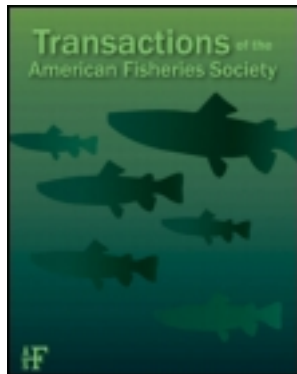


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ARTICLE

# Seasonally Dynamic Diel Vertical Migrations of *Mysis diluviana*, Coregonine Fishes, and Siscowet Lake Trout in the Pelagia of Western Lake Superior

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## Abstract

Diel vertical migrations are common among many aquatic species and are often associated with changing light levels. The underlying mechanisms are generally attributed to optimizing foraging efficiency or growth rates and avoiding predation risk ( $\mu$ ). The objectives of this study were to (1) assess seasonal and interannual changes in vertical migration patterns of three trophic levels in the Lake Superior pelagic food web and (2) examine the mechanisms underlying the observed variability by using models of foraging, growth, and  $\mu$ . Our results suggest that the opossum shrimp *Mysis diluviana*, kiyi *Coregonus kiyi*, and siscowet lake trout *Salvelinus namaycush* migrate concurrently during each season, but spring migrations are less extensive than summer and fall migrations. In comparison with *M. diluviana*, kiyis, and siscowets, the migrations by ciscoes *C. artedi* were not as deep in the water column during the day, regardless of season. Foraging potential and  $\mu$  probably drive the movement patterns of *M. diluviana*, while our modeling results indicate that movements by kiyis and ciscoes are related to foraging opportunity and growth potential and receive a lesser influence from  $\mu$ . The siscowet is an abundant apex predator in the pelagia of Lake Superior and probably undertakes vertical migrations in the water column to optimize foraging efficiency and growth. The concurrent vertical movement patterns of most species are likely to facilitate nutrient transport in this exceedingly oligotrophic ecosystem, and they demonstrate strong linkages between predators and prey. Fishery management strategies should use an ecosystem approach and should consider how altering the densities of long-lived top predators produces cascading effects on the nutrient cycling and energy flow in lower trophic levels.

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An understanding of how and why diel vertical migration (DVM) patterns are dynamic among species, seasons, and years is important for understanding within-lake processes, such as species interactions, energy transfer, and nutrient cycling (Iwasa 1982; Salonen et al. 1984). Diel vertical migrations occur in many aquatic ecosystems within most groups of organisms,

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including zooplankton (Worthington 1931; Gliwicz 1986), planktivores (Bohl 1980; Janssen and Brandt 1980), and piscivores (Weng and Block 2004; Hrabik et al. 2006). For most species, DVM patterns correspond to fluctuations in light levels (Appenzeller and Leggett 1995; Gal et al. 1999), while thermal gradients may influence the magnitude of many migrations (Gal et al. 2004; Boscarino et al. 2007). The mechanism underlying this migratory pattern is commonly attributed to optimization of foraging efficiency (Narver 1970; Levy 1990) or growth rates (McLaren 1963; Brett 1971; Wurtsbaugh and Neverman 1988) while avoiding predation risk ( $\mu$ ; Zaret and Suffern 1976; Lampert 1993). Consequently, seasonal and annual variation in the abiotic and biotic environments within lake ecosystems can cause differences in vertical migration patterns among species. These differences have a direct influence on predator–prey interactions, energy flow, and nutrient cycling rates, which can ultimately affect entire aquatic ecosystems (Iwasa 1982; Steinberg et al. 2002).

In Lake Superior, the pelagic food web is composed of species that are known to perform—and to be well adapted for—DVMs. The offshore pelagic community is dominated by the opossum shrimp *Mysis diluviana* (formerly *M. relicta*), kiyi *Coregonus kiyi*, cisco *Coregonus artedi*, and siscowet lake trout *Salvelinus namaycush* (hereafter, “siscowet”); the shortjaw cisco *Coregonus zenithicus*, bloater *Coregonus hoyi*, and rainbow smelt *Osmerus mordax* are also present but at relatively low densities (Bronte et al. 2003; Yule et al. 2009). Vertical migrations by mysids are known to occur in many systems (Dakin and Latache 1913; Beeton and Bowers 1982), including Lake Superior (Bowers 1988; Jensen et al. 2009). The DVM pattern exhibited by various coregonines has been documented in Lake Michigan (TeWinkel and Fleischer 1999) and Lake Superior (Hrabik et al. 2006; Yule et al. 2007). In addition, siscowets are known to migrate vertically in Lake Superior (Hrabik et al. 2006; Stockwell et al. 2010).

Although vertical movements have been documented for *M. diluviana*, kiyis, ciscoes, and siscowets, most DVM research has focused on coregonines in Lake Superior (Hrabik et al. 2006; Jensen et al. 2006; Stockwell et al. 2010). Hrabik et al. (2006) provided the first empirical documentation that coregonine fishes in Lake Superior migrate vertically, although species-specific DVM patterns were not examined. Jensen et al. (2006) used foraging, growth, and predation models to explore the mechanisms driving movements of coregonines; those authors concluded that the movements were related to growth potential and  $\mu$ , but the conclusions were based on limited field data and the study failed to incorporate a seasonal component. Stockwell et al. (2010) added detail by examining DVM patterns of kiyis and ciscoes separately; they found that kiyis have more extensive vertical movements than ciscoes. In addition, Stockwell et al. (2010) observed that spring migrations by kiyis were less pronounced than summer and fall migrations. It is clear that many of the important species in the Lake Superior pelagia migrate vertically, but the following remain unclear: (1) how mi-

grations change seasonally for each dominant species, (2) how those movements are interrelated in a food web context, and (3) the mechanisms driving those changes for each species across seasons.

Seasonal changes in temperature, light, prey availability, and predator distributions may alter DVM behavior for a particular species among seasons, thereby dictating how the trophic levels interact (Lampert 1993; Hays 2003). For example, *M. diluviana* migrate less extensively in spring than in other seasons and are found throughout the water column at night, probably because of isothermal conditions in the Great Lakes during that time period (Gal et al. 2004; Boscarino et al. 2009). For some fish species, such as juvenile kokanee *Oncorhynchus nerka* and walleye pollock *Theragra chalcogramma*, DVM patterns are influenced by seasonal changes in water temperature, light, and prey–predator densities and distributions (Hardiman et al. 2004; Adams et al. 2009). However, for the vendace *Coregonus albula* and Fontane cisco *Coregonus fontanae*, the DVM patterns do not change significantly by season (Mehner et al. 2007). Overall, seasonal changes in the physical and biological environment could modify DVM patterns for a particular species depending on the mechanisms driving those movements.

Models of foraging, growth, and  $\mu$  have been used to explore factors influencing movement patterns of many species (Wright and O’Brien 1984; Mason and Patrick 1993; Jensen et al. 2006). In general, foraging rate models predict where predators can maximize foraging opportunity based on prey densities, prey and predator swimming speeds, and predator reaction distances (Gerritsen and Strickler 1977). Growth rate models build upon the general foraging model framework by incorporating prey availability and water temperature to predict areas with the highest growth rate potential (GRP) for a given organism based on fundamental bioenergetic principles (Kitchell et al. 1977). Although foraging and growth models may provide explanations for the movements of top predators in aquatic ecosystems, they commonly fail to explain the movements of organisms at lower trophic levels, where  $\mu$  may be a driving factor (Iwasa 1982; Werner et al. 1983). Therefore, it is important to consider models that incorporate foraging opportunity, GRP, and  $\mu$  when trying to understand general movement patterns.

The purpose of this study was to quantify characteristics of DVM patterns among seasons and years for three trophic levels in the Lake Superior food web. Our first objective was to empirically characterize diel movement patterns of the three trophic levels simultaneously by using hydroacoustics (for fish) and an optical plankton counter (OPC; for zooplankton); both methods enable the collection of data at a fine temporal resolution. Our second objective was to explore the mechanisms driving movement patterns by using a modeling approach, which was similar to that of Jensen et al. (2006) and used various abiotic (i.e., temperature and light) and biotic (i.e., predator–prey diets, distributions, and densities) inputs. An understanding of how and why organisms migrate in Lake Superior is important because it will help to elucidate nutrient and energy flow pathways through

the system and to clarify predator–prey linkages, thus aiding in fishery management decisions. Based on previous studies, we hypothesized that all four dominant species would migrate during all seasons and that less-extensive migrations would occur during spring, when the lake is isothermic and prey resources are dispersed throughout the water column (Gal et al. 2004; Stockwell et al. 2010). Alternatively, we hypothesized that ciscoes would exhibit less-consistent migration patterns among seasons because of their larger size and lower  $\mu$ . In addition, we hypothesized that foraging or bioenergetic efficiency and  $\mu$  would drive the movement patterns of *M. diluviana* and kiyis, whereas  $\mu$  would have a lesser influence on movements by ciscoes because of their decreased vulnerability to predation (Jensen et al. 2006; Stockwell et al. 2010). Lastly, we hypothesized that siscowets would migrate concurrently with kiyis during all seasons and would also feed upon deepwater sculpin *Myoxocephalus thompsonii* in bottom areas to satisfy their energetic requirements as the top predator in the pelagia of Lake Superior.

## METHODS

**Study site and sampling regime.**—This study was conducted in the western arm of Lake Superior (Figure 1). A 50-km-long transect was sampled with hydroacoustics and an OPC from end to end continuously over the course of each research cruise. In addition, midwater and bottom trawls were periodically carried out (see next section). When the research vessel reached the end of the sampling transect, it traveled approximately 1 km at a right angle to the transect before heading back to the original starting point to limit sampling of the same organisms. Along the sampling transect, bottom depth ranged between 140 and 160 m. This location was selected because it represents a deep pelagic area that is typical of offshore Lake Superior. Based on midwater trawl sampling along the study transect from 2005 to 2008 (total  $n = 957$  fish), the fish community was composed of coregonines (kiyis: 70%; ciscoes: 24%; bloaters: 2%), siscowets (<1%), ninespine sticklebacks *Pungitius pungitius* (<1%), and rainbow smelt (3%). Analyses of diets and DVMs focused only on kiyis, ciscoes, and siscowets because bloaters, ninespine sticklebacks, and rainbow smelt were present at low densities. Research cruises were scheduled during the spring isothermal period (May), the summer stratified period (July), and the fall isothermal period (October). Sampling occurred during the summer in 2005–2006 and during spring, summer, and fall in 2007–2008. Because moon phase influences the movement patterns of fish (e.g., fish generally occupy greater depths during full moons than new moons; Luecke and Wurtsbaugh 1993; Yule et al. 2007), the research cruises were scheduled to occur near the new moon phase to minimize this source of variability. During each of the eight research cruises, continuous sampling occurred over the course of about 3 d, thus allowing changes in vertical migrations over multiple day–night cycles to be detected.

**Fish sampling and diets.**—Daytime bottom trawls and nighttime midwater trawls were used to determine the species composition of demersal and pelagic fish along the study transect. Bottom trawls were performed by use of a 3/4 Yankee bottom trawl (11.9-m headrope, 15.5-m footrope, and 2.2-m winglines) with a 13-mm-mesh liner in the cod end. Trawl wingspread data were recorded with a NETMIND net mensuration system (Northstar Technical, St. John's, Newfoundland and Labrador). Bottom trawls ( $n = 12$ ) were fished for 30 min at two locations near the study transect (Figure 1) during each season in 2007 and 2008. Nighttime midwater trawl tows were performed by use of a Gourcock box-type midwater trawl (20 × 20 m) with a 5-mm-mesh liner in the cod end. The midwater trawl was monitored with an Imagenex trawl mensuration system (Imagenex Technology, British Columbia) attached at the headrope; this system measured the trawl opening and depth. All midwater trawls ( $n = 8$ ) targeted the primary scattering layer observed with hydroacoustics and were fished between 20 and 60 m at a constant headrope depth for 0.5–1.0 h during summer in 2005–2006 and during spring, summer, and fall in 2007–2008. Fish that were captured in bottom and midwater trawls were sorted by species, enumerated, and measured for total length (nearest mm).

Length-frequency distributions were constructed for kiyis, ciscoes, and siscowets that were captured in midwater trawls and for kiyis and siscowets that were captured in bottom trawls. A length-frequency distribution was not constructed for ciscoes captured in bottom trawls because only one individual was caught. Similarly, in the eight midwater trawls, only one siscowet was captured. To get a better representation of the size distribution of fish captured in midwater trawls (particularly siscowets, but also kiyis and ciscoes), midwater trawl data collected from 2003 to 2009 in the western arm of Lake Superior were used along with the data that were collected directly along the study transect (91 total trawl tows). These ancillary trawls were performed by using the same midwater trawl and the same methods as described above for the trawls conducted along the sampling transect. Of the midwater trawls performed in the western arm of Lake Superior from 2003 to 2009, only those trawls with a maximum depth greater than 120 m were used; this was done to avoid variability in size distributions of fish found in other areas of the lake or near shore.

Diet analyses were performed on up to 50 individual kiyis, ciscoes, and siscowets collected from each research cruise along the study transect (daytime bottom trawls and nighttime midwater trawls). When analyzing an individual stomach, the contents were subsampled when necessary (i.e., when more than 100 individual prey items were present), identified to genus and species when possible, enumerated, and measured. Siscowet diet items were dried and weighed to determine their dry mass, and length–weight regressions used by the U.S. Environmental Protection Agency's Great Lakes National Program Office (2003) were applied to determine the taxonomic composition (percent dry

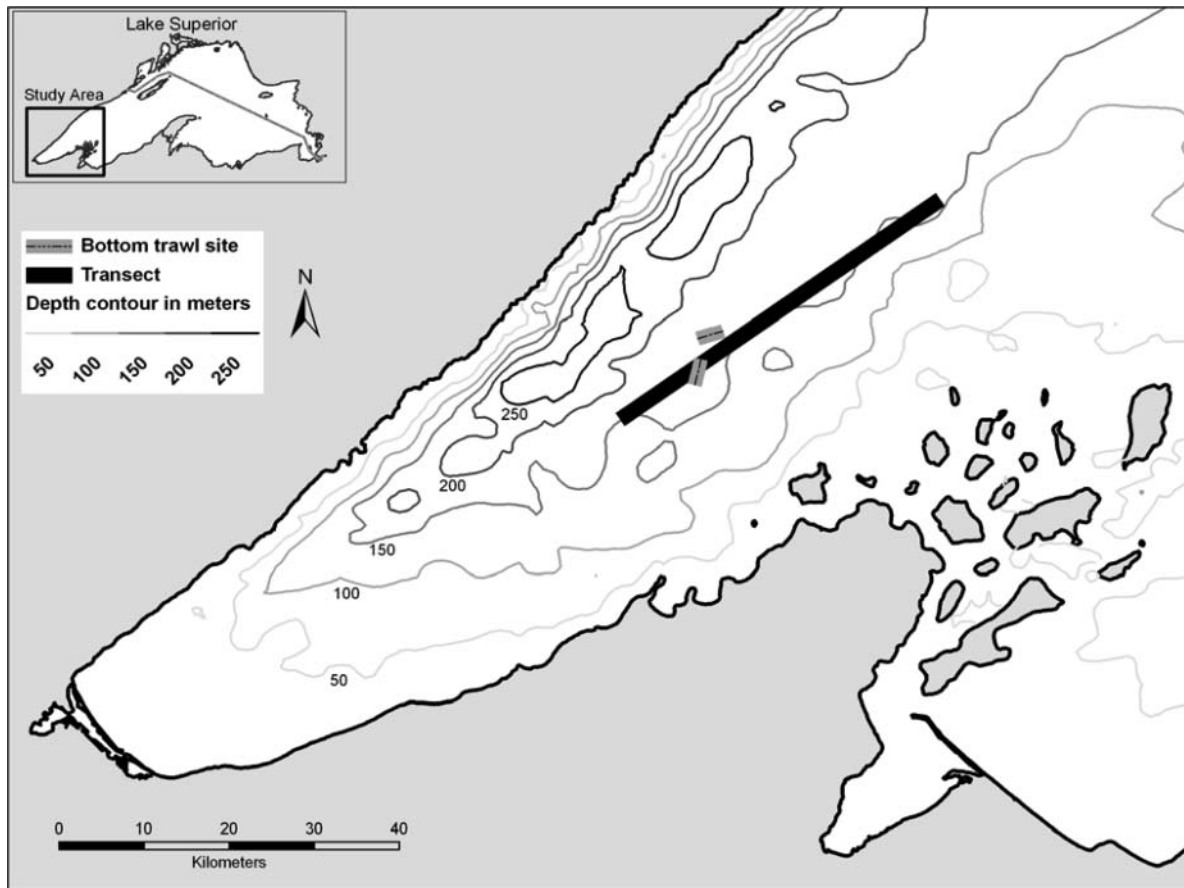


FIGURE 1. Survey transect in the western arm of Lake Superior, sampled seasonally from 2005 to 2008. The study transect was approximately 50 km long, and depths ranged from 140 to 160 m.

mass) of the diets consumed by kiyis and ciscoes during each season and year from 2005 to 2008.

*Zooplankton vertical migrations.*—To determine the extent of vertical migrations by zooplankton, an OPC (Focal Technologies, Dartmouth, Nova Scotia) was mounted on a Triaxus tow body (MacArtney Offshore, Houston, Texas). The OPC uses a rectangular light beam to size and count zooplankton as they pass through the aperture (Herman 1992). The Triaxus tow body is capable of maneuvering in a sinusoidal pattern from the bottom of the lake to the surface. It was towed at a speed of 2–3 m/s, which equates to one full water column profile being sampled about every 7 min (horizontal distance of ~1 km).

Because the OPC provides only the estimated sizes of objects, zooplankton net tow data were used to verify the size distribution and to identify the taxonomic composition of zooplankton in the water column. Zooplankton samples were gathered once during the day and night of each research cruise along the study transect. During the day and night, a 0.5-m-diameter, 250- $\mu$ m-mesh, conical plankton net was lowered to four different predetermined depths and was retrieved at a speed of 1 m/s. Three replicate samples were collected from each depth: 5 m off the bottom to the surface, 100 m to the surface, 50 m to the surface,

and 10 m to the surface. Samples were immediately preserved in 95% ethanol, and individuals were later identified, enumerated, and measured (by subsampling) to provide diel, seasonal, and annual size distribution data describing the zooplankton community.

Vertical distributions of large zooplankton taxa (e.g., spiny water flea *Bythotrephes longimanus*, *Daphnia* spp., and the calanoid copepod *Limnocalanus macrurus*) and *M. diluviana* were analyzed with the OPC and net tow data because these taxa were the primary prey resources consumed by ciscoes and kiyis, respectively. When the OPC collects data, it digitally records each organism's size, which is proportional to the peak cross-sectional area of the particle measured. The OPC software then converts the digital size to an equivalent spherical diameter (ESD) by use of an empirical equation (Herman 1992). However, most zooplankton are not spherical but instead tend to be elliptical in shape and have a major axis : minor axis ratio of approximately 1.33:1.00 (Sprules et al. 1998). For *M. diluviana*, this ratio is reportedly as high as 4.5:1.0 (Jensen et al. 2009). Therefore, large zooplankton taxa were considered to be 1.5–2.5 mm ESD (actual length of ~1.7–2.9 mm based on a ratio of 1.33:1.00), which encompasses the average size of zooplankton

taxa found in cisco diets (e.g., *B. longimanus*, *Daphnia* spp., and *L. macrurus*). Any particle that was over 2.5 mm ESD (actual length of ~5.3 mm based on a ratio of 4.5:1:0) was assumed to be an *M. diluviana* target because it is the largest zooplankton species present in Lake Superior. This cutoff was based on the net tow size distribution data and the findings reported by Sprules (1998, 2000).

The movement patterns of large zooplankton (1.5–2.5 mm ESD) and *M. diluviana*-sized targets (>2.5 mm ESD) were determined during the spring, summer, and fall of 2007–2008. Densities (individuals/m<sup>3</sup>) of the large zooplankton taxa were averaged for each research cruise based on the OPC data collected during the day and night in 5-m depth intervals from just below the surface to the bottom of the lake. Densities of *M. diluviana* at depth, as determined with the OPC, were averaged in 30-min × 5-m depth bins (up to the maximum depth) for a 24-h period. The DVM pattern for *M. diluviana* was then evaluated statistically with a smoothing spline as described below. For large zooplankton and *M. diluviana*, average densities were determined based on the assumption that DVM trajectories did not vary over the short time scale (3 d) and spatial extent of the survey.

*Coregonine and siscowet vertical migrations.*—During each research cruise, the day and night size distribution, depth distribution, and density of fish were estimated by using a DT-X hydroacoustic echosounder (BioSonics, Seattle, Washington) with a split-beam, 70-kHz transducer mounted on a BioSonics Biofin tow body. Hydroacoustic sampling, data collection, and calibration methods were analogous to the methods of Hrabik et al. (2006). During calibration, the measured target strength (TS) of the calibration sphere never varied significantly from its expected TS (i.e., measured TS was always within 1 dB of expected TS); therefore, no calibration offset values were applied to the data. Acoustic signals were collected with BioSonics Visual Acquisition Software version 4.1 and saved to a computer hard drive. Fish densities were estimated from the BioSonics file data by using Echoview version 4.0.73.6254 (Miriax, Hobart, Australia). Single-target detection parameters and methods described by Hrabik et al. (2006) were used for all data analyses. The data were analyzed in 30-min time intervals over 5-m depth bins from 2 m below the surface to the maximum depth for each segment.

To estimate size-based densities of pelagic fish, single targets were separated from the hydroacoustic data into three size-classes (small targets:  $-45 \text{ dB} < \text{TS} < -35.6 \text{ dB}$ ; medium targets:  $-35.6 \text{ dB} < \text{TS} < -32 \text{ dB}$ ; large targets:  $\text{TS} > -32 \text{ dB}$ ) similar to the classifications used by Hrabik et al. (2006), Yule et al. (2006), and Stockwell et al. (2010). Based on Love's (1977) equation, these TSs corresponded to lengths of 100–250 mm for small targets, 250–478 mm for medium targets, and over 478 mm for large targets. Although it is possible that some targets could have been assigned to the wrong size category if the fish were immature or significantly large, the midwater trawl data suggested that the majority of the small targets were kiyis (94%),

the majority of the medium targets were ciscoes (98%), and all of the large targets were siscowets (100%).

For each bin or cell, the volumetric fish density ( $P_{VS}$ ; fish/m<sup>3</sup>) of kiyi-, cisco-, and siscowet-sized targets was calculated with the following equation:

$$P_{VS} = \frac{P_S}{\sum \left[ P_S \times 10^{\left(\frac{TS_S}{10}\right)} \right]} \times S_V, \quad (1)$$

where  $P_S$  is the proportion of fish in size-class  $S$ ,  $TS_S$  is the mean TS for each size-class in each cell (calculated by using a single-target analysis), and  $s_V$  is the linear mean volume backscattering coefficient obtained for each cell from the echo integration file for the echogram. Once fish densities were calculated for each size-class in each cell for the 3-d research cruise, average fish densities over one 24-h period were calculated for each size-class in the same depth and time cells.

The hydroacoustic equipment is not capable of sampling organisms that are present on or near the bottom of the lake, but such information is valuable for describing DVM behavior (Stockwell et al. 2007, 2010). Bottom trawl information from the spring, summer, and fall of 2007–2008 was used to estimate bottom densities of kiyis, ciscoes, and siscowets. Only daytime bottom trawls were performed because nighttime densities of the study organisms on or near the bottom are known to be very low owing to vertical migration behavior (Stockwell et al. 2010). Density estimates for the bottom trawl tows were calculated for each species in each season and year based on the actual wingspread of the trawl and the time spent sampling the bottom as determined with the trawl mensuration system. Calculated densities were then extrapolated to the entire daytime period for each species and each research cruise and were used in vertical migration modeling.

*Statistical analysis of vertical migration patterns.*—To estimate variability in vertical distributions for each species over a 24-h period, a weighted, penalized cubic smoothing spline (i.e., generalized additive mixed model [GAMM]) was used with time as the predictor, densities as the weights, and depth as the response variable (Wood and Augustin 2002; Wood 2006). A cubic spline is a curve made up of sections of cubic polynomials that are joined together by knots so that they are continuous. The number and placement of knots control the smoothness of the model. Too many knots will cause the model to have too much sensitivity, while too few knots will cause the model to be too smooth to approximate the underlying pattern. By using a penalized model, a suitable number of knots based on the data was chosen via generalized cross validation (Wood and Augustin 2002). A GAMM with an autoregressive covariance structure was used (instead of simply a generalized additive model) to control for the effects of temporal autocorrelation present in the data. The statistical software package R version 2.11.1 was used to model the depth distribution data for each species during each research cruise (GAMM was conducted via the mgcv package

version 1.6–2 for R). A 95% pointwise confidence interval was then fitted to each modeled distribution to allow for an easier comparison of vertical migrations among species, seasons, and years. In addition, the coefficient of determination ( $R^2$ ) was calculated to describe the proportion of depth variability explained by each modeled distribution.

*Foraging, growth, and predation risk models.*—To better understand why species may migrate differently among seasons, several models for predicting the distribution of organisms were considered. First, a foraging rate potential (FRP) model was considered for kiyis and ciscoes by using the encounter rate model developed by Gerritsen and Strickler (1977) as applied by Mason and Patrick (1993) and Jensen et al. (2006):

$$\text{FRP} = \left( \frac{\pi R_{ij}^2}{3} \right) \left( \frac{3v_j^2 + v_i^2}{v_j} \right) d_i, \quad (2)$$

where  $R_{ij}$  is the reaction distance (m) of predator  $j$  (kiyi or cisco) to prey  $i$  (*M. diluviana* or other zooplankton);  $v_j$  and  $v_i$  are the swimming speeds (m/min) of predator and prey, respectively; and  $d_i$  is the prey density (individuals/m<sup>3</sup>).

Reaction distance was determined by using the  $R_{ij}$  model developed by Wright and O'Brien (1984) and modified by Jensen et al. (2006) for use with coregonine fishes:

$$R_{ij} = \frac{[1.44\beta(l - 0.2)]}{1,000}, \quad (3)$$

where  $l$  is the average length (mm) of prey (*M. diluviana* or zooplankton) and the  $\beta$  parameter is a function of light intensity at depth  $x$  ( $I_x$ ; lx) and turbidity ( $\tau$ ; nephelometric turbidity units):

$$\beta = 1.65[1.49 + 7.86 \times \arctan(\log_{10} I_x)] \left( 1 - \frac{\tau}{30} + 4.6 \right), \quad (4)$$

An  $R_{ij}$  value of 2 cm at a light level of 0 lx was used for coregonines (similar to the value used by Jensen et al. 2006) because coregonines are known to feed in the dark (TeWinkel and Fleischer 1999). To determine  $I_x$ , surface light intensity data from the National Solar Radiation Data Base (NSRDB 2005; measured at Duluth, Minnesota) were used for all seasons during 2005. Average irradiance (W/m<sup>2</sup>) was converted to visible light (lx) by means of a conversion factor (1 W/m<sup>2</sup> = 120 lx; Lampert and Sommer 1997). The  $I_x$  was then modeled by using the Beer–Lambert equation (Hutchinson 1957):

$$I_x = I_0 e^{-kx}, \quad (5)$$

where  $I_0$  is light intensity at the surface and  $k$  is the extinction coefficient (per m) as obtained from Koenings and Edmundson (1991).

Because the swimming speeds of kiyis and ciscoes are unknown, their swimming speeds were estimated with an allometric equation developed by Rudstam et al. (1994) for the bloater,

a closely related coregonine species in Lake Michigan:

$$v_j = 7.23W^{0.25}, \quad (6)$$

where  $v_j$  is the swimming speed (cm/s) and  $W$  is the average weight (g) of an individual organism. Zooplankton swimming speed was assumed to be negligible relative to planktivore swimming speed, and *M. diluviana* swimming speed was assumed to be 0.6 m/min, a value that has been used in similar modeling studies (Mason and Patrick 1993; Jensen et al. 2006) and is reasonable based on measured values (Ramcharan and Sprules 1986).

Prey density ( $d_i$ ) was determined for zooplankton and *M. diluviana* with the OPC as described previously. Prey inputs in the cisco models were the densities of large zooplankton (1.5–2.5 mm ESD) from all seasons in 2007–2008, corresponding to the size range of organisms found in cisco diets. For kiyi modeling, *M. diluviana* densities were calculated for each research cruise performed in 2007–2008 except spring 2007. Therefore, data from spring 2008 were used as the prey model input for 2007.

A GRP model was also evaluated in an attempt to understand factors influencing vertical migration patterns. Potential growth rates throughout the water column were predicted by incorporating basic bioenergetic constituents, such as temperature-dependent consumption, respiration, specific dynamic action, egestion, and excretion (Kitchell et al. 1977). The fundamental bioenergetic equations were from Hanson et al. (1997). Many of the model parameters were physiological constants that were acquired from the generalized coregonine model derived by Rudstam et al. (1994). Other model inputs were site specific, such as water temperature, preferred prey resources, and predator consumption rates. Water column temperatures were collected twice during each research cruise along the study transect with a bathythermograph (Model ABT-1; Alec Electronics, Kobe, Japan). Preferred prey items were determined by performing diet analyses as described previously. Lastly, consumption rates were estimated from the FRP model, in which all encounters with preferred prey species were assumed to have resulted in consumption up to a maximum consumption rate for each species (Jensen et al. 2006). The FRP and GRP model predictions for kiyis and ciscoes were estimated for spring, summer, and fall of 2007–2008 (day and night) in 5-m depth bins up to the maximum depth.

Predation risk ( $\mu$ ) was also incorporated into the FRP and GRP models because  $\mu$  is known to influence the movement patterns of organisms (Dill and Fraser 1984; Werner and Hall 1988). Predation risk to the planktivores (kiyis or ciscoes) was defined as the encounter rate with predators (siscowets), similar to the work of Mason and Patrick (1993). Therefore,  $\mu$  can be modeled with an equation that is analogous to equation (2) by substituting predator density ( $d_j$ ) for prey density ( $d_i$ ). Swimming speeds of kiyis and ciscoes were the same as calculated previously; siscowet reaction distance and swimming

speed were also calculated. Reaction distance for siscowets was determined with a function developed by Vogel and Beauchamp (1999) for  $I_x$  values less than or greater than the saturation intensity threshold of 17.83 lx as follows:

for  $I_x$  less than 17.83 lx,

$$R_{ij} = 26.84 + 2.81I_x - 6.09 \log_e(\tau) - 0.025 \log_e(\tau)I_x, \quad (7)$$

and for  $I_x$  of 17.83 lx or greater,

$$R_{ij} = 77.79 + 0.046I_x - 6.09 \log_e(\tau) - 0.025 \log_e(\tau)I_x. \quad (8)$$

Siscowet swimming speed (m/min) was calculated as a function of body weight and water temperature at depth (Stewart et al. 1983):

$$v_j = 11.7W^{0.05}e^{(0.0405T)}, \quad (9)$$

where  $W$  is weight (g) and  $T$  is temperature ( $^{\circ}\text{C}$ ).

Four models (FRP; ratio of FRP :  $\mu$  [FRP/ $\mu$ ]; GRP; and ratio of GRP :  $\mu$  [GRP/ $\mu$ ]) were considered in evaluating the factors influencing the movement patterns of kiyis and ciscoes. The parameter inputs for each model are outlined in Table 1. The performance of each model was evaluated by comparing the percent overlap between the observed and predicted depth distributions of each species based on Schoener's (1970) index. The calculated percent overlap values were then averaged (across time of day, season, and year) for each of the four models, and comparisons were made by using a Wilcoxon rank-sum test with a Bonferroni correction (i.e.,  $\alpha = 0.05/4 = 0.0125$ ) to determine whether any model performed significantly better than the others in predicting the depth distributions of kiyis and ciscoes.

## RESULTS

### Species and Length Frequency

Bottom trawls performed during the day along the study transect in the spring, summer, and fall of 2007–2008 captured 21,965 individual fish ( $n = 12$  trawls). Of those fish, deepwater sculpin were the most abundant (19,654 individuals), followed by kiyis (2,167 individuals) and siscowets (120 individuals). Other species captured at low densities included the bloater, burbot *Lota lota*, slimy sculpin *Cottus cognatus*, rainbow smelt, and spoonhead sculpin *Cottus ricei*. Midwater trawl tows along the study transect during the summer of 2005–2006 and spring, summer, and fall of 2007–2008 captured 957 individual fish ( $n = 8$  trawls). Kiyis were the most abundant species (670 individuals), followed by ciscoes (226 individuals). Other species included the bloater, ninespine stickleback, rainbow smelt, and siscowet.

Length-frequency distributions were constructed based on both bottom trawl and midwater trawl data for kiyis and sis-

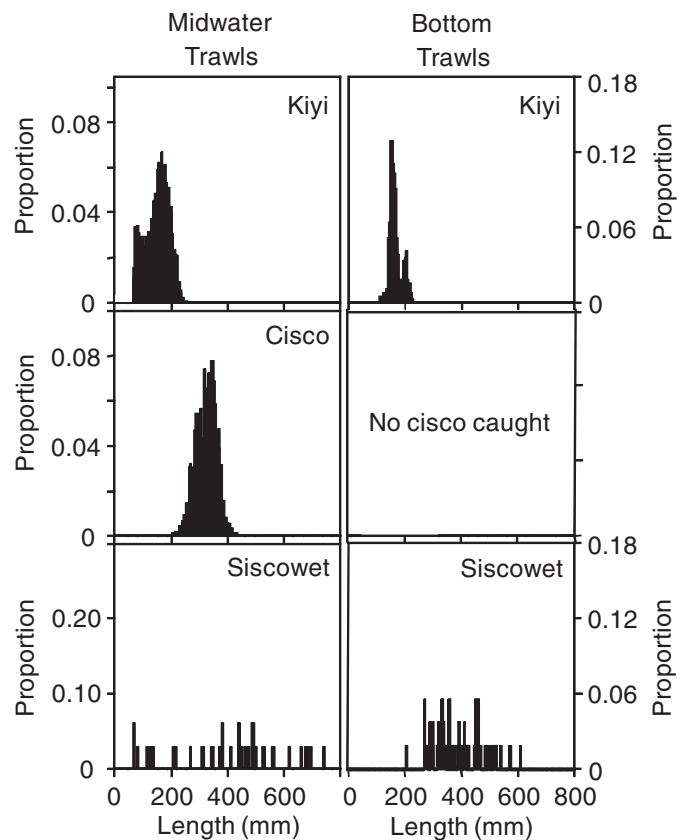


FIGURE 2. Length-frequency (mm total length) distributions for kiyis, ciscoes, and siscowet lake trout captured during all seasons in midwater trawls (2003–2009) and bottom trawls (2007–2008).

cowets and based on only midwater trawl data for ciscoes (i.e., because only one cisco was captured in bottom trawls; Figure 2). Kiyi sizes (total length) ranged between 111 and 229 mm (mean = 167 mm) in bottom trawls and between 61 and 275 mm (mean = 155 mm) in midwater trawls, and two distinct modes were observed for each distribution. Cisco sizes ranged between 203 and 451 mm (mean = 324 mm) in the midwater trawls, and there was only one noticeable mode. Siscowet length-frequency distributions, which were broader and exhibited no distinct modes, ranged between 209 and 610 mm (mean = 386 mm) in bottom trawls and between 70 and 740 mm (mean = 402 mm) in midwater trawls.

### Diet Composition

Kiyis that were captured in midwater and bottom trawls primarily consumed *M. diluviana* (~98% by mass) regardless of season and year ( $n = 656$  stomachs analyzed; Figure 3A). Cisco diets were more variable among seasons and years; ciscoes primarily consumed cladocerans, such as *B. longimanus* and *Daphnia* spp., as well as copepods ( $n = 253$  stomachs analyzed; Figure 3B). Other prey items found in cisco stomachs at less than 1% of the total biomass included *Bosmina* spp., chironomid larvae,



TABLE 1. Biological and physical parameters used in the foraging rate potential, growth rate potential, and predation risk models (NTU = nephelometric turbidity units).

Parameter	Symbol	Value or units	Source
Densities of prey <i>i</i> and predator <i>j</i>			
Zooplankton	$d_i$	individuals/m <sup>3</sup>	Measured
<i>Mysis diluviana</i>	$d_i$	individuals/m <sup>3</sup>	Measured
Siscowet	$d_j$	fish/m <sup>3</sup>	Measured
Depth	$x$	m	Measured
Extinction coefficient	$k$	0.15 per m	Koenings and Edmundson 1991
Foraging rate potential (encounter rate with prey)	FRP	individuals·m <sup>-3</sup> ·min <sup>-1</sup>	Gerritsen and Strickler 1977
Growth rate potential	GRP	g·g <sup>-1</sup> ·d <sup>-1</sup>	Hanson et al. 1997
Lengths			
Zooplankton	$l$	2.5 mm	Measured
<i>M. diluviana</i>	$l$	15 mm	Measured
Light level at depth $x$	$I_x$	lx	Hutchinson 1957
Light level at surface	$I_0$	0–5 × 10 <sup>-4</sup> lx	NSRDB 2005
Predation risk (encounter rate with predator)	$\mu$	individuals·m <sup>-3</sup> ·min <sup>-1</sup>	Gerritsen and Strickler 1977
Reaction distances			
Kiyi and cisco	$R_{ij}$	m	Wright and O'Brian 1984
Siscowet	$R_{ij}$	m	Vogel and Beauchamp 1999
Swimming speeds for prey <i>i</i> and predator <i>j</i>			
<i>M. diluviana</i>	$v_i$	0.6 m/min	Mason and Patrick 1993
Kiyi	$v_i$ or $v_j$	10.2 m/min	Rudstam et al. 1994
Cisco	$v_i$ or $v_j$	16.3 m/min	Rudstam et al. 1994
Siscowet	$v_j$	18–26 m/min	Stewart et al. 1983
Temperature	$T$	3–12°C	Measured
Turbidity	$\tau$	0.5 NTU	Koenings and Edmundson 1991
Weights			
Kiyi	$W$	30 g	Measured
Cisco	$W$	200 g	Measured
Siscowet	$W$	675 g	Jensen et al. 2006

*Daphnia* resting eggs, amphipods *Diporeia* spp., oligochaetes, ostracods, peaclams *Pisidium* spp., and terrestrial insects. Siscowet diets, which were used to determine their preferred prey resources, only varied slightly among seasons and years ( $n = 111$  stomachs analyzed; Figure 3C). Deepwater sculpin were the primary prey resource consumed by siscowets in terms of biomass, followed by coregonines and unknown fish. Other prey items consumed by siscowets included *M. diluviana*, terrestrial invertebrates, and parts of birds.

### Diel Vertical Migration Patterns of Three Trophic Levels

*Mysis diluviana*, kiyis, ciscoes, and siscowets all displayed DVMs during at least part of the year (Figure 4). Weighted, penalized regression spline fits that used density as weights and time as the predictor accounted for 17–98% of the variability in

the depth distribution of organisms (Table 2). *Mysis diluviana* showed vertical migrations from near the bottom (depths of ~140–160 m) during the day to shallower depths at night during all seasons. However, *M. diluviana* did not migrate as high into the water column at night during spring (depth ~60 m) in comparison with summer and fall (depth ~30 m). Kiyis underwent migrations that were similar in magnitude to those of *M. diluviana*, exhibiting a less-extensive upward migration at night during spring (up to a depth of ~60 m) than during summer and fall (depth ~40 m). Variations in DVM patterns were consistent among years for *M. diluviana* during summer and fall and for kiyis during the spring, summer, and fall. Cisco movement patterns varied between seasons and, to some extent, within seasons among years. During spring 2007, variable vertical movements were observed, and the majority of the cisco population migrated between a depth of 60 m at night and a depth of 100 m

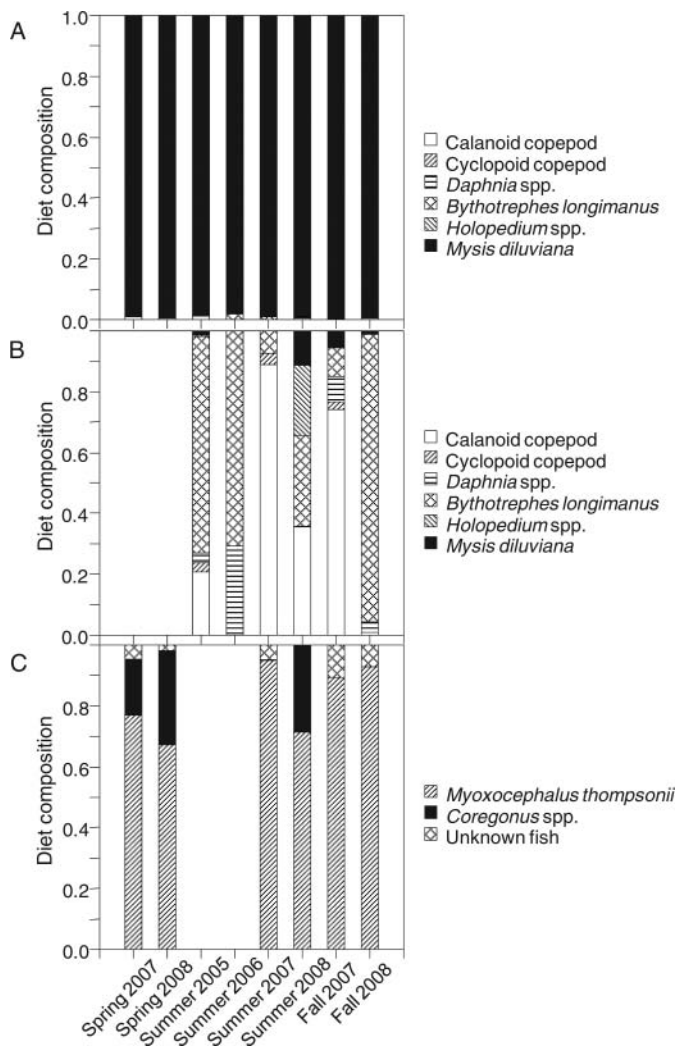


FIGURE 3. Taxonomic composition of the diet (proportion by mass) for (A) kiyis ( $n = 656$ ), (B) ciscoes ( $n = 253$ ), and (C) siscowet lake trout ( $n = 111$ ) captured in midwater and bottom trawls along the study transect during each season, 2005–2008 (*Myoxocephalus thompsonii* = deepwater sculpin). Diet items that were present at less than 1% of the total biomass are not included.

during the day. Diel differences in cisco distributions were negligible during spring 2008. During summer, ciscoes migrated from shallower depths at night (~30 m) to deeper areas during the day (~130 m), and some variation was evident among years. During fall of 2007 and 2008, ciscoes were found near a depth of 30 m during the day and night. Siscowets migrated vertically during all seasons. Spring migrations brought siscowets up to a depth of 45 m on average at night, whereas during summer and fall they were found at a depth of 30 m at night, which was consistent with the upper depths occupied by *M. diluviana* and kiyis during the nighttime.

## Empirical Estimates of Biological and Physical Modeling Parameters

Based on the results of the diet analyses, the density and distribution data for large zooplankton (1.5–2.5 mm ESD) as calculated with the OPC were used as the prey input for the cisco model (Figure 5). This size-class was selected because it encompassed the size range of zooplankton in cisco diets during each season and year (average zooplankton length in cisco diets = 2.18 mm; median length = 2.03 mm). Zooplankton densities calculated with the OPC and zooplankton net tows have been shown to be similar (Sprules et al. 1998). For kiyi prey inputs, seasonal *M. diluviana* density and distribution data (Figure 2) determined with the OPC were used. For *M. diluviana*, estimates of whole-water-column density from the OPC and zooplankton net tows were not significantly different during each season and year (two-tailed  $t$ -test: all  $P > 0.05$ ).

Light intensity at depth, which was used to calculate reaction distance, varied slightly among seasons; water temperature, which was used to calculate swimming speeds and growth potential, varied by season and, to a lesser extent, by year (Figure 6). Maximum depth of light penetration reached approximately 35 m in spring, 45 m in summer, and 30 m in fall. Most organisms began migrating downward in the morning as surface light levels began increasing past 5 lx. Upward migrations in the evening began just after sunset once the light levels were approaching 0 lx throughout the water column. During 2007–2008, water temperatures were isothermal in spring, were stratified in summer, and gradually decreased with depth during the fall. Spring temperatures were approximately 2.5°C throughout the water column in 2007–2008. The thermocline was found at 5 m during summer 2007 and was only slightly deeper (at 6 m) during summer 2008. Fall water temperatures varied from 9°C at the surface to about 3°C at 160 m during 2007–2008 but never changed by more than 1°C over a 1-m depth interval.

## Modeling Results

Kiyi movement patterns were best predicted with the FRP and the FRP/ $\mu$  models; the highest daytime FRP was predicted for depths between 125 and 175 m, and the highest nighttime FRP was predicted to occur between 15 and 50 m during all seasons and years (Figure 7). Percent overlap between the observed and predicted depth distributions of kiyis averaged 56.7% for the FRP model and 56.3% for the FRP/ $\mu$  model, and no significant difference was detected between the two models. The GRP and GRP/ $\mu$  models also had similar performance, as the calculated overlap percentages were 45.1% and 44.7%, respectively, and there was no detectable difference between models. Both of the FRP models performed better than the GRP models, but the results were not significantly different after Bonferroni correction ( $\alpha = 0.0125$ ; FRP versus GRP:  $P = 0.03$ ; FRP versus GRP/ $\mu$ :  $P = 0.02$ ; FRP/ $\mu$  versus GRP:  $P = 0.05$ ; FRP/ $\mu$  versus GRP/ $\mu$ :  $P = 0.04$ ).

TABLE 2. Weighted, penalized regression spline fits predicting the depths occupied by *Mysis diluviana*, kiyis, ciscoes, and siscowet lake trout based on time of day during spring, summer, and fall 2005–2008 ( $N$  = the number of 5-m  $\times$  30-min intervals for which data were available;  $df$  = model degrees of freedom;  $R^2$  = proportion of depth variability explained by the model).

Season	Year	<i>M. diluviana</i>			Kiyi			Cisco			Siscowet		
		$N$	$df$	$R^2$	$N$	$df$	$R^2$	$N$	$df$	$R^2$	$N$	$df$	$R^2$
Spring	2007				423	7.7	0.98	164	6.3	0.83	72	4.5	0.93
	2008	207	4.7	0.82	692	7.3	0.97	280	4.9	0.71	117	5.0	0.82
Summer	2005				825	7.6	0.94	365	6.9	0.80	111	3.5	0.64
	2006				527	7.5	0.92	202	4.9	0.68	138	4.0	0.59
	2007	230	6.3	0.89	583	7.6	0.98	206	5.6	0.51	165	6.8	0.87
Fall	2008	238	6.8	0.97	634	7.7	0.94	196	6.2	0.85	150	4.2	0.17
	2007	145	4.8	0.91	599	7.7	0.96	258	5.6	0.29	118	5.1	0.43
	2008	345	7.5	0.96	471	7.8	0.96	134	2.4	0.28	77	6.2	0.86

For ciscoes, movement patterns were best predicted by the FRP/ $\mu$  model (average overlap = 41.8%), and most of the predictions placed ciscoes between 5 and 50 m during the day and night (Figure 8). The overlap percentages for the FRP (31.7%),

GRP (38.2%), and GRP/ $\mu$  (37.9%) models were only slightly less than that calculated for the FRP/ $\mu$  model. No significant difference was observed among calculated overlap percentages for any of the cisco model predictions.

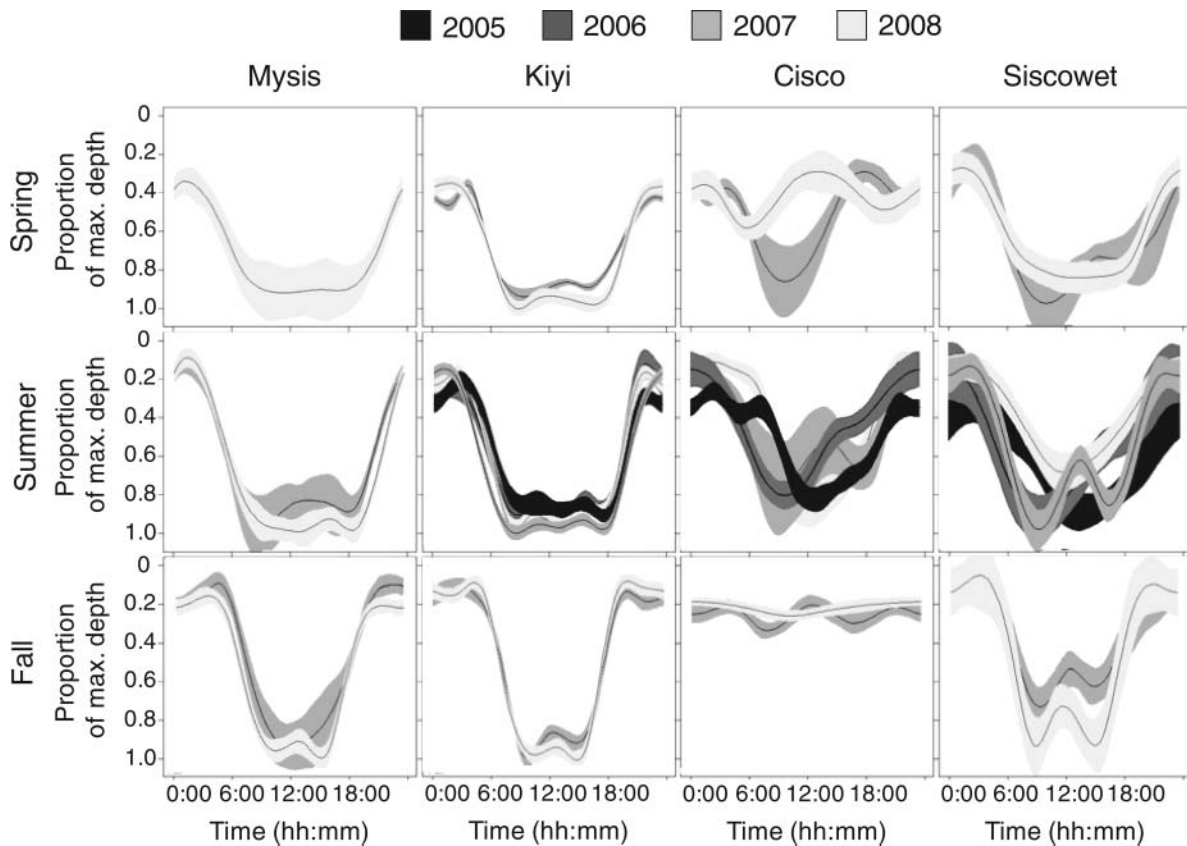


FIGURE 4. Weighted, penalized regression splines (generalized additive mixed model using mgcv; see Methods) modeling the diel vertical migration behavior of *Mysis diluviana*, kiyis, ciscoes, and siscowet lake trout with time as the predictor and depth as the response and weighted by density during spring, summer, and fall 2005–2008. Species are shown in columns, seasons are shown in rows, and different years are represented by different shades of gray. A 95% pointwise confidence interval band is presented for each species and year.

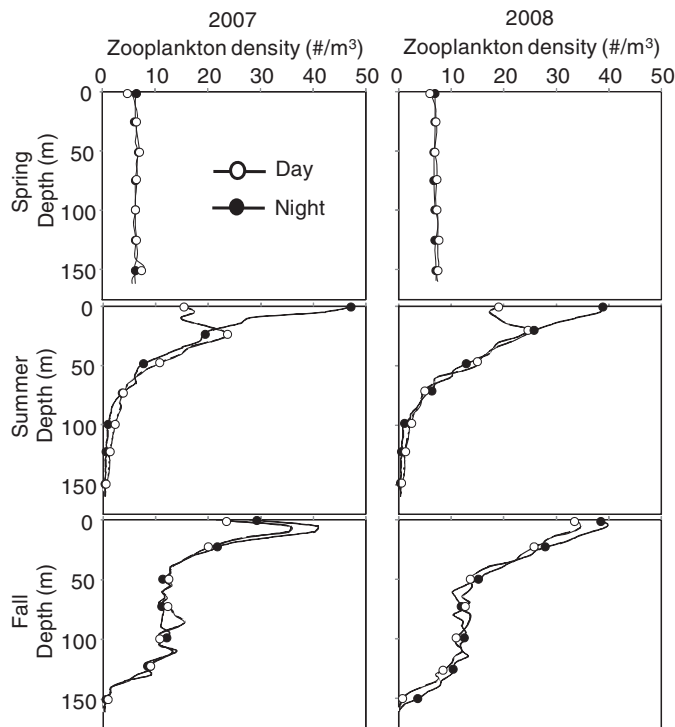


FIGURE 5. Zooplankton density (individuals/m<sup>3</sup>) estimates in 5-m depth bins for organisms between 1.5 and 2.5 mm equivalent spherical diameter as sampled by the optical plankton counter along the survey transect during the day and night in spring, summer, and fall 2007–2008.

## DISCUSSION

Vertical distributions of *M. diluviana* varied seasonally, as has been observed in other studies (Gal et al. 2004; Boscarino et al. 2007), and seem to be driven by the location of predators and prey. For example, in Lake Ontario the highest *M. diluviana* densities were deeper and broader at night during spring and fall (at a depth of ~50 m) compared with a shallower and more distinct *M. diluviana* layer (at ~10 m) in the summer (Gal et al. 2004). In our study, *M. diluviana* vertical migrations were deeper at night in the spring (depth ~60 m) than in summer and fall (depth ~30 m). The lower magnitude of migration in spring is probably attributable to the state of mixing and isothermic conditions in the lake, causing the prey of *M. diluviana* to disperse more evenly throughout the water column (Bowers 1988; Gal et al. 2004). Spring diatom blooms and the subsequent death and sinking of the diatoms may also provide a source of prey for *M. diluviana* such that they do not need to migrate as extensively (Conley and Scavia 1991). Johannsson et al. (2001) found that diatoms represented 50% of the diet for *M. diluviana* during May in Lake Ontario, and this percentage was much higher than observed in other seasons. During summer and fall, *M. diluviana* migrations were more extensive and at night extended to shallower depths, where the highest phytoplankton and zooplankton resources were located (Yurista et al. 2009; present study). The movement patterns of *M. diluviana* are probably driven by their

prey as well as by  $\mu$ , although we were unable to quantitatively test this with modeling because *M. diluviana* are omnivorous (Johannsson et al. 2001) and have many potential predators (A. Gamble, University of Minnesota–Duluth, unpublished data). Our findings are consistent with those of Gal et al. (2004) and Boscarino et al. (2007), who concluded that *M. diluviana* migrate to maximize feeding rates and to minimize  $\mu$ . Foraging opportunity alone cannot explain the movements of *M. diluviana* in Lake Superior because most plankton resources are located in the upper 30 m of the water column during periods of thermal stratification (Bowers 1988). In addition, Bowers (1988) noted that *M. diluviana* rarely migrated above 50 m at night. Our results show that *M. diluviana* migrate to a depth of approximately 20 m at night during summer and fall, indicating that the present migration pattern of *M. diluviana* in Lake Superior differs from the pattern observed in the 1980s. The observed differences in the magnitude of migration between the two time periods could be attributed to different sampling techniques (staged net tows versus OPC, respectively) or to changes in  $\mu$ , food availability, or other factors. In the study by Bowers (1988) and the present study, most of the *M. diluviana* migrated to areas near the bottom instead of simply to a safe depth where  $\mu$  was low; this probably occurred because the bottom affords greater foraging opportunities (e.g., detritus) than a deep pelagic layer (Scavia and Fahnenstiel 1987). However, not all *M. diluviana* migrate to the bottom, as increased  $\mu$  from deepwater sculpin or increased energetic costs may discourage *M. diluviana* from undertaking deep migrations (McLaren 1963). Overall, *M. diluviana* movements appear to be consistent with risk-sensitive foraging (McNamara and Houston 1992) that exemplifies a tradeoff between foraging and  $\mu$ .

Kiyi vertical migrations closely followed the *M. diluviana* migrations while simultaneously avoiding areas of highest  $\mu$  throughout the year. This pattern suggests the importance of both prey and predators in driving the movements of kiyis. Consistent with findings reported by Stockwell et al. (2010), kiyis migrated less extensively in spring than in summer and fall. Our empirical and modeling results suggest that *M. diluviana* are important in driving the movements of kiyis in Lake Superior. This finding is important when considering nutrient transport and energy flow between trophic levels and habitats (e.g., benthic and pelagic). Although foraging and growth were important in predicting kiyi movements, it was more difficult to assess the influence of  $\mu$  because kiyi distributions followed the distributions of their *M. diluviana* prey, which coincided directly with the areas of lowest  $\mu$  from siscowets. As a result, incorporating  $\mu$  into the models (i.e., FRP/ $\mu$  and GRP/ $\mu$  models) did not significantly improve predictions of kiyi vertical movement patterns. Because  $\mu$  was confounded with prey, it was difficult to determine the complete influence of  $\mu$  on kiyi movements. We believe that  $\mu$  from siscowets does influence kiyi distributions, but we were unable to assess the importance of predation relative to foraging. Thus, a model that includes a  $\mu$  component and an FRP component would probably be more accurate if predator risk and foraging

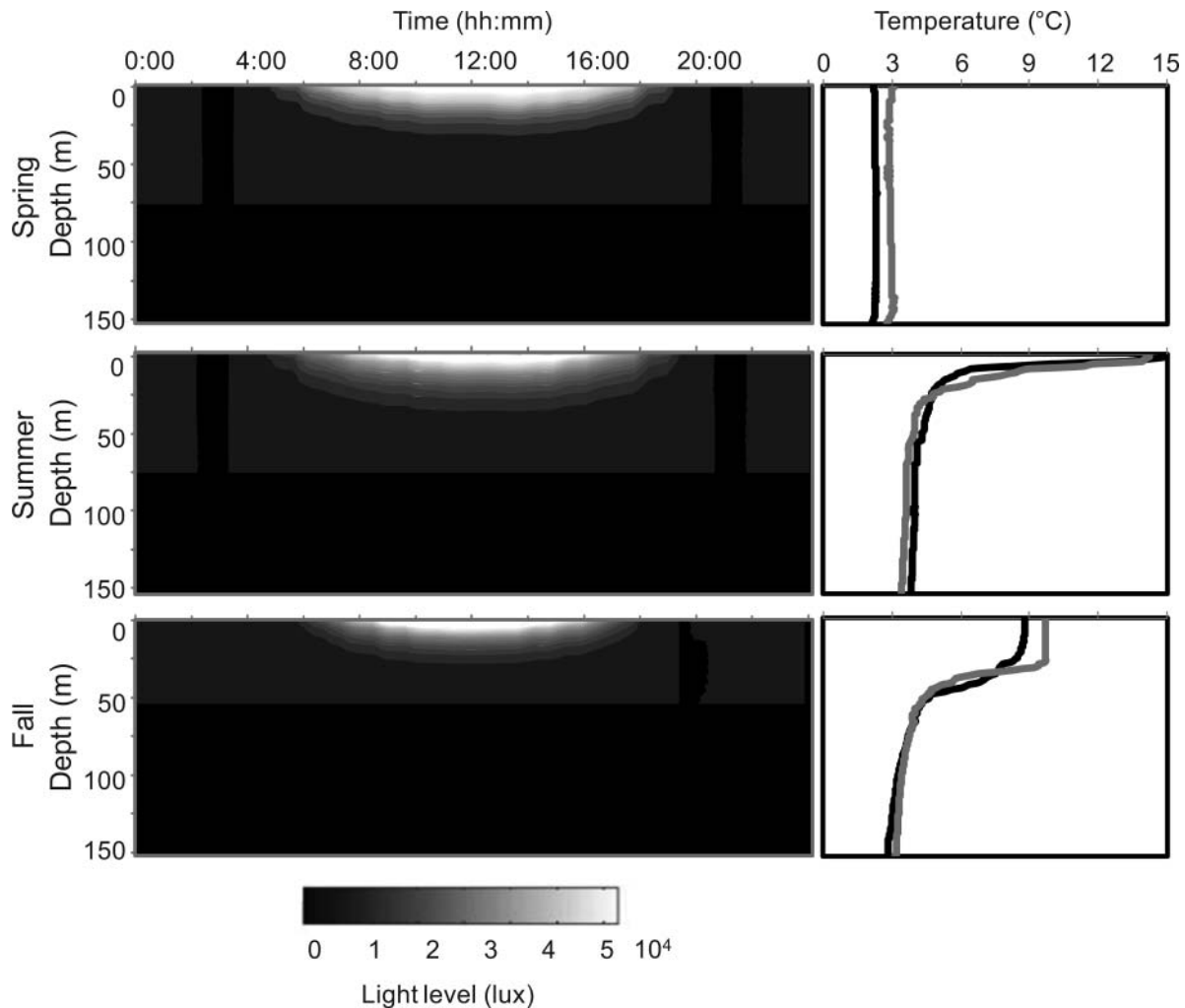


FIGURE 6. Seasonal light levels (lx) and water temperature ( $^{\circ}\text{C}$ ) by depth along the survey transect. Light levels were based on surface light intensity data recorded in 2005 at Duluth, Minnesota (NSRBD 2005). Water temperatures were collected during each season in 2007 (black line) and 2008 (gray line).

opportunities were decoupled. Future changes to the food web of Lake Superior may provide additional information that could help assess the overall importance of  $\mu$  to kiyis.

Comparison of multiple competing models is often useful for identifying important mechanisms that underlie the observed dynamics. However, we could not determine whether FRP or GRP models were more effective at predicting the distribution of kiyis. The FRP models were better than the GRP models for describing the movements of kiyis, but the differences were not significant. Given the minimal temperature gradient ( $\sim 2^{\circ}\text{C}$ ) experienced by kiyis during vertical movements and the fact that the primary data input difference between the models was temperature, it is not surprising that the models predicted similar distribution patterns. Our results were similar to those from studies of movements by alewives *Alosa pseudoharengus* and bloaters in Lake Michigan, where the locations of potential prey items (e.g., *M. diluviana*, *Daphnia* spp., and *Diporeia* spp.) were identified as the mechanism driving the observed move-

ment patterns (Janssen and Brandt 1980; TeWinkel and Fleischer 1999).

Ciscoes are large-bodied coregonine fish with a diverse diet, and they are less susceptible than kiyis to predation by siscowets (Stockwell et al. 2010). However, cisco vertical migrations were driven by the location of prey resources and, to a lesser extent, by predation pressure. Although the migration pattern of ciscoes was less pronounced than that of kiyis, the response of ciscoes to each source of variability resulted in shallower migrations during the day in comparison with *M. diluviana* and kiyis, regardless of season. The FRP/ $\mu$  model appeared to be the best for predicting the distribution of ciscoes. However, the results of the model could not be differentiated statistically from the performance of the FRP, GRP, and GRP/ $\mu$  models. It is possible that foraging, growth, and  $\mu$  all play a role in determining cisco movements or that some other factors are also important. Previous research by Stockwell et al. (2010) suggests that predation pressure on adult ciscoes is low in offshore areas of Lake

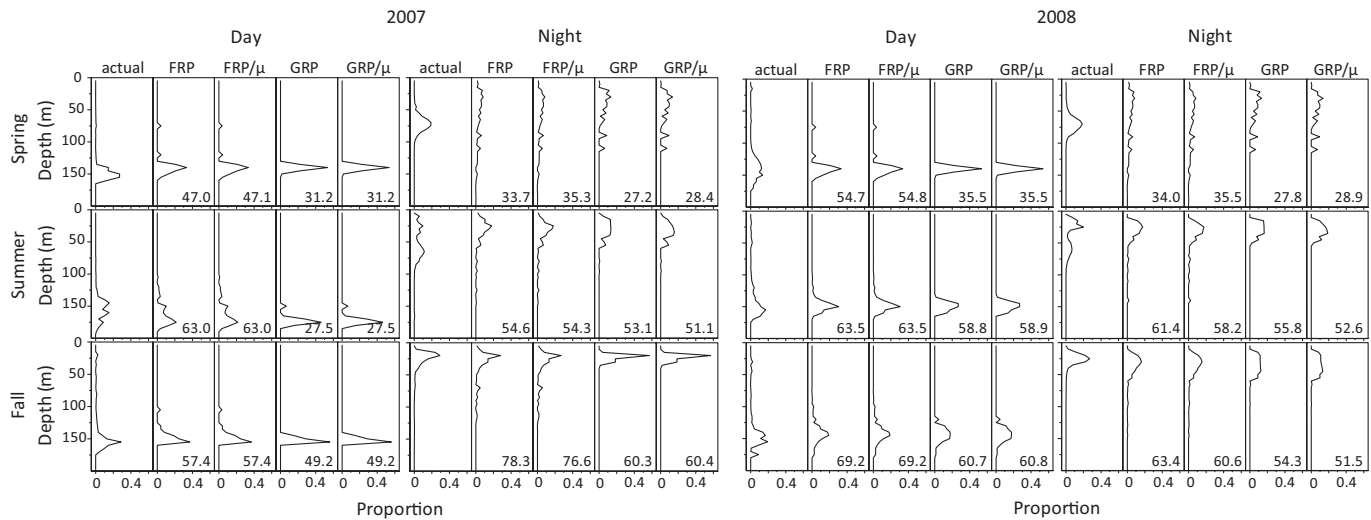


FIGURE 7. Observed (actual) and predicted depth distributions for kiyis during day and night in spring, summer, and fall 2007–2008. Predictions are from four models: foraging rate potential (FRP) model; ratio of FRP to predation risk ( $\mu$ ; FRP/ $\mu$ ); growth rate potential (GRP) model; and ratio of GRP :  $\mu$  (GRP/ $\mu$ ). The value in the lower right corner of each box is the percentage of overlap between the modeled distribution and the observed distribution.

Superior and may have little effect on DVM patterns, primarily because ciscoes have relatively large body sizes. Based on the large size of ciscoes relative to siscowets and the diet information gathered here and in other studies (Harvey et al. 2003; Negus et al. 2008), the vulnerability of large ciscoes to predation by siscowets is probably low. However, it is difficult to completely discount  $\mu$  because predation does occur on smaller ciscoes and there may be a perceived  $\mu$  from the largest siscowet (>600 mm) predators. There also may be some lasting effect of dealing with  $\mu$  from lake trout (i.e., the lean morphotype) in nearshore areas, where juvenile ciscoes spend most of their time (Stockwell et al.

2010). Ciscoes were regularly found in deep water below the areas of highest FRP during the day, indicating that they avoid areas of high light, where search volumes for large siscowets would be high. Even very low predator density or a perceived  $\mu$  is capable of influencing habitat use by prey species in other systems (Werner et al. 1983; He et al. 1993). A drastic reduction of siscowet densities would yield insight into the overall influences of  $\mu$  on cisco movements (Hrabik et al. 2006). Studies of cisco DVM patterns in years with very different siscowet densities would allow a more thorough understanding of the role of predation.

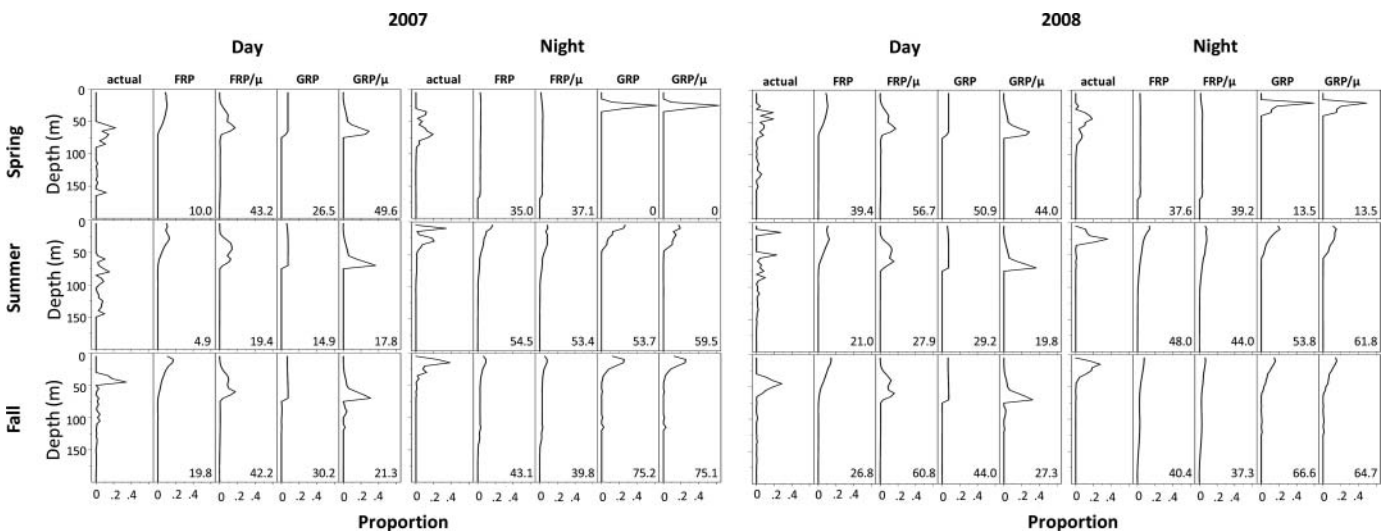


FIGURE 8. Observed (actual) and predicted depth distributions for ciscoes during day and night in spring, summer, and fall 2007–2008. Predictions are from four models: foraging rate potential (FRP) model; ratio of FRP to predation risk ( $\mu$ ; FRP/ $\mu$ ); growth rate potential (GRP) model; and ratio of GRP :  $\mu$  (GRP/ $\mu$ ). The value in the lower right corner of each box is the percentage of overlap between the modeled distribution and the observed distribution.

Coregonine DVM patterns were thought to be driven by  $\mu$  and *M. diluviana* prey resources during the summer (Jensen et al. 2006); however, we now know that the DVM patterns for kiyis and ciscoes are driven by predators and by the location of *M. diluviana* or zooplankton prey, respectively, throughout the spring, summer, and fall. Specifically, our study is unique in comparison with other studies because we separated coregonines by species, considered data from multiple seasons and years, and collected concurrent *M. diluviana* and plankton information. Jensen et al. (2006) concluded that coregonines migrate to minimize the ratio of  $\mu$  to growth, and this conclusion cannot be refuted by our results. Jensen et al. (2006) observed two migration trajectories that minimized the risk-to-growth ratio when *M. diluviana* were used as the prey input for their modeling exercises. One trajectory was relatively shallow, starting just below the thermocline (depth  $\sim$ 25 m) at night and following low light levels down to a depth of about 80 m during the day. The other was a deep trajectory from just below the thermocline at night to near the bottom of the lake (depth  $>$  150 m) during the day, and this trajectory tracked the highest *M. diluviana* densities. Because we never observed *M. diluviana* higher in the water column during the day, our modeling results never predicted the shallow, high-risk, high-growth trajectory when we used the measured *M. diluviana* densities as the prey input. Jensen et al. (2006) suggested that the presence of low *M. diluviana* densities just below the thermocline during the day could lead to this result. However, the low densities of *M. diluviana* used in modeling by Jensen et al. (2006) were from only a few samples collected in 1986 (Bowers 1988). Ciscoes were predicted to follow—and generally did follow—the shallow, high-risk, high-growth trajectory when large zooplankton (1.5–2.5 mm ESD) were used as the prey input for modeling. The two migration trajectories predicted by Jensen et al. (2006) were consistent with our findings; the differences between studies were probably attributable to the fact that we separated the distributions for kiyis and ciscoes and considered them independently, as was done by Stockwell et al. (2010). However, unlike Stockwell et al. (2010), we incorporated direct measures of the preferred prey of ciscoes and kiyis and measured the distribution patterns over an entire 24-h cycle.

Previous findings have indicated a possible change in the participation of siscowets in vertical migration behavior in recent years. Hrabik et al. (2006) and Jensen et al. (2006) observed the shallow, high-risk, high-growth trajectory for coregonines in 2001 and the deeper, low-risk, low-growth trajectory in 2004. This change in coregonine migration trajectories among years was attributed to a higher density of siscowets participating in DVM during 2004, thus increasing  $\mu$  and causing coregonines to migrate to greater depths. Conversely, Stockwell et al. (2010) found no relationship between coregonine migration amplitude and siscowet densities. Our results were consistent with those of Stockwell et al. (2010) in that we could not identify a relationship between the migration patterns of kiyis or ciscoes

and siscowet densities. However, this was probably because the densities and vertical movements of siscowets did not vary significantly along our study transect across years.

Siscowets feed substantially on benthic and pelagic prey (Dryer et al. 1965; Ray et al. 2007) and have extensive vertical migrations (Hrabik et al. 2006; Stockwell et al. 2010). Now we understand that this migration pattern is relatively consistent between seasons and years and is probably driven by prey resources. It is likely that siscowets feed on coregonines higher in the water column at night and on coregonines and sculpins near the bottom during the day (Conner et al. 1993). Although coregonines were found at lower proportions in siscowet diets than were sculpins, the greater nutritional value of coregonines (ciscoes: 6,922 J/g; bloaters: 9,879 J/g) relative to sculpins (5,421 J/g) makes them a valuable prey resource (Rottiers and Tucker 1982; Vondracek et al. 1996). Siscowet migrations to the bottom of the lake during the day are intriguing because the modeled search volume for siscowets could be as much as 500 times greater in the upper water column (27.0 m<sup>3</sup>/min) than at the bottom (0.056 m<sup>3</sup>/min). However, the lack of prey observed near the thermocline during the day probably drives siscowets to migrate to the bottom, where densities of sculpins and kiyis are considerably higher. Because the siscowet capture efficiencies for different prey types on the bottom probably vary due to differences in habitat use and predator avoidance, FRP and GRP models were not used for siscowets (Breck 1993; Mason and Brandt 1996). It is unlikely that capture rates would have been accurately described by the encounter rate model we used. Further research investigating the siscowet capture efficiencies for different prey items would help to better understand the factors underlying siscowet DVM patterns.

A variety of factors, including light, prey distributions, temperature–energetic maximization, and predation, are probably important determinants of species distributions under certain conditions (e.g., Magnuson et al. 1979; Mason and Patrick 1993). In Lake Superior, the upper extent of vertical migrations seems to be limited by temperature. *Mysis diluviana*, kiyis, ciscoes, and siscowets all remained below the thermocline during evening ascents and occupied approximately 5°C water at night. Other studies have reported that *M. diluviana* avoid strong thermal gradients, generally prefer water temperatures between 6°C and 8°C, and rarely move into waters that exceed 15°C (Mauchline 1980; Rudstam et al. 1999; Boscarino et al. 2007). Pelagic fishes in Lake Superior prefer cold temperatures as well and generally avoid waters warmer than 10–12°C (Wismer and Christie 1987; Negus 1995; Yule et al. 2007). Vertical migration patterns were also closely related to changing light levels over the day–night cycle in our study and other studies (Gal et al. 1999; Van Gool and Ringelberg 2003). In addition, light was clearly a factor dictating the timing of upward and downward migrations. Although it was difficult to determine the exact light levels that were preferred or avoided by the organisms in our study, previous studies have reported that *M. diluviana* prefer light levels



not exceeding  $10^{-2}$  to  $10^{-4}$  lx (Teraguchi et al. 1975; Moen and Langeland 1989). Coregonines generally remain at light levels below  $10^{-3}$  lx (Yule et al. 2007), and their reaction distances decrease significantly at levels below  $10^{-2}$  lx (Link and Edsall 1996; Vogel and Beauchamp 1999). Overall, our results and past studies indicate that daily and seasonal changes in temperature and light are important factors in modifying vertical migrations of organisms but are not the primary mechanisms driving DVM behavior in Lake Superior, where  $\mu$  and the distribution of food resources seem to be more important. Diel vertical migration behavior also may be influenced by maximum lake depth, horizontal movement patterns, spatial structure and patchiness of zooplankton, or age structures of fish populations, but these factors are not known to drive vertical migrations and therefore were not analyzed here.

In summary, *M. diluviana*, kiyis, and siscowets all underwent vertical migrations during the seasons studied. Ciscoes did not migrate considerably during spring or fall but did exhibit DVM in summer. These seasonal changes in vertical migration patterns among species appear to be related to temperature and light, the location of preferred prey resources, and potential predation pressure for the lower trophic levels (i.e., *M. diluviana*, kiyis, and ciscoes). Overall, our results are unique in that they provide a clearer picture of the seasonal and annual DVM patterns exhibited by three trophic levels of organisms. Our findings highlight the importance of *M. diluviana* in driving the distribution of kiyis. However, under the current food web configuration, we are unable to determine the overall influence of  $\mu$  from siscowets on the migratory prey species. Nonetheless, the close association of vertical movement patterns among pelagic organisms emphasizes the importance of ecosystem-based fishery management in Lake Superior. Small population changes in upper trophic levels, such as through increased harvest, could have significant population effects on lower trophic levels in the food web. Recent findings suggest that vertically moving organisms, including *L. macrurus*, *M. diluviana*, kiyis, and siscowets, regenerate and translocate a significant amount of nutrients relative to that available to the deep chlorophyll maximum just below the thermocline (S. Mueller and T. Hrabik, University of Minnesota–Duluth, unpublished data). Alterations of fishing regulations that decrease the densities of predatory siscowets in open-water areas would probably have a cascading effect, increasing the density of kiyis and other planktivores in the pelagia and reducing the net flux of nutrients via *M. diluviana* and other zooplankton, which represent the bulk of the transport. Effective ecosystem-scale management should consider the overall ramifications of increasing fishing effort for long-lived pelagic predators, such as siscowets, on nutrient regeneration and energy flow throughout the lower trophic levels. The majority of the species belonging to the pelagic food web in Lake Superior perform vertical migrations, suggesting a need for research to track nutrient cycling between benthic and pelagic habitats and to determine the role that migrations play in energy flow throughout the aquatic food web.

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## REFERENCES

- Adams, C. F., R. J. Foy, J. J. Kelley, and K. O. Coyle. 2009. Seasonal changes in the diel vertical migration of walleye pollock (*Theragra chalcogramma*) in the northern Gulf of Alaska. *Environmental Biology of Fishes* 86:297–305.
- Appenzeller, A. R., and W. C. Leggett. 1995. An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:504–511.
- Beeton, A. M., and J. A. Bowers. 1982. Vertical migration of *Mysis relicta* Loven. *Hydrobiologia* 93:53–61.
- Bohl, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia* 44:368–375.
- Boscarino, B. T., L. G. Rudstam, J. L. Eillenberger, and R. O’Gorman. 2009. Importance of light, temperature, zooplankton and fish in predicting the nighttime vertical distribution of *Mysis diluviana*. *Aquatic Biology* 5:263–279.
- Boscarino, B. T., L. G. Rudstam, S. Mata, G. Gal, O. E. Johannsson, and E. L. Mills. 2007. The effects of temperature and predator-prey interactions on the migration behavior and vertical distribution of *Mysis relicta*. *Limnology and Oceanography* 52:1599–1613.
- Bowers, J. A. 1988. Diel vertical migration of the opossum shrimp *Mysis relicta* in Lake Superior: observations and sampling from the Johnson-Sea-Link II submersible. *Bulletin of Marine Science* 43:730–738.
- Breck, J. E. 1993. Foraging theory and piscivorous fish: are forage fish just big zooplankton? *Transactions of the American Fisheries Society* 122:902–911.
- Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist* 11:99–113.
- Bronte, C. R., M. P. Ebener, D. R. Schreiner, D. S. DeVault, M. M. Petzold, D. A. Jensen, C. Richards, and S. J. Lozano. 2003. Fish community change in Lake Superior, 1970–2000. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1552–1574.
- Conley, D. J., and D. Scavia. 1991. Size structure of particulate biogenic silica in Lake Michigan. *Journal of Great Lakes Research* 17:18–24.
- Conner, D. J., C. R. Bronte, J. H. Selgeby, and H. L. Collins. 1993. Food of salmonine predators in Lake Superior, 1981–1987. *Great Lakes Fishery Commission Technical Report* 59.
- Dakin, W. J., and M. Latarche. 1913. The plankton on Lough Neagh: a study of the seasonal changes in the plankton by quantitative methods. *Proceedings of the Royal Irish Academy* 30:20–96.
- Dill, L. M., and A. H. G. Fraser. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behavioral Ecology and Sociobiology* 16:65–71.



- Dryer, W. R., L. F. Erkkila, and C. L. Tetzloff. 1965. Food of lake trout in Lake Superior. *Transactions of the American Fisheries Society* 94:169–176.
- Gal, G., E. R. Loew, L. G. Rudstam, and A. M. Mohammadian. 1999. Light and diel vertical migration: spectral sensitivity and light avoidance by *Mysis relicta*. *Canadian Journal of Fisheries and Aquatic Sciences* 56:311–322.
- Gal, G., L. G. Rudstam, and O. E. Johannsson. 2004. Predicting *Mysis relicta* vertical distribution in Lake Ontario. *Archiv für Hydrobiologie* 159:1–23.
- Gerritsen, J., and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of the Fisheries Research Board of Canada* 37:73–82.
- Gliwicz, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature (London)* 320:746–748.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin System Sea Grant Institute, Madison.
- Hardiman, J. M., B. M. Johnson, and P. J. Martinez. 2004. Do predators influence the distribution of age-0 kokanee in a Colorado reservoir? *Transactions of the American Fisheries Society* 133:1366–1378.
- Harvey, C. J., S. T. Schram, and J. F. Kitchell. 2003. Trophic relationships among lean and siscowet lake trout in Lake Superior. *Transactions of the American Fisheries Society* 132:219–228.
- Hays, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503:163–170.
- He, X., R. Wright, and J. F. Kitchell. 1993. Fish behavioral and community responses to manipulation. Pages 69–84 in S. R. Carpenter and J. F. Kitchell, editors. *The trophic cascade in lakes*. Cambridge University Press, Cambridge, UK.
- Herman, A. W. 1992. Design and calibration of a new optical plankton counter capable of sizing small zooplankton. *Deep Sea Research* 39:395–415.
- Hrabik, T. R., O. P. Jensen, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2286–2295.
- Hutchinson, G. E. 1957. *A treatise on limnology, volume 1. Geology, physics, and chemistry*. Wiley, New York.
- Iwasa, Y. 1982. Vertical migration of zooplankton: a game between predator and prey. *American Naturalist* 120:171–180.
- Janssen, J., and S. B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 37:177–184.
- Jensen, O. P., T. R. Hrabik, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006. Diel vertical migration in the Lake Superior pelagic community. II. Modeling trade-offs at an intermediate trophic level. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2296–2307.
- Jensen, O. P., P. M. Yurista, T. R. Hrabik, and J. D. Stockwell. 2009. Densities and diel vertical migration of *Mysis relicta* in Lake Superior: a comparison of optical plankton counter and net-based approaches. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 30:957–963.
- Johannsson, O. E., M. F. Leggett, L. G. Rudstam, M. R. Servos, M. A. Mohammadian, G. Gal, R. M. Dermott, and R. H. Hesslein. 2001. Diet of *Mysis relicta* in Lake Ontario as revealed by stable isotope and gut content analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1975–1986.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 34:1922–1935.
- Koenings, J. P., and J. A. Edmundson. 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: effects of yellow color and turbidity. *Limnology and Oceanography* 36:91–105.
- Lampert, W. 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Archiv für Hydrobiologie* 39:79–88.
- Lampert, W., and U. Sommer. 1997. *Limnology: the ecology of lakes and streams*. Oxford University Press, Oxford, UK.
- Levy, D. A. 1990. Reciprocal diel vertical migration behaviour in planktivores and zooplankton in British Columbia lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1755–1764.
- Link, J., and T. A. Edsall. 1996. The effect of light on lake herring (*Coregonus artedii*) reactive volume. *Hydrobiologia* 332:131–140.
- Love, R. H. 1977. Target strength of an individual fish at any aspect. *Journal of the Acoustical Society of America* 62:1397–1403.
- Luecke, C., and W. A. Wurtsbaugh. 1993. Effects of moonlight and daylight on hydroacoustic estimates of pelagic fish abundance. *Transactions of the American Fisheries Society* 122:112–120.
- Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. *American Zoologist* 19:331–343.
- Mason, D. M., and S. B. Brandt. 1996. Effects of spatial scale and foraging efficiency on the predictions made by spatially-explicit models of fish growth rate potential. *Environmental Biology of Fishes* 45:283–298.
- Mason, D. M., and E. V. Patrick. 1993. A model for the space-time dependence of feeding for pelagic fish populations. *Transactions of the American Fisheries Society* 122:884–901.
- Mauchline, J. 1980. The biology of mysids and euphausiids. *Advances in Marine Biology* 18:1–681.
- McLaren, I. A. 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. *Journal of the Fisheries Research Board of Canada* 20:685–727.
- McNamara, J. M., and A. I. Houston. 1992. Risk-sensitive foraging: a review of the theory. *Bulletin of Mathematical Biology* 54:355–378.
- Mehner, T., P. Kasprzak, and F. Holker. 2007. Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish. *Canadian Journal of Fisheries and Aquatic Sciences* 64:874–886.
- Moen, V., and A. Langeland. 1989. Diurnal vertical and seasonal horizontal distribution patterns of *Mysis relicta* in a large Norwegian lake. *Journal of Plankton Research* 11:729–745.
- Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. *Journal of the Fisheries Research Board of Canada* 27:281–316.
- Negus, M. T. 1995. Bioenergetics modeling as a salmonine management tool applied to Minnesota waters of Lake Superior. *North American Journal of Fisheries Management* 15:60–78.
- Negus, M. T., D. R. Schreiner, T. N. Halpern, S. T. Schram, M. J. Seider, and D. M. Pratt. 2008. Bioenergetics evaluation of the fish community in the western arm of Lake Superior in 2004. *North American Journal of Fisheries Management* 28:1649–1667.
- NSRDB (National Solar Radiation Data Base). 2005. NSRDB hourly data files for Duluth. Available: [rredc.nrel.gov/solar/old\\_data/nsrdb/](http://rredc.nrel.gov/solar/old_data/nsrdb/). (February 2009).
- Ramcharan, C. W., and G. W. Sprules. 1986. Visual predation in *Mysis relicta* Loven. *Limnology and Oceanography* 31:414–420.
- Ray, B. A., T. R. Hrabik, M. P. Ebener, O. T. Gorman, D. R. Schreiner, S. T. Schram, S. P. Sitar, W. P. Mattes, and C. R. Bronte. 2007. Diet and prey selection by Lake Superior lake trout during spring, 1986–2001. *Journal of Great Lakes Research* 33:104–113.
- Rottiers, D. V., and R. M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish and Wildlife Service, Technical Paper 108, Washington, D.C.
- Rudstam, L. G., F. P. Binkowski, and M. A. Miller. 1994. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. *Transactions of the American Fisheries Society* 123:344–357.
- Rudstam, L. G., A. L. Hetherington, and A. M. Mohammadian. 1999. Effect of temperature on feeding and survival of *Mysis relicta*. *Journal of Great Lakes Research* 25:363–371.
- Salonen, K., R. I. Jones, and L. Arvola. 1984. Hypolimnetic phosphorus retrieval by diel vertical migrations of lake phytoplankton. *Freshwater Biology* 14:431–438.

- Scavia, D., and G. L. Fahnenstiel. 1987. Dynamics of Lake Michigan phytoplankton: mechanisms controlling epilimnetic communities. *Journal of Great Lakes Research* 13:103–120.
- Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- Sprules, W. G. 2000. Spatial estimates of prey consumption by *Mysis relicta* Loven using an optical plankton counter. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 27:3275–3278.
- Sprules, W. G., E. H. Jin, A. W. Herman, and J. D. Stockwell. 1998. Calibration of an optical plankton counter for use in fresh water. *Limnology and Oceanography* 43:726–733.
- Steinberg, D. K., S. A. Goldthwait, and D. A. Hansell. 2002. Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. *Deep Sea Research Part I: Oceanographic Research Papers* 49:1445–1461.
- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*, application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences* 40:681–698.
- Stockwell, J. D., T. R. Hrabik, O. P. Jensen, D. L. Yule, and M. Balge. 2010. Empirical evaluation of predator-driven diel vertical migration in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences* 67:473–485.
- Stockwell, J. D., D. L. Yule, T. R. Hrabik, O. T. Gorman, and B. V. Holbrook. 2007. Vertical distribution of fish biomass in Lake Superior: implications for day bottom trawl surveys. *North American Journal of Fisheries Management* 27:735–749.
- Teraguchi, M., A. D. Hasler, and A. M. Beeton. 1975. Seasonal changes in the response of *Mysis relicta* Loven to illumination. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 19:2989–3000.
- TeWinkel, L. M., and G. W. Fleischer. 1999. Vertical migration and nighttime distribution of adult bloaters in Lake Michigan. *Transactions of the American Fisheries Society* 128:459–474.
- U.S. Environmental Protection Agency's Great Lakes National Program Office. 2003. Standard operating procedure for zooplankton analysis. U.S. Environmental Protection Agency, SOP-LG403, Chicago. Available: [www.epa.gov/greatlakes/monitoring/sop/chapter\\_4/LG403.pdf](http://www.epa.gov/greatlakes/monitoring/sop/chapter_4/LG403.pdf). (November 2011).
- Van Gool, E., and J. Ringelberg. 2003. What goes down must come up: symmetry in light-induced migration behaviour in *Daphnia*. *Hydrobiologia* 491:301–307.
- Vogel, J. L., and D. A. Beauchamp. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1293–1297.
- Vondracek, B., B. D. Giese, and M. G. Henry. 1996. Energy densities of three fishes from Minnesota waters of Lake Superior. *Journal of Great Lakes Research* 22:757–764.
- Weng, K. C., and B. A. Block. 2004. Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital retia mirabilia. *U.S. National Marine Fisheries Service Fishery Bulletin* 102:221–229.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk in habitat use in fish. *Ecology* 64:1540–1548.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:1352–1366.
- Wismer, D. A., and A. E. Christie. 1987. Temperature relationships of Great Lakes fishes: a data compilation. Great Lakes Fishery Commission, Special Publication 87-3, Ann Arbor, Michigan.
- Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall, Boca Raton, Florida.
- Wood, S. N., and N. H. Augustin. 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modeling. *Ecological Modeling* 157:157–177.
- Worthington, E. B. 1931. Vertical movements of fresh-water macroplankton. *Internationale Revue der Gesamten Hydrobiologie* 25:394–436.
- Wright, D. I., and W. J. O'Brien. 1984. The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis annularis*). *Ecological Monographs* 54:65–98.
- Wurtsbaugh, W. A., and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. *Nature (London)* 333:846–848.
- Yule, D. L., J. V. Adams, J. D. Stockwell, and O. T. Gorman. 2007. Using multiple gears to assess acoustic detectability and biomass of fish species in Lake Superior. *North American Journal of Fisheries Management* 27:106–126.
- Yule, D. L., J. D. Stockwell, G. A. Cholwek, L. M. Evrard, S. Schram, M. Seider, and M. Symbal. 2006. Evaluation of methods to estimate lake herring spawner abundance in Lake Superior. *Transactions of the American Fisheries Society* 135:680–694.
- Yule, D. L., J. D. Stockwell, D. R. Schreiner, L. M. Evrard, M. Balge, and T. R. Hrabik. 2009. Can pelagic forage fish and spawning cisco (*Coregonus artedii*) biomass in the western arm of Lake Superior be assessed with a single summer survey? *Fisheries Research* 96:39–50.
- Yurista, P. M., J. R. Kelly, and S. E. Miller. 2009. Lake Superior zooplankton biomass: alternate estimates from a probability-based net survey and spatially extensive LOPC surveys. *Journal of Great Lakes Research* 35:337–346.
- Zaret, T. M., and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnology and Oceanography* 21:804–813.