column to the top (<1 min) and their random distribution in control columns soon after experimental commencement, we believe the 45-min observation period was sufficient to capture thermal response behaviors, even though mysids are exposed to pelagic conditions over much longer time periods (11–13 h in the field). The successful application of our experimentally derived model to field distributions is further evidence to suggest that the 45-min

observation period effectively captured the thermal preferences of *M. relicta*.

Since research on temperature preferences in fish suggests that final thermal preference and upper temperature thresholds increase with increasing acclimation temperatures (see review by Beitinger et al. 2000), we maintained room and, therefore, region 1 temperatures at 10°C for the temperature threshold and acclimation experiments and at 4°C in the temperature experiments. Our results indicate that thermal preferences and thresholds for temperature choices of 10°C and above are independent of acclimation temperatures of 4°C or 10°C for *M. relicta*.

Both the size and sex ratio of mysids used in the experiments mimicked those of adult field populations in the fall and summer of Lake Ontario. However, we did not test for potential size differences in temperature preference or in temperature–prey density or temperature–predator density interactions in these experiments because mysids smaller than 12 mm were difficult to see with the camera. We therefore only tested the responses of mysids >12 mm, and it is possible that juvenile mysids respond differently to the environmental factors manipulated in this study. For example, Beeton and Bowers (1982) and Rudstam et al. (1989) both reported that juvenile mysids move to shallower depths than adults and speculated that smaller mysids may venture higher into the water column to feed on zooplankton because they are at less risk of predation than larger mysids. However, we were able to accurately predict both the range and peak of mysid vertical distribution in Lake Ontario for both the fall and summer seasons, suggesting that either size differences were not playing a large role in the temperature preferences of mysids on the sampling nights we examined or the acoustic sampling of Gal (1999) did not accurately detect mysids <12 mm.

The estimated preferred temperature of 6.07°C for *M. relicta* in this study is several degrees lower than the reported optimal temperature for feeding (10–12°C, Chipps 1998; Rudstam et al. 1999). Our results therefore contradict the strong correlation between maximum feeding rates and final thermal preference observed in many species of fish (McCauley and Casselman 1980; Jobling 1981; Larsson 2005). In addition, zooplankton biomass is greater in the upper metalimnion and epilimnion than at the lower temperatures preferred by mysids (Boscarino unpubl. data; Gal et al. 2006); therefore, mysids do not appear to select for temperatures that would maximize feeding rates on zooplankton.

Our results also support the existence of an upper temperature threshold for *M. relicta*. Smith (1970) demonstrated >50% mortality for *M. relicta* in 16°C waters when acclimated to low temperatures and very low mortalities at temperatures lower than 10°C. Mysids avoid temperatures greater than 16°C, with reduced abundance in the field above 12–13°C (DeGraeve and Reynolds 1975; Rudstam et al. 1989; Gal et al. 2004). Our results are consistent with these upper threshold values for *M. relicta*. Mysids began to be deterred by temperatures of 12°C and above in the laboratory and showed strong avoidance responses to

temperatures greater than 16°C. In the absence of other variables, mysids were never found in temperatures of 16°C or higher and only ventured into 16°C waters when prey was present at these temperatures. Although mysids survive and feed at 18°C when held at that temperature for 4 h (Rudstam et al. 1999), they apparently will not voluntarily enter 18°C or higher temperatures, since mysids were never found in 18°C waters regardless of prey density.

Inclusion of our temperature preference function in the Gal et al. (2004) vertical distribution model resulted in significantly improved predictions of both the peak and range of depths inhabited by mysids during both the summer and fall seasons in Lake Ontario. In August, the Gal model I predicted a wider distribution and therefore lower peak abundance than observed, whereas the modified model reflected the observed distribution. Differences in percentage overlap with observed distributions were even more dramatic in the fall (percentage overlap improved from 25% to 77%) when the Gal model I predicted mysids to be 42 m higher in the water column than observed. Thus, our modified temperature preference function represents a significant improvement over the feeding rate based curve of Gal et al. (2004). Clearly, maximum feeding rate is not a good predictor of temperature preference for mysids.

Contrary to Beeton's (1960) hypothesis that mysid migration is limited by temperature changes greater than 1.2°C m<sup>-1</sup>, we did not find that the rate of temperature change alone limits mysid movements. Results from the temperature and temperature threshold and acclimation experiments demonstrate that mysids move easily through temperature gradients much sharper than the 1.2°C m<sup>-1</sup> hypothesized by Beeton (1960) to limit movements. The ability of our modified model to predict field distributions without a temperature gradient function is further support that temperature gradients do not directly modify mysid movements.

Our laboratory experiments and comparisons with field distributions indicate that mysid temperature preferences peak at lower temperatures than previously reported and that mysids occupy a range of temperatures that are suboptimal for consumption of zooplankton. A preference to this lower temperature could be an adaptation to optimize growth rates under restricted rations (Crowder and Magnuson 1983; Despatie et al. 2001) or an adaptation to reducing risk of predation by fish that are often more abundant in the warmer epilimnion (Gal et al. 2004), or some combination of both.

Optimum growth temperature for mysids in Lake Ontario is several degrees lower than the temperature that maximizes consumption rate. Although juvenile *M. relicta* grew faster at 8°C than at 4°C when fed zooplankton ad libitum (Berrill and Lasenby 1983), growth estimates are sensitive to changes in feeding rates. For example, Gorokhova (2002) demonstrated that *Mysis mixta* fed limited rations of zooplankton grew better at 5°C than at 12°C, but those fed ad libitum rations grew better at 12°C. Mysids in Lake Ontario are most likely not feeding at the maximum rates observed under ad libitum conditions in the laboratory. Johannsson et al. (1994) calculated feeding rates of 50–80% of maximum rates (assuming a mean prey

energy density of 811 calories per gram wet weight) to cover the caloric demands of individual adult mysids in Lake Ontario based on a mysid bioenergetics model (Rudstam 1989). Given these feeding rates, this bioenergetics model would predict maximum growth for *M. relicta* to occur between 5°C and 6°C for both a 12-mm and a 15-mm mysid in Lake Ontario. This range of optimal growth temperatures is similar to the preferred temperature estimated in our experiments, suggesting that Lake Ontario mysids may be adapted to choose temperatures for maximizing growth rather than optimum temperatures for feeding.

An alternative explanation for low temperature preference is an adaptation to reducing predation risk. Mysids are large, lipid-rich prey with slow reproductive rates relative to other zooplankton and fish, and there should be a strong selection pressure to reduce predation mortality (Rudstam et al. 1998; Johannsson et al. 2003). Alewives, the most abundant predator on mysids in Lake Ontario, prefer temperatures above 10°C (Coutant 1977; Brandt et al. 1980) and are primarily found in the epilimnion during the summer and fall in Lake Ontario (Olson et al. 1988). A preference for temperatures between 6°C and 8°C would prevent mysids from moving into this high-risk environment.

Our results also indicate that mysids move deeper in the water column and away from their preferred temperatures as a response to alewife kairomones in the laboratory. Sensitivity to the presence of fish kairomones was expected given the prevalence of this response in other crustaceans (Neil 1990; Loose 1993; Ringelberg and Van Gool 1995) and given the reported anticannibalistic responses of juvenile and immature mysids to adult mysid kairomones (Quirt and Lasenby 2002). Very little work has been done on *M. relicta*'s ability to sense the presence of fish, and researchers have only investigated effects of fish exudates on mysid feeding rates (Hamrén and Hanssen 1999; Lindén et al. 2003). Our results are the first to indicate both that mysids can sense the kairomones of the alewife and that they will actively avoid these areas if kairomone concentrations are high enough and a predator kairomone-free refuge is available. Since the summer and fall thermal stratification regime of Lake Ontario prevents the mixing of hypolimnetic and epilimnetic waters, alewife kairomones should therefore be restricted primarily to epilimnetic waters. By restricting mysid migrations into the epilimnion, fish will also restrict the feeding rates of mysids both because feeding rates are lower at lower temperatures and because zooplankton densities in the metalimnion are lower below the thermocline (Rudstam et al. 1999; Gal et al. 2006).

Our results also indicate that final depth and thermal preferences can be modified if prey densities are sufficiently high in upper waters. We noted significantly shallower depth distributions for the 4°C:16°C trials when both a high and low prey density was introduced into the upper column and recorded multiple observations of mysids in 16°C waters when food was available. These results are in direct contrast to the temperature experiments in which no mysids were recorded in 16°C waters, suggesting that mysids are sensing the presence of prey in these waters and actively entering otherwise undesirable temperatures to

feed. Ability to move into warmer waters for short periods of time to feed on abundant epilimnetic or upper-metalimnetic zooplankton would be a clear advantage to mysids in the field.

It is important to note, however, that while we provide evidence to indicate that mysids will alter their depth distributions depending on relative prey and predator abundances, we were able to accurately predict mysid vertical distributions in both the summer and fall profiles without incorporating prey and predator density functions into our model. It may be that the responses to predator and prey densities cancelled each other on the nights we modeled these migration patterns and, therefore, may not have been necessary factors to consider in our predictions. Typically, the epilimnion has both higher prey and predator densities in Lake Ontario during stratified conditions. While we tested for the effects of temperature-prey density and temperature-predator kairomone interactions in the laboratory, we did not perform a prey-predator combination experiment, and we do not have detailed information on prey distribution for the field observations. To what degree our model can predict mysid distribution in lakes with other primary mysid predators is not known at this time. Future studies may help address these remaining questions. However, we believe that our model should be generally applicable to a deep-water ecosystem where the primary mysid predator and prey items are epilimnetic.

The development of our modified model of mysid vertical distribution has important implications for the spatial modeling of aquatic species. The vast majority of DVM literature has focused on the influence that exogenous factors such as light, temperature, and prey and predator densities have on the choice of optimal habitat, or vertical position of a migrating organism in the water column that would maximize individual fitness (Mason and Patrick 1993; Fiksen 1997). These studies are therefore limited to predictions concerning the "optimal" individual. Here, we demonstrate that preference functions for factors influencing vertical movement can be used to predict the entire vertical distribution of a migrating population (*see also* Rudstam and Magnuson 1985; Andersen and Nival 1991) and will therefore no longer be constrained to depth maxima predictions. This is important because many feeding interactions between fish and zooplankton occur at the edges of their respective distributions, when organisms make brief forays out of their thermal or light optima (Stuntz and Magnuson 1976). Fitness-maximization models alone cannot account for interactions occurring at the edges of a distribution. We believe that models similar to ours—models based on field and laboratory-derived preferences to exogenous factors—could be similarly derived for a wide variety of migrating organisms.

This study is also novel in that it highlights the importance of temperature, not just light and chemical cues, as a main proximate factor influencing vertical distribution of an invertebrate. While temperature is typically mentioned as an important modifier of zooplankton migratory behavior, few studies have investigated how

temperature changes along a thermal gradient can interact with light and chemical cues to influence zooplankton's entire vertical distribution. For example, a review of temperature effects on zooplankton DVM (Moore et al. 1996) does not mention temperature preference as a main determinant of depth distribution but focuses more on feeding rate and growth as functions of temperature—both of which are apparently weak predictors of vertical distribution of mysids. The importance of temperature preference for fish habitat selection has been widely explored in the literature (Bulkley and Pimentel 1983; Despatie et al. 2001; see review by Beitinger et al. 2000), and temperature preference curves have been successfully used in predictive models of vertical distribution of fish (Rudstam and Magnuson 1985). We argue that temperature preference should be given more attention as a primary determinant of distribution in zooplankton as well.

We also believe our model can be used to predict distribution patterns of *M. relicta* across a variety of different temporal scales in Lake Ontario. For example, moon phase and cloud cover have repeatedly been shown to modify mysid position in the water column, with deeper distributions of mysids on full moon or clear nights versus new moon or cloudy nights (Teraguchi et al. 1975; Janssen and Brandt 1980), and this response should be predictable from our model. Computer programs that predict sun and moon illuminance are currently available (see Janiczek and DeYoung 1987), and our results indicate that mysid responses to variable cloud cover or moon phase could be modeled if temperature profiles are either known or estimated. Response functions for *M. relicta*'s primary prey and predators could be similarly derived and used to model how diurnal or seasonal changes in light or temperature can affect the degree of overlap between the different trophic levels.

These predator-prey overlap dynamics could also be modeled over a larger, ecosystem-wide or climactic scale. For example, warmer air temperatures due to global climate change may cause gradual warming and deepening of the epilimnion over time and lead to earlier spring breakup of thermal structure or later autumn freezing (Anderson et al. 1996; Magnuson et al. 2000), but very little is known about how zooplankton populations may respond to these changes. DeStasio et al. (1993, 1996) modeled the impact of climate change on the vertical movements of *Daphnia* spp. and predicted significant decreases in migration amplitude in all global warming scenarios for four different Wisconsin lakes, potentially altering the availability of this food resource to the planktivorous fish community. Models investigating the impacts of climate change on thermal niche have been similarly developed for a variety of fish (Magnuson et al. 1990; McDonald et al. 1996; Schindler et al. 2005). Therefore, the derivation of our mysid temperature preference curve represents an important step in determining how larger climactic changes may influence the distribution patterns and accessibility of food resources, like mysids, to the planktivorous fish community.

This paper extends previous efforts by Gal et al. (2004) to model the full extent of the vertical distribution of *M.*

*relicta* during stratified conditions in Lake Ontario and analyze the different environmental factors influencing the spatial and temporal overlap of mysids, their prey and predators. The improved ability of the model derived from our experimental results to predict independently collected field distributions suggests that the assumption of Gal et al. (2004) that mysid temperature preference is directly proportional to feeding rate is not valid. Predictions of vertical distribution require preference functions derived from behavioral observations, and we therefore argue that our modified model more accurately describes mysids' migratory responses to temperature in Lake Ontario. This study is the first to (1) describe a temperature preference curve for *M. relicta* based on behavioral observations independent of the field data used to test it, (2) show that rate of temperature change does not limit mysid movement, (3) show that mysid vertical movements are influenced by relative densities of fish kairomones and prey in upper waters, and (4) successfully model mysid vertical distribution in the field across different seasons based on experimentally derived temperature and light preferences.

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