Diel Vertical Migrations and Trophic Interactions of Freshwater Organisms

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Abstract

Abiotic and biotic conditions interact to cause dynamic diel vertical migrations (DVM) of organisms in the pelagic area of freshwater lakes. This dissertation includes four unique studies to improve our knowledge of how and why DVM patterns change between species, ecosystems, seasons, and years. The first study documented a normal DVM of the endangered Hovsgol grayling (*Thymallus nigrescens*) in Lake Hovsgol, Mongolia, during the summer season. This migration was driven by the distribution of prey because there were no pelagic predators. Next, I examined how different abiotic and biotic conditions between 11 inland lakes in Minnesota and northern Wisconsin caused differences in DVM patterns of cisco (*Coregonus artedi*) during the summer season. I found cisco populations that performed normal DVM, no DVM, and reverse DVM, resulting from differences in temperature, oxygen, prey density, growth potential, and predation risk between lakes. To determine differences in DVM patterns between seasons and years, I followed up this study by analyzing reverse DVM patterns of cisco in Ten Mile Lake, Minnesota, during the spring, summer, fall, and winter over multiple years. I observed a small reverse DVM of cisco during the spring and fall, a large reverse DVM during summer, with no DVM during winter. These differences were attributable to seasonal changes in the abiotic and biotic conditions of the lake. Lastly, I examined seasonal and yearly changes in normal DVM patterns of four pelagic species in Lake Superior. DVM patterns changed between seasons, but were more consistent among years, and were driven by changes in prey and predator densities and distributions.

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Forward

This is a doctoral dissertation submitted as partial fulfillment for the degree of Doctor of Philosophy from the University of Minnesota. Chapter 2 is currently published in Environmental Biology of Fishes. Chapter 3 is currently accepted with revisions in Oecologia. Chapter 5 is currently published in Transactions of the American Fisheries Society. All of the chapters were prepared for publication with co-authors, so the collective "we" is used instead of "I" throughout the dissertation.

Ahrenstorff, T.D., O.P. Jensen, B.C. Weidel, B. Mendsaikhan, and T.R. Hrabik. 2012. Abundance, spatial distribution, and diet of endangered Hovsgol grayling (*Thymallus nigrescens*). Environmental Biology of Fishes 94:465-476. http://link.springer.com/article/10.1007/s10641-011-9961-5#page-1

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Ahrenstorff, T.D., T.R. Hrabik, J.D. Stockwell, D.L. Yule, and G.G. Sass. 2011. Seasonally dynamic diel vertical migrations of *Mysis diluviana*, coregonine fishes, and siscowet lake trout in the pelagia of western Lake Superior. Transactions of the American Fisheries Society 140:1504-1520. http://www.tandfonline.com/doi/abs/10.1080/00028487.2011.637004#

Chapter 1

Introduction

Diel vertical migrations (DVM) are commonly observed in many aquatic

ecosystems among most groups of organisms, including zooplankton (Gliwicz 1986),

planktivores (Bohl 1980), and piscivores (Weng and Block 2004). Normal diel vertical

migrations are characterized by the vertical movement of organisms from deeper water

during the day to shallower water at night. Reverse diel vertical migrations, which are

comparatively uncommon, are described as the vertical movement of organisms from

shallower water during the day to deeper water at night. Normal or reverse DVM

patterns are known to be influenced by proximate (e.g. light and temperature) and

ultimate (e.g. foraging, growth, and predation risk) factors (Ringelberg and Van Gool

2003). However, there are gaps in our knowledge of DVM behavior (Mehner 2012). For

example, it is unclear what mechanisms may cause a fish species to perform normal,

reverse, or no vertical migrations in different aquatic environments. Similarly, the

influence of seasonal changes in abiotic and biotic conditions on DVM patterns is not

well understood. This dissertation includes a synthesis of four unique studies from

different species around the world in an attempt to improve knowledge of how and why

DVM patterns change between species, ecosystems, seasons, and years.

The proximate causes that influence DVM behavior are generally thought of as

the factors that guide an organism during migrations. The main proximate trigger of

DVM behavior is changing light levels over a daily cycle (Appenzeller and Leggett

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1995). Organisms typically migrate up or down in the water column concurrently with

the rapid change in light during crepuscular periods (i.e. dawn and dusk) (Appenzeller

and Leggett 1992; Scheuerell and Schindler 2003). For example, when light levels do not

change considerably throughout a 24-hour period (e.g. summer in the Arctic or under ice)

organisms do not typically migrate (Gjelland et al. 2009; Steinhart and Wurtsbaugh

1999). Other proximate factors that may influence DVM patterns include temperature

and oxygen conditions. Strong thermal gradients in the metalimnion, or warmer

temperatures near the surface and low oxygen content near the bottom of a lake, may

influence the magnitude of many migrations by constraining total habitat available

(Magnuson et al. 1979; Rudstam and Magnuson 1985).

　　　The ultimate factors, or adaptive significance, of migrating can be summarized

into three main hypotheses, including, (1) optimal foraging, (2) bioenergetic efficiency,

(3) predator avoidance, and combinations therein (Mehner 2012). The optimal foraging

hypothesis states that an organism may migrate in order to maximize consumption of

prey resources despite other influences (Levy 1990; Narver 1970). Increased foraging

potential seems to drive the normal DVM pattern of alewife (*Alosa pseudoharengus*) and

bloater (*Coregonus hoyi*) in Lake Michigan which feed on normally migrating *Mysis*

diluviana (Janssen and Brandt 1980; TeWinkel and Fleischer 1999). The bioenergetics

efficiency hypothesis is based on the premise that organisms migrate in order to

maximize growth efficiency (McLaren 1963). This hypothesis has been supported by

studies on sockeye salmon (*Oncorhynchus nerka*) and dogfish (*Scyliorhinus canicula*)

where these species gained a growth advantage by migrating (Brett 1971; Sims et al.

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2006). Lastly, the predator avoidance hypothesis states that organisms may migrate to

avoid predation risk from visually feeding predators (Lampert 1993; Zaret and Suffern

1976). This is the most common explanation for normally migrating species (Eggers

1978; Jensen et al. 2006), but may also be important for some species that perform

reverse migrations (Jensen et al. 2011; Stockwell and Johnson 1999).

Chapter 2 examines DVM patterns of the Hovsgol grayling (*Thymallus*

nigrescens), in Lake Hovsgol, Mongolia. This study provided a unique scenario in which

to study DVM behavior because the Hovsgol grayling was the only pelagic fish species

present in the lake (i.e. no predation risk). It allowed us to test the potential influence of

foraging and growth potential on DVM behavior. This study also provides the first

publication in the English literature on the Hovsgol grayling that examines their

abundance, spatial distribution, and feeding behaviors.

While the study in Mongolia allowed tests of individual hypotheses, it is rare that

a single factor drives the movements of an organism (Mehner 2012). Instead, there are

typically tradeoffs among proximate and ultimate factors that ultimately determine

migration patterns. For example, the anti-predation window combines foraging and

predation models, to predict that planktivores may migrate to low light areas during the

day and night, where they can sufficiently capture prey resources, while still avoiding

predation due to the higher light intensities required for their predators to feed efficiently

(Clark and Levy 1988; Scheuerell and Schindler 2003). In addition, the importance of

these tradeoffs between proximate and ultimate factors may change given different

environmental conditions among lakes. For example, when food availability is high

throughout the water column, *Daphnia hyalina* avoid predation risk by remaining in the hypolimnion (Gliwicz and Pijanowska 1988); however, when food availability is low throughout the water column, *Daphnia* spp. spend most of their time feeding near the surface despite the higher predation risk (Johnson and Jakobsen 1987). Clearly, different migration patterns are driven by a variety of factors that must be explored in diverse ecosystems to identify the extent of behavioral plasticity for a given species.

The study designed in Chapter 3 examined different DVM patterns, and the potential tradeoffs in the mechanisms influencing DVM behavior, by studying vertical movements of cisco (*Coregonus artedi*) in 11 inland lakes throughout Minnesota and northern Wisconsin. This study was the first to document normal, reverse, and no DVM for a fish species in lake ecosystems. It also examines the mechanisms causing different DVM behavior between lakes through the use of foraging, growth, and predation risk models.

Chapter 2 and 3 examine DVM patterns of pelagic species during summer; however, seasonal changes in temperature, light, prey availability, and predator distributions may alter DVM behavior for a particular species among seasons. For example, *Mysis diluviana* have been found to migrate less extensively in spring, likely because of water mixing and isothermal conditions in the Great Lakes during that time period (Boscarino et al. 2009; Gal et al. 2004). For some fish species, such as juvenile kokanee salmon and walleye pollock (*Theragra chalcogramma*), DVM patterns are influenced by seasonal changes in water temperature, light, and prey/predator densities and distributions (Adams et al. 2009; Hardiman et al. 2004; Stockwell et al. 2010).

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However, for vendace (*Coregonus albula*) and Fontane cisco (*C. fontanae*), DVM patterns do not change significantly by season (Mehner et al. 2007). Overall, seasonal changes in the abiotic and biotic environment could modify DVM patterns for a particular species, depending on the mechanisms driving those movements.

Chapter 4 examines seasonal and yearly changes in reverse DVM patterns of cisco in Ten Mile Lake, Minnesota. There have been relatively few studies which have documented reverse DVM behavior for a fish species (Jensen et al. 2011; Sims et al. 2005). Of those studies, none of them have examined the impact of seasonal changes on reverse DVM behavior. Therefore, this study is the first to document the mechanisms causing different reverse DVM behavior throughout the year.

Lastly, chapter 5 examines seasonally dynamic DVM patterns of the dominant species in the pelagic food-web of Lake Superior. While there have been some studies documenting that species within the pelagic food-web migrate vertically (Hrabik et al. 2006; Stockwell et al. 2010), the following was unclear: (1) how migrations 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. This study provides a nice summary of how competing models can be used to describe seasonal differences in normal DVM behavior of an entire food-web.

Overall, this dissertation uses four unique and novel studies to provide additional information about how and why species perform DVM in different aquatic ecosystems. Chapter 2 provides a simple example of DVM behavior where there are limited factors influencing the movements of Hovsgol grayling. Chapter 3 examines tradeoffs in the

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mechanisms influencing different DVM patterns of cisco in inland lakes. Chapter 4

studies seasonal changes in reverse DVM behavior of cisco in Ten Mile Lake, Minnesota.

Lastly, chapter 5 documents seasonal changes in normal diel vertical migrations of the

Lake Superior pelagic food-web. Understanding how and why DVM patterns change

among ecosystems, species, seasons, and years is summarized in the final chapter 6.

Chapter 2

Abundance, spatial distribution, and diet of endangered Hovsgol grayling

(*Thymallus nigrescens*)

Introduction

Anthropogenic environmental changes are increasing worldwide and causing

decreases in biological diversity in both terrestrial and aquatic ecosystems (Vitousek

1994). Freshwater ecosystems may be particularly vulnerable (Abell 2002).

Conservation of endangered species in the face of increased anthropogenic influences

requires knowledge of basic species demographics, including abundance, spatial

distribution, and behavior (Campbell et al. 2002). Conservation action plans for

threatened and endangered Mongolian fishes (e.g. Hovsgol grayling) have been initiated

but there is little direct monitoring and limited ecological understanding of these fish

populations (Ocock et al. 2006b). This is cause for concern given that Mongolia had one

of the fastest growing human populations in the 20th century (Ramankutty et al. 2002)

and is undergoing rapid environmental changes characterized by an increase in the

average annual air temperature by 1.66°C in the last 60 years (Punsalmaa et al. 2005),

shortened ice cover duration in rivers and lakes (Punsalmaa et al. 2004), increasing

precipitation (Namkhaijantsan 2006), and changing stream flow regimes (Ma et al. 2003).

The Hovsgol grayling (*Thymallus nigrescens*) is listed as an endangered species

on Mongolia's Red List (Ocock et al. 2006a), and is endemic to Mongolia's largest lake,

Lake Hovsgol, yet no peer-reviewed publications exist about its ecology in the English-

language literature. As a taxonomic group, grayling can be susceptible to anthropogenic influences as has been seen with the extirpation or reduction in population sizes of North American Arctic grayling (*Thymallus articus*) in Montana and Wyoming (Northcote 1995). The Hovsgol grayling is closely related to the Arctic grayling. Some researchers designate the Hovsgol grayling as a subspecies of the Arctic grayling (Reshetnikov et al. 2002), some classify it as its own species (Berg 1962; Kottelat 2006; Scott and Crossman 1998), and others await additional morphological and genetic analyses before making subspecies or species classifications (Froufe et al. 2005). Most of what is known about the Hovsgol grayling is based on informal reports and unpublished studies, briefly summarized in Dulmaa (1999) and Sideleva (2006). While empirical evidence is lacking, it is thought that Hovsgol grayling primarily inhabit the littoral zone and surface layers of the pelagia of Lake Hovsgol, as well as inflowing rivers mainly during the early-summer spawning period (Dulmaa 1999). It is also thought that they are omnivorous, feeding mostly on zooplankton (Sideleva 2006). There has been no assessment of their abundance, lakewide distribution, vertical distribution, diel vertical migration tendencies, or ontogenetic or habitat-related diet shifts.

Densities, distributions, and feeding behaviors of planktivores in large lake ecosystems are typically controlled by a host of factors, such as resource limitation from the bottom-up (Power 1992), top-down control from piscivores (McQueen et al. 1986), the amount of available habitat (Magnuson et al. 1979), and direct exploitation (Post et al. 2002). Lake Hovsgol is a large, ultra-oligotrophic (Urabe et al. 2006) body of water. Although still relatively pristine owing to its remote location, it faces a number of

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anthropogenic pressures including changing habitat conditions due to global climate change (Punsalmaa et al. 2005) and increasing exploitation caused by an increase in tourism and population growth (Ramankutty et al. 2002; Yu and Goulden 2006). However, unlike most large lake ecosystems, Lake Hovsgol has very few piscivores present in the pelagia, with much higher densities in littoral areas. The low pelagic piscivore density provides a low predation risk scenario in the pelagia for Hovsgol grayling, which may influence their distribution, diel vertical migration behavior, and ultimately the consumption of prey resources (Carpenter and Kitchell 1993).

The purpose of this study was to characterize the ecology of the endemic, endangered Hovsgol grayling population in Lake Hovsgol. Specifically, our objectives were to (*i*) assess lakewide densities of two size classes of Hovsgol grayling (small, 100 – 170 mm; large, > 170 mm), (*ii*) describe their vertical and horizontal distributions during day and night, and (*iii*) examine their feeding behaviors in littoral and pelagic areas. Given the potential for rapid environmental change in this region and the limited ecological understanding of Hovsgol grayling, our research provides a baseline for interpreting the effects of future environmental changes and implementing proper conservation and monitoring strategies.

Materials and Methods

Study Site

Lake Hovsgol, Mongolia (51°05'50.00" N, 100°30'00.00" E), is located in the mountains of northern Mongolia, at the southern edge of the Siberian taiga forest. It is

the 19th largest lake in the world by volume (480 km^3), with a maximum depth of 262 m, and a surface area of 2,760 km^2 (Goulden et al. 2006; Herdendorf 1982). For size reference, Lake Hovsgol is similar to Lake Erie in volume (545 km^3). Lake Hovsgol is dimictic, with ice cover from November to June, an established thermocline by late July (10 – 14 m depth), and summer surface water temperatures reaching 14 – 15°C (Edlund et al. 2003; Urabe et al. 2006). It is an ultra-oligotrophic lake; characterized by low primary production (2 – 5 mg C·m^{-3}·day^{-1}), high oxygen content year-round throughout the water column (8 – 11.5 mg O$_2$·l^{-1}), and clear water (Secchi disk readings commonly up to 20 m) (Kozhova et al. 1994; Urabe et al. 2006). The abundance of submergent and emergent vegetation is low throughout the lake, except near inflowing streams and rivers.

Biological sampling

We sampled the lake from July 20th to July 30th, 2009, and collected data on Hovsgol grayling population densities, vertical and horizontal distribution patterns, and feeding behaviors. Specific sampling techniques employed horizontal gillnets ($N = 8$ locations), vertical gillnets ($N = 6$ locations), hydroacoustics ($N = 8$ locations), and staged vertical zooplankton net tows ($N = 2$ locations) (Figure 1). The various locations were selected in order to sample the entire lake at littoral and pelagic areas, as well as points and embayments.

The littoral fish community was sampled at eight locations using three monofilament experimental horizontal gillnets (Figure 1). Two of the gillnets were 2 m deep and 20 m long, made up of 4 m panels of 25.4, 38.1, 50.8, 63.5, and 76.2 mm bar

mesh. The other gillnet was 2 m deep and 28 m long, consisting of 4 m panels of 12.7, 25.4, 38.1, 50.8, 63.5, 76.2, and 88.9 mm bar mesh. The gillnets were deployed using a stationary bottom set, perpendicular to shore, in water less than 10 m deep (Hubert 1983). Nets were fished throughout the night, for 8.5 – 11.5 hours, at each location. All fish captured were measured to the nearest mm in total length, weighed to the nearest gram, and stomach contents were removed and analyzed from grayling ranging in total length (described below).

The pelagic fish community was sampled using vertical gillnets at six locations distributed throughout the lake (Figure 1). The vertical gillnets were 40 m long by 4 m wide, with spreader bars placed every 10 m. At station 2, we used a 19.1 and 38.1 mm bar mesh gillnet. At station 5, we used a 12.7, 19.1, 25.4, and 38.1 mm bar mesh net. Finally, at stations 4, 7, 8, and 9 we used a 12.7, 19.1, 25.4, and 31.8 mm bar mesh net. The vertical gillnets were deployed with the top of the net at the surface and the bottom of the net at 40 m, in bottom depths ranging from 40 – 110 m. We set each net in the evening and fished them for 7 – 13.5 hours. Upon retrieval, fish were identified, measured to the nearest millimeter (total length), weighed to the nearest gram, had their stomachs dissected, and had the depth of capture measured to the nearest 0.5 m. Horizontal and vertical gillnet catch rates (ind.$\cdot$h$^{-1}\cdot$m^{-2}) with associated standard errors were calculated to compare the littoral and pelagic areas.

Entire stomachs were removed from the Hovsgol grayling caught in horizontal and vertical gillnets, and stomach contents were identified, enumerated, and weighed (to the nearest 0.1 mg wet weight). To examine ontogenetic and habitat related diet shifts,

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we examined the diet composition (% by mass) of at least 5 grayling (range: 5 – 39) in each 50 mm length bin (e.g. 100 – 150 mm) captured in the horizontal and vertical gillnets. Diet items were classified into major taxonomic categories as follows: primarily benthic invertebrates (Amphipoda, Chironomidae, Ephemeroptera, Hirudinea, Mollusca, Plecoptera, Simuliidae, and Trichoptera), zooplankton (Calanoida, Cyclopoida and Cladocera) and terrestrial insects (Coleoptera, Diptera adults, Ephemeroptera adults, and Hymenoptera).

Hydroacoustic data to determine the size distribution, density, and vertical distribution of the pelagic fish community were collected concurrently with gillnet sampling. For all hydroacoustic sampling we used a 120 kHz Biosonics DTX hydroacoustic echosounder (Biosonics, Inc., Seattle, Washington) mounted on a 1.75 m tow body. Eight transects were sampled during the day or night to examine lakewide densities and diel changes in vertical distributions (Figure 1). Each transect was sampled for between 30 to 300 minutes with bottom depths ranging from 26 m to 222 m (Table 1). Data were collected according to Rudstam et al. (2009). The acoustic signals were collected with Biosonics Visual Acquisition Software (version 4.1) and saved to a computer hard drive for later analyses. At the beginning and end of the research cruise, a standard sphere calibration of the hydroacoustic system was performed and little difference ($< \pm 1$ dB) was detected in the observed and theoretical target strength of the calibration sphere.

Fish densities were estimated from the hydroacoustic data using Echoview software (version 4.10, SonarData Ply Ltd., Tasmania). Post-processing procedures

included removing bottom dead zone echoes, the near-field exclusion zone, and non-fish echoes. Data were classified into 5 m depth bins from just below the near-field exclusion zone (~ 2 m) to the maximum depth for each transect. For each depth bin, within each transect, densities of Hovsgol grayling were calculated. Based on length modes in the vertical gillnet catch data (Figure 2B), and because only Hovsgol grayling were captured in the vertical gillnets, we classified grayling into two size groups: 100 – 170 mm (smaller) and > 170 mm (larger). In the absence of a target strength to length relationship for grayling, we chose to use the general equation provided in Love (1977) for measurements of fish in the dorsal aspect. The lengths in each size category correspond to target strengths ranging from -44.77 to -40.37 dB for smaller sized grayling and > -40.37 dB for larger sized grayling.

To calculate densities of smaller and larger grayling in each depth bin, we first calculated the proportion (P_s) and mean target strength ($\overline{TS}_s$; dB re 1 m^2) for each size class (s) in each bin using a single target analysis with single target detection parameters described in Rudstam et al. (2009). If fewer than 30 single targets were present in a depth bin shallower than 50 m we used an average P_s and $\overline{TS}_s$ value for all organisms in less than 50 m of water along that transect. Likewise, if fewer than 30 single targets were present in a depth bin greater than 50 m of water we used an average P_s and $\overline{TS}_s$ value for all organisms in greater than 50 m of water along that transect. We used 50 m as a cutoff because proportionally more small individuals were present below 50 m causing differences in P_s and $\overline{TS}_s$. Next, we used P_s, $\overline{TS}_s$, and s_V, which is the linear mean volume backscattering coefficient determined from the echo integration file for the echogram

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$(m^2 \cdot m^{-3})$, to calculate the volumetric fish density (P_{VS}; ind.·m^{-3}) for each size class in each bin using the following equation:

$$(1) \qquad P_{VS} = \frac{P_s}{\Sigma\left(P_s \times 10^{\left(\frac{TS_s}{10}\right)}\right)} \times s_V$$

Volumetric fish densities (ind.·m^{-3}) were converted to areal densities (ind.·ha^{-1}) when necessary by summing volumetric fish densities in each meter of the water column and multiplying by 10,000 (10,000 m^2 = 1 ha). Only night estimates were used when estimating Hovsgol grayling population densities throughout the lake because fish forming large and dense schools during the day could potentially lead to inaccuracies (Appenzeller and Leggett 1992). However, this does not appear to be a major concern given the similar day and night density estimates between most transects (Table 1). Due to these similarities, day and night density estimates were used to evaluate diel vertical migration patterns. All density estimates are accompanied by estimates of one standard error. Two-sample Kolmogorov-Smirnov tests were used to compare day versus night vertical distributions of smaller and larger Hovsgol grayling for each transect when the data were available.

We used staged vertical plankton net tows to gather information on the species composition, abundance, and vertical distribution of the zooplankton community. We sampled the zooplankton community at 2 locations, providing day and night samples (Figure 1). At each location, a 0.25 m opening, 153 ųm conical mesh plankton net was deployed and retrieved at a speed of ~1 m·s^{-1}. Staged net tows were used with three replicates collected at each depth. We took replicates from 5 m off the bottom to the

surface, 50 m to the surface, and 20 m to the surface. Zooplankton samples were preserved with 95% ethanol. We analyzed each zooplankton sample by identifying and counting all of the organisms in four 5 ml subsamples. Cladocerans were identified to family and copepods were identified to order. This coarse taxonomic resolution was appropriate given that our study objectives focused on zooplankton only as a component of grayling diets.

Results

Species composition, size distributions, and catch rates

We captured 565 fish at the eight littoral stations using horizontal gillnets. Hovsgol grayling represented a little more than half of all the fish captured in littoral areas (N = 301; 53.3%). Other species captured less frequently included burbot (*Lota lota*; N = 90; 16%), roach (*Rutilus rutilus lacustris*; N = 65; 11.5%), lenok (*Brachymystax lenok*; N = 57; 10.1%), Eurasian perch (*Perca fluviatilis*; N = 51; 9%) and stone loach (*Barbatula toni*; N = 1; <1%). A length-frequency distribution for Hovsgol grayling caught in the littoral zone was unimodal (270 mm, Figure 2A) and ranged from 207 – 385 mm with a mean of 272 mm.

We captured 127 fish (all Hovsgol grayling) in the vertical gillnets. The pelagic Hovsgol grayling population showed a bimodal length distribution, with modes at 140 mm and 230 mm (Figure 2B). The smaller size group ranged between 108 – 156 mm (mean = 138 mm) while the larger group was between 175 – 339 mm (mean = 230 mm).

The mean gillnet catch rate of Hovsgol grayling, standardized for soak time and net area, was 7.5 times lower in pelagic set vertical gillnets (0.0031 ± 0.001 ind.$\cdot$h$^{-1}\cdot$m^{-2}, $N = 22$) compared to the littoral horizontal gillnets (0.0234 ± 0.004 ind.$\cdot$h$^{-1}\cdot$m^{-2}, $N = 24$). Pelagic vertical gillnet catch rates were 4 times higher along the western and northern shore stations 2, 5, 7, and 9 (0.004 ± 0.001 ind.$\cdot$h$^{-1}\cdot$m^{-2}, $N = 14$) compared to the eastern shore stations 4 and 8 (0.001 ± 0.0004 ind.$\cdot$h$^{-1}\cdot$m^{-2}, $N = 8$). Littoral horizontal gillnet catch rates did not vary between the western/northern shore and the eastern shore stations (0.023 and 0.024 ind.$\cdot$h$^{-1}\cdot$m^{-2}, respectively).

Hovsgol grayling diet composition

Diet composition (% by mass) of Hovsgol grayling varied as a function of length and habitat (littoral vs. pelagic). In pelagic vertical gillnets, 65 diets were analyzed from grayling between 108 – 339 mm, including 13 fish < 150 mm, 5 fish from 150 – 199 mm, 25 fish from 200 – 249 mm, 17 fish from 250 – 299 mm, and 5 fish > 300 mm. Diets of smaller grayling caught in pelagic vertical gillnets were dominated by zooplankton (Calanoida, Cyclopoida, and Cladocera). Larger grayling, however, consumed proportionally more benthically associated invertebrates (e.g. Amphipoda, Chironomidae, Ephemeroptera, Hirudinea, Mollusca, Plecoptera, Trichoptera, and Simuliidae) (Figure 3A). Terrestrial insects (e.g. Coleoptera, Diptera, and Hymenoptera) made up about 20% or less of pelagic grayling diets regardless of size. From the littoral horizontal gillnets, 73 diets were analyzed from grayling between 210 – 385 mm, including 13 fish from 200 – 249 mm, 39 fish from 250 – 299 mm, 14 fish from 300 – 349 mm, and 7 from fish >

350 mm. Only larger Hovsgol grayling (>200 mm) were captured in the horizontal

gillnets set in littoral areas and their diets were dominated by species associated with the

bottom (~75%), followed by terrestrial insects (~20%), and zooplankton (~5%) (Figure

3B).

Hovsgol grayling densities and diel vertical migrations

Hovsgol grayling densities calculated using hydroacoustics at night averaged 34.2

± 6.8 ind.·ha^{-1} (4.4 ± 0.9 kg·ha^{-1}), however, densities of smaller and larger individuals

varied throughout the lake (Figure 4; Table 1). Smaller grayling densities ranged

between 5.1 – 23.7 ind.·ha^{-1} (averaged 15.1 ± 3.1 ind.·ha^{-1}) for transects sampled at night.

Nighttime densities of larger individuals ranged between 5.5 – 34.4 ind.·ha^{-1} and

averaged 19.1 ± 3.8 ind.·ha^{-1}. Although similar depths were sampled, stations located on

the western and northern shores (stations 2, 5, 7, and 9) contained higher average

densities of smaller and larger Hovsgol grayling (21.5 ± 1.5 and 26.2 ± 2.8 ind.·ha^{-1},

respectively) compared to average densities (6.6 ± 1.4 and 9.5 ± 2.5 ind.·ha^{-1},

respectively) from the eastern shore stations 4, 6, and 8.

Hydroacoustic sampling over a day-night cycle allowed examination of changes

in vertical distribution over changing light levels. We observed diel vertical migrations

of smaller and larger Hovsgol grayling at the majority of the stations sampled (Figure 5).

For all transects with complimentary day and night data, the distribution of Hovsgol

grayling during the daytime was significantly deeper compared to night distributions for

both size classes (Kolmogorov-Smirnov test, all *P* values < 0.05). For most transects,

nighttime distributions of smaller grayling were concentrated around 15 m although they

ranged between about 2 – 40 m. During the day densities were highest in deeper water

along most transects, with modal peaks near 30 m, and the majority of the population

present between 10 – 50 m. Vertical migration patterns of larger individuals were similar

to smaller individuals, with densities concentrated around 15 m at night and 30 m during

the day. Similar nighttime vertical distributions of both sizes of grayling were observed

using vertical gillnets and hydroacoustics (figure not shown).

Zooplankton population characteristics

The deepwater zooplankton community was dominated by cyclopoid copepods,

calanoid copepods, and the cladoceran families Bosminidae and Daphniidae. Copepod

average volumetric densities were approximately 100 times greater than cladoceran

densities (1,145 and 11 ind.$\cdot$m^{-3}, respectively). We observed diel vertical migrations for

calanoid copepods, *Bosmina* spp., and *Daphnia* spp. where densities were highest

between 0 – 20 m in depth at night and 20 – 50 m in depth during the day (Figure 6A, C,

and D). The vertical distribution of cyclopoid copepods did not appear to differ between

day and night (Figure 6B).

Discussion

Hovsgol grayling biomass estimates were low (4.4 $\pm$ 0.9 kg$\cdot$ha^{-1}) compared to fish

populations in other large oligotrophic lakes. For example, Lake Superior, the most

oligotrophic Laurentian Great Lake, has planktivore densities about 3.5 times higher than

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Lake Hovsgol, averaging 15.6 kg·ha^{-1} (Mason et al. 2005). Other more productive

Laurentian Great Lakes, such as Lakes Michigan and Ontario, historically had pelagic

fish biomass estimates about 20 – 40 times higher than Lake Hovsgol, at 94 and 191

kg·ha^{-1}, respectively (Brandt et al. 1991; Mason et al. 2001). In Lake Tanganyika, near

the peak of the seasonal biomass pulse, fish densities have been estimated at 880 kg·ha^{-1}

using hydroacoustics (Coulter 1977). With no previous quantitative fish sampling in

Lake Hovsgol available for comparison, it is unclear whether this low pelagic fish density

represents the natural ultra-oligotrophic condition of the lake or whether it is the result of

anthropogenic change. Given the lack of large scale fisheries (small scale, nearshore

gillnetting and angling were occasionally observed) and invasive species, it seems likely

that the low fish density is natural.

Pelagic grayling densities concentrated along the western and northern areas of

the lake suggest that catchment morphometry or landscape-scale factors may influence

Hovsgol grayling distributions in Lake Hovsgol. The western portion of the catchment is

steeper than the eastern shore and soils may potentially experience a greater amount of

weathering and therefore deposit more mineral nutrients on the western side of the lake.

Alternatively, the prevailing west wind in conjunction with the steeper western shorelines

may result in more terrestrial insects being deposited on the western shores.

Interestingly, despite the difference in pelagic fish densities, there was little difference in

grayling catch rates nearshore along the western/northern areas compared to the eastern

areas. While our data suggests a difference in grayling densities in pelagic areas, it is

important to recognize that our observations represent a single, seasonal snapshot of

densities at the lakewide scale. Future work should determine if this large-scale spatial pattern is consistent across seasons and years and explore potential causal mechanisms.

Littoral areas had more Hovsgol grayling than pelagic areas; however, smaller grayling were only present in pelagic areas where predator densities were low. Piscivores (e.g. burbot, lenok, and Eurasian perch) were abundant in littoral samples but entirely absent pelagically. We speculate that smaller grayling, and many larger grayling, use the pelagia as a predation refuge or low risk, low reward (because of presumably lower food density than in the littoral zone) habitat. In smaller lakes, similar ontogenetic shifts between littoral and pelagic habitats occur for bluegill balancing the foraging rate – predation risk trade-off (Werner and Hall 1988).

Diel vertical migration is another common mechanism by which pelagic fish balance predation risk and growth opportunities. For example, amphipods (*Macrohectopus branickii*) in Lake Baikal and juvenile sockeye salmon (*Oncorhynchus nerka*) in British Columbia lakes, undergo diel vertical migrations to increase consumption and decrease predation risk in pelagic areas (Clark and Levy 1988; Rudstam et al. 1992). In Lake Hovsgol, since there appear to be few pelagic predators of grayling, the presumed goal of migrating vertically is to track vertically migrating zooplankton resources. Although our zooplankton data were collected at a relatively coarse vertical resolution, it is apparent that most zooplankton show similar vertical migrations as grayling. The observed DVM trajectories of Hovsgol grayling are notably shallower (change in depth of ~15 m) than the observed DVM trajectory of other species, such as amphipods in Lake Baikal (change of ~100 m) (Rudstam et al. 1992) and kiyi

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(*Coregonus kiyi*) in Lake Superior (change of ~150 m) (Ahrenstorff et al. 2011; Stockwell et al. 2010), which may be due to the lack of predators in the pelagic areas of Lake Hovsgol. It is unclear why large Hovsgol grayling undergo similar vertical migrations as small individuals since they do not feed heavily on zooplankton resources. Perhaps the input of terrestrial invertebrates at night and subsequent death and sinking during the day plays a role in the similar movements because the percentage of terrestrial invertebrates consumed is similar (~20%) among all size classes of grayling. The movement pattern of larger individuals may also be a lasting relict of migrating when younger, or could provide a growth or a bioenergetic benefit due to the temperature differences experienced by grayling during migrations (Bevelhimer and Adams 1993; Brett 1971).

The ontogenetic diet shift of Hovsgol grayling observed in our study has also been observed in studies on Arctic grayling in inland lakes. Juvenile Arctic grayling are commonly planktivorous (Merrick et al. 1992; Schmidt and O'Brien 1982), while adults rely more heavily on benthic production (O'Brien et al. 1979; Sierszen et al. 2003). In fact, Schmidt and O'Brien (1982) found that grayling larger than 170 mm could not be enticed to feed on zooplankton in the laboratory. Arctic grayling gill raker spacing increases with body size, up to 130 mm, suggesting a morphological mechanism for the shift in diets (Schmidt and O'Brien 1982).

Diets from larger Hovsgol grayling collected offshore suggest that they rely heavily on benthic production. However, we rarely observed grayling of any size below 50 m during the day or night. This is unlikely to be a physiological limitation as water

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temperatures and oxygen levels below 50 m are sufficiently high (> 4°C and > 8 mg $O_2 \cdot l^{-1}$). The predominance of benthic invertebrates in larger grayling diets suggests that they are either migrating to littoral areas to feed benthically or are consuming emerging or vertically migrating benthic organisms in the water column. The former is not likely given that day and night density estimates were similar for grayling at most transects and depths. The latter is more likely given the diversity of bottom invertebrates, approaching 300 known species in Lake Hovsgol, some of which migrate off the bottom at night to feed or emerge as adults (Erbaeva et al. 2006; Erbaeva and Safronov 2006; Safronov 2006). Our fine mesh zooplankton net was likely unsuitable for capturing these larger organisms. Future research should include sampling with larger nets and mesh sizes.

Because Hovsgol grayling use a variety of habitats (e.g. littoral and pelagic areas) they are vulnerable to a variety of threats (e.g. climate change, invasive species, poaching, etc.). This emphasizes the importance of effective monitoring and management strategies (Grumbine 1994), which should be based on the results found here. Given the relatively low population densities of grayling, and the threat of a changing climate around Lake Hovsgol (Punsalmaa et al. 2005), we recommend regular lakewide monitoring of the grayling population. In addition to climate change, the introduction of invasive species to Lake Hovsgol offers significant threats to grayling, because they are the only fish species present in the pelagia. A successful introduction of a competitor, such as omul (*Coregonus migratorius*), or a predator, such as lake trout (*Salvelinus namaycush*), could significantly reduce the forage base available for grayling or increase their predation risk in pelagic areas. Interestingly, omul were introduced to

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Lake Hovsgol from Lake Baikal in 1956 – 1957 (Sideleva 2006) but we found no evidence of their presence. Prevention of the spread of invasive species should come in the form of education and awareness in high-use areas of the lake (e.g. in the towns of Hatgal and Khankh). Illegal fishing, gillnetting, and beach seining also threatens the grayling population, despite the closure of the fishery in 1995 when Hovsgol National Park was established. The minimal resources available for enforcement of current regulations should focus on areas with highest grayling densities which, based on our results, are located in littoral areas along the western shores of the lake.

Our study indicates that Hovsgol grayling densities are low compared to pelagic fish densities in other large lakes; however, this difference may simply represent the natural ultra-oligotrophic conditions of Lake Hovsgol. Hovsgol grayling diets and spatial distributions suggest that they are generalists, able to feed on a variety of food resources in different habitats throughout their lives. Despite this, it is important to develop conservation strategies to ensure the long-term health of this species. Specifically, conservation decisions should consider the primary threats to grayling in regards to their current lakewide densities and distributions. While our study provides important knowledge not previously documented, future research should investigate seasonal and yearly changes to the grayling population throughout the lake. In addition, examining Hovsgol grayling reproduction in terms of spawning site fidelity and success rates of in-lake versus stream spawning would be beneficial. Ultimately, a better understanding of the broader ecology and food-web of Lake Hovsgol will improve our ability to manage and monitor Hovsgol grayling and this unique ecosystem.

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Chapter 3

Food resource effects on diel movements and body size of cisco (*Coregonus artedi*) in north-temperate lakes

Introduction

Diel vertical migration (DVM) patterns of aquatic species have been widely studied (see reviews by Haney 1988; Mehner 2012). Normal DVM is the vertical movement of organisms from deeper water during the day to shallower water at night, and has been frequently documented for phytoplankton, zooplankton, and fishes (Bohl 1980; Clark and Levy 1988). Reverse DVM, characterized by an evening descent and morning ascent in the water column, has been infrequently documented for zooplankton and even more rarely for fishes (Jensen et al. 2011; Levy 1990; Sims et al. 2005). No diel change in the vertical distribution of organisms is not commonly documented, but occurs regularly (Gliwicz and Pijanowska 1988). Hutchinson (1957) posited that there is a continuum of potential diel movements for organisms (see also Haney 1988). For example, normal or reverse DVM patterns may range from a few meters to a few hundred meters in magnitude for different species in different aquatic environments (Ahrenstorff et al. 2012; Sims et al. 2005). DVM patterns may also vary for the same species among lakes, where there may be no DVM pattern of a particular species in one lake while normal or reverse DVM patterns may exist for the same species in other lakes (Gliwicz and Pijanowska 1988; Johnson and Jakobsen 1987). While considerable variability in movement patterns of species has been observed, no studies have examined a variety of

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normal DVM, no DVM, and reverse DVM patterns for a single fish species in a range of aquatic ecosystems. This type of systematic comparison of migration patterns along a gradient of environmental conditions between lakes is necessary to advance our knowledge of DVM behavior (Mehner 2012).

The diverse movement patterns of aquatic species are perhaps not surprising given the range of environmental conditions among lakes that are known to influence species distributions (see reviews by Clark and Levy 1988; Mehner 2012). Combinations of factors such as light, temperature, oxygen, foraging, growth, and predation risk are all known to influence vertical movement patterns of various species. Light levels, which are a determinant of foraging ability and predation risk, are commonly listed as the proximate stimulus for migrations to occur during dawn or dusk, and may be important for determining the depth at which organisms reside during the day or night (Appenzeller and Leggett 1995; Forward 1988). Temperature and oxygen conditions often limit the extent of many migrations, because strong thermal gradients in the metalimnion or warmer temperatures near the surface and low oxygen content near the bottom of a lake may make these habitats unsuitable for many organisms (Magnuson et al. 1979; Rudstam and Magnuson 1985). Additionally, the ability of an organism to forage at different depths under different light regimes may further influence movements, where organisms typically migrate to areas of highest foraging potential in the water column (Ahrenstorff et al. 2011; Werner and Mittelbach 1981). Growth potential, or bioenergetic optimization, may also influence movements because migrating individuals may gain a metabolic advantage over non-migrating individuals by feeding in warmer surface waters

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and then migrating to cooler areas to digest their food (Brandt et al. 1992; Mason and Brandt 1996). Lastly, predation risk may modify the movement patterns of species, where organisms tend to migrate out of areas of highest predation risk in the water column (Iwasa 1982; Werner et al. 1983). Models of temperature/oxygen (Rudstam and Magnuson 1985), foraging (Gerritsen and Strickler 1977), growth (Rudstam et al. 1994), and predation risk (Gerritsen and Strickler 1977) have been developed in order to empirically examine the potential role of each of these selective forces or a combination therein (See also Ahrenstorff et al. 2011; Jensen et al. 2011).

It is rare that a single factor drives the movements of an organism (Mehner 2012). Instead, there are likely tradeoffs among selective forces that ultimately determine migration patterns. The importance of these tradeoffs may change given different environmental conditions among lakes. For example, when food availability is high throughout the water column, *Daphnia hyalina* avoid predation risk by remaining in the hypolimnion (Gliwicz and Pijanowska 1988); however, when food availability is low throughout the water column, *Daphnia* spp. spend most of their time feeding near the surface despite the higher predation risk (Johnson and Jakobsen 1987). Similar behavioral changes in movement patterns have been observed for juvenile fishes (Walters and Juanes 1993), anuran tadpoles (*Rana* spp.) (Anholt and Werner 1995), and Serengeti wildebeest (*Connochaetes taurinus*) (Sinclair and Arcese 1995). In general, it appears that as food becomes limiting animals will take greater risks to obtain it. Clearly, different migration patterns are driven by a variety of factors that must be explored in diverse ecosystems to identify the extent of behavioral plasticity for a given species.

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Differences in environmental conditions (e.g. food availability, water temperatures, etc.) among lakes and movement patterns of organisms within lakes may cause differences in growth rates among individuals between populations. This tendency was first recognized for coregonines 150 years ago in central European lakes (von Siebold 1863), and has since been studied for coregonines in northern Wisconsin lakes (Hile 1938) and in Lake Superior (Todd et al. 1981). One of the most common differences between cisco populations throughout the northern hemisphere is growth, where dwarfing, or stunting, is common resulting in slower growth rates of individuals within a population (Shields and Underhill 1993). Environmental factors, such as density dependence, low food availability, or lake characteristics likely play a larger role in altering growth rates of coregonines compared to genetic factors (Loch 1974; Todd et al. 1981). For example, when dwarf cisco (*Coregonus artedi*) were transferred from Ten Mile Lake, Minnesota, into three experimental lakes previously void of cisco, they lived longer and grew to larger sizes (Shields and Underhill 1993). While environmental factors are thought to influence cisco growth, the specific mechanisms are largely unresolved.

The objectives of this study were to examine cisco populations in a variety of inland lakes in order to (1) investigate variability in DVM patterns, (2) explore the causal mechanisms influencing different movements, and (3) examine factors that may cause variations in cisco body size. To address objective one, we used hydroacoustic and vertical gillnet data from 11 study lakes collected in 1996-1997 and 2010-2011 to empirically characterize the dynamic movements of cisco. We hypothesized that cisco

movements would be variable among lakes with differing characteristics. To address

objective 2, we used temperature/oxygen, foraging, growth, and predation risk models to

determine the potential role of each of these factors in influencing cisco vertical

distributions. Based on previous studies, we hypothesized that lakes with low foraging

potential would have cisco that exhibited risk taking behavior that maximized foraging,

while lakes with higher food availability would have cisco that either moved little or

exhibited normal DVM and predator avoidance behavior during the day. Finally, we

combined information on cisco movements and environmental conditions within lakes to

examine mechanisms underlying phenotypic plasticity in cisco populations. We

hypothesized that cisco body size would vary among lakes and would be driven by

differences in the environmental conditions and movements of cisco in each lake (e.g.

Todd et al. 1981).

Materials and Methods

Study locations

        During summer, we sampled 11 lakes in northern Wisconsin (*n*=7) and across

Minnesota (*n*=4) in 1996-1997 and 2010-2011, respectively (Figure 7). These lakes

varied considerably in their physical conditions in terms of surface area (105 – 2042 ha),

maximum depth (14 – 63 m), and Secchi depth (2 – 6 m) (Table 2). The lakes varied in

biological conditions as well. Zooplankton densities and species composition varied in

each lake with most containing some combination of copepods, cladocerans, and macro-

zooplankton (e.g. *Chaoborus* spp. and *Leptodora kindti*), but only a few having either

high proportions of copepods or abundant macro-zooplankton. The fish communities were similar among lakes, with cisco and walleye being abundant in each. The abundance and morphology (e.g. average size) of cisco were variable between lakes (Table 2). These differences in physical and biological traits provided a diverse set of conditions to identify the mechanisms influencing vertical movements and the overall impact of habitat on the average size of cisco among lakes.

Fish communities

The composition of pelagic fish species present in each lake was determined using vertical gillnets with varying mesh sizes set overnight (6 – 20h) during each sampling date. Each vertical gillnet (of each size) was 3 m wide and set from the surface to the bottom of the lake in the deepest location of each lake. In the Wisconsin lakes, we used individual vertical gillnets with mesh sizes of 10, 13, 16, 19, 26, and 32 mm bar mesh. In the Minnesota lakes, mesh sizes of 10, 13, 19, 32, and 51 mm bar measure mesh were used for individual nets. Fish captured in each vertical gillnet were identified, enumerated, and measured for total length to the nearest mm. Length-frequency distributions were constructed for cisco captured in each lake in order to determine the range and average size of cisco present.

Cisco densities and vertical distributions

Densities and vertical distributions of cisco were determined using a combination of hydroacoustics and ground truthing data collected with vertical gillnets in each lake.

Hydroacoustic data was collected during the day and night in each lake by sampling transects in a systematic zig-zag design throughout water greater than 10 m in depth. The amount of hydroacoustic data collected in each lake was proportional to the size of each lake, and followed the recommendations of Aglen (1983). In the Wisconsin lakes, a 70 kHz Simrad echosounder was used in 1996 and a Hydroacoustic Technologies 120 kHz split-beam echosounder was used in 1997. In the Minnesota lakes, a 70 or 120 kHz split-beam, Biosonics, Inc., DT-X hydroacoustic echosounder was used in 2010 and 2011. Hydroacoustic collection and analysis methods were analogous to the standard operating procedure for the Great Lakes for all lakes sampled (Rudstam et al. 2009). Each acoustic unit was calibrated in each research lake and the measured target strength of the calibration sphere never varied significantly from its expected target strength in any lake.

To estimate the density and vertical distribution of cisco during the day and night in each lake, we calculated the volumetric fish density (fish m^{-3}) of cisco-sized targets in 30 min time intervals over 2 m depth bins. Fish density in each bin was estimated using the echo integration method (Parker-Stetter et al. 2009; Echoview software version 4.10, SonarData Ply Ltd., Tasmania), which uses the linear mean volume backscattering coefficient (s_v), and the proportion and mean target strength of cisco-sized targets. The lower s_v threshold was lake dependent, and was set 6 dB below the minimum target strength of cisco in each lake (Rudstam et al. 2009). This method avoided including backscatter from targets smaller than the smallest sized cisco, such as *Chaoborus* or other zooplankton species. Proportions and mean target strengths for cisco were determined using vertical gillnet catch data from each lake. Average cisco sizes (mm) were

converted to decibel (dB) readings according to Love's (1977) equation for fish in the dorsal aspect. Because cisco were the dominant pelagic species in each lake, we are confident our hydroacoustic estimates for cisco are accurate. Average density estimates of cisco in each inland lake were determined using night-time hydroacoustic estimates because of schooling behavior during the day (Appenzeller and Leggett 1992). Day and night hydroacoustic density estimates, in the 2 m depth bins, were used to determine the diel movements of cisco during the day and night in each lake.

Temperature/oxygen, foraging, growth, and predation risk models

In order to determine the factors influencing cisco movement patterns, we used temperature/oxygen, foraging, growth, and predation risk models. We then compared the observed distribution of cisco in each lake with each model's prediction during the day and night by using Schoener's index (1970). This index calculates a percent overlap between the observed and predicted distribution of animals:

(1) $\quad 100\left(1 - \frac{1}{2}\Sigma|p_{x,i} - p_{y,i}|\right)$

where $p_{x,i}$ and $p_{y,i}$ are the observed and predicted proportions of cisco in each depth bin i. The percent overlap indicates the strength that factor may play in driving cisco distributions in each lake. We calculated an average percent overlap value for the day and night estimates across all years for each lake. We used a two-factorial ANOVA to test for differences in the performance among models across all lakes and for differences in the performance of each model within groups of lakes with differing migration patterns of cisco (i.e. no DVM, reverse DVM, and normal DVM) ($\alpha = 0.05$). Lastly, we used a

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linear regression to compare the performance of each model across lakes with different

sized cisco populations ($\alpha = 0.05$). All values were log transformed which normalized

the data set for statistical analyses (verified using Shapiro-Wilk and Anderson-Darling

normality tests).

The temperature/oxygen (T/O) model created for cisco by Rudstam and

Magnuson (1985) was used to predict the proportion of cisco that should be found at each

depth (in 2 m intervals) during the day and night in each lake. According to the model,

cisco have an optimal temperature preference of 12°C and avoid temperatures above

17°C. They prefer oxygen levels above 4.4 mg/L, and have a lower lethal limit of 1.9

mg/L. We collected temperature and oxygen data in each lake in 1996 – 1997 using a

YSI model 57 unit, and in 2010 – 2011 using a YSI model 85 unit. Further information

about the T/O model can be found in Rudstam and Magnuson (1985).

To determine areas in the water column where foraging potential would be

maximized for cisco, we used a foraging rate potential (FRP) model developed by

Gerritsen and Strickler (1977) as applied by Ahrenstorff et al. (2011) for cisco in Lake

Superior:

(2) $\qquad FRP = \left(\dfrac{\pi R_{ij}^2}{3} \right) \left(\dfrac{3v_j^2 + v_i^2}{v_j} \right) d_i$

where R_{ij} is the reaction distance (m) of a predator j (cisco) to prey i (zooplankton), v_j and

v_i are the swimming speeds (m min^{-1}) of predator and prey, and d_i is the prey density (#

m^{-3}). Reaction distance was calculated using a function created by Wright and O'Brien

(1984) and swimming speeds were estimated using an allometric equation developed by

Rudstam et al. (1994). For detailed descriptions of these equations, or how the FRP

model can be applied to predict cisco distributions, refer to Ahrenstorff et al. (2011).

Light levels in the water column (used to determine reaction distances) were collected

using a Li-Cor model LI-1400 light meter during the day and night in each lake. In order

to determine prey densities in the water column, we first determined which prey items

were consumed by cisco in each lake, and then used that information to determine the

density of those prey items throughout the water column. We analyzed up to 50 cisco

diets from each lake and date to determine their average diet composition (% by mass).

Mass estimates for zooplankton species were determined from length-weight regressions

provided by the U.S. Environmental Protection Agency (SOP-LG403, 2003). Next, we

examined the vertical distribution of those prey items by collecting zooplankton samples

using a Schindler-Patalas plankton trap in 2 m intervals from the surface to the bottom of

each lake during the day and night. In the Wisconsin lakes, a 2 m tall, 45 L trap, was

used with a 53 μm mesh collecting cup. In the Minnesota lakes, a 1/2 m tall, 30 L trap,

was used with a 63 μm mesh collecting cup.

Estimates of growth rate potential (GRP) were derived by incorporating estimates

of foraging potential inputs and temperature dependent bioenergetics equations acquired

from the generalized coregonine model (Rudstam et al. 1994). We simulated growth

potential for cisco in 2 m depth intervals in each study lake during the day and night. See

Ahrenstorff et al. (2011) for a detailed description of the GRP model application for

cisco.

Predation risk (μ) for cisco in the water column was determined using an equation similar to equation (2), with the density term (d_j) excluded. By not including predator densities, we were simulating where predation risk would be highest in the water column under the assumption that predators could move anywhere to maximize their foraging ability. In this case, our simulations predicted that predation risk is higher for cisco near the surface where light intensities are greater compared to other areas. Other inputs into equation (2) include swimming speeds for piscivores j (e.g. walleye) and prey i (cisco), and reaction distances for predator and prey. Piscivore swimming speeds were estimated to be 3 m min^{-1} (Bahr 1977) while cisco swimming speeds were determined using an allometric equation developed by Rudstam et al. (1994). Reaction distance for piscivores and cisco were calculated using a function created by Wright and O'Brien (1984) which incorporates prey size and light intensity from each lake. A lower percent overlap between the predation risk model and the observed distribution of cisco indicates that cisco are avoiding predation, while a higher percent overlap indicates they are located in higher predation risk areas.

Determinants of cisco size

We used linear regression to compare the average size of cisco to cisco density across all lakes, with zooplankton density as a covariate, to test for the influence of density dependence on the average size of cisco (α=0.05). We then tested for the influence of resource limitation on cisco sizes, by comparing the average size of cisco,

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and maximum size of cisco, to zooplankton densities across all lakes using linear
regression (α=0.05). All values were log transformed to normalize the data set.

Results

Fish communities

In the 11 study lakes we captured a total of 3,203 cisco and numerous piscivores
including walleye (*Sander vitreus*; *n*=18), northern pike (*Esox luscius*; *n*=5), and
largemouth bass (*Micropterus salmoides*; *n*=2) using vertical gillnets. Other non-
piscivores captured less frequently than cisco included black crappie (*Pomoxis
nigromaculatus*; *n*=2), lake whitefish (*Coregonus clupeaformis*; *n*=4), white sucker
(*Catostomus commersonii*; *n*=2), and yellow perch (*Perca flavescens*; *n*=196). We
measured total length for a subset of all cisco captured, and created length-frequency
distributions to estimate differences in cisco body size between lakes (Figure 8). There
was a gradient in the average size of cisco caught in the study lakes (Table 2), with the
smallest sized cisco being found in Ten Mile Lake (average=124 mm) and the largest in
Papoose Lake (average=300 mm).

Cisco densities and vertical distributions

Cisco density estimates calculated using hydroacoustics at night averaged
between 168 – 4,214 fish ha^{-1} in the study lakes (Table 2). Cisco vertical migrations were
variable in the study lakes (Figure 9). No discernible DVM pattern of cisco was observed
in Clear, Elk, Papoose, or White Iron Lake (~0 m average change in depth between the

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day and night). Reverse DVM patterns of different magnitudes were documented in Lake

Carlos (~5 m change in depth), Manitowish Lake (~8 m movement), Ten Mile Lake (~22

m movement), and Trout Lake (~12 m movement). In Trout and Manitowish lakes, only

a portion of the cisco population performed a reverse DVM while the other portion did

not migrate. Normal DVM patterns were documented in Big Lake (~5 m change in

movement), Dead Pike Lake (~ 6 m movement), and Little Star Lake (~5 m movement).

Model predictions

The T/O, FRP, GRP, and μ models require empirical inputs including the

temperature and oxygen conditions of each lake, the composition of prey items in cisco

diets (Figure 10), and the location and density of those prey items in the water column.

In many of the lakes, water temperatures were either too warm near the surface (> 17°C)

or oxygen levels were too low near the bottom of the lake (< 1.9 mg L^{-1}) to support cisco

populations for extended periods. Cisco diets were variable between lakes and also

variable between years in the same lake. The primary prey items consumed included

copepods, *Daphnia* spp., *Bosmina longirostris*, *Hexagenia* spp., *Leptodora kindti*, and

Chaoborus spp. Other prey species consumed less frequently (< 5% of the total mass

consumed) included *Chydorus sphaericus*, chironomid larvae, chironomid pupae,

Diaphanasoma birgei, and terrestrial insects. Because cisco diets were so variable

among lakes and years in the same lake, we used the density and distribution of all

zooplankton species found in cisco diets in each lake as the input into our foraging and

growth models.

Based on the average percent overlap between the expected and predicted distribution of cisco for each of the models (for example see Figure 11) across all lakes, the T/O model performed significantly than the FRP, GRP, and μ models (P=0.006; Figure 12). By splitting the lakes into categories defined by the type of movement pattern shown (no DVM, reverse DVM, and normal DVM), there was no significant difference in model performance for the T/O, FRP, GRP, or μ models among each group of lakes (all P-values > 0.05).

Model performance for each of the four models varied with changes in the average size of cisco present in each lake. For the T/O model, model performance was lowest for lakes with the smallest sized cisco and model performance increased significantly as the average size of cisco increased in each lake ($F_{1,9}$=5.28; P=0.047) (Figure 13). The opposite pattern was observed for the FRP ($F_{1,9}$=6.34; P=0.033) and GRP ($F_{1,9}$=5.40; P=0.045) models, where lakes with the smallest sized cisco had the highest model performance and model performance decreased significantly as the average size of cisco increased (Figure 13). For the μ model there was a general, albeit non-significant, trend where lakes with the smallest sized cisco were located in areas of highest predation risk, and model performance decreased as the average size of cisco increased in each lake ($F_{1,9}$=1.02; P=0.34; Figure 13).

Determinants of cisco size

There was no relationship between the average size of cisco and cisco density in the study lakes, with zooplankton density as a covariate ($F_{3,8}$=1.95; P=0.21). However,

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zooplankton density was positively correlated with the average size of cisco ($F_{1,9}$=5.41; P=0.045; Figure 14) and maximum size of cisco ($F_{1,9}$=9.33; P=0.014) in all inland lakes.

Discussion

Our findings are consistent with other studies in that we observed different vertical movement patterns of a planktivore (i.e. no DVM, reverse DVM, or normal DVM) in lakes that varied in physical and biological characteristics. For example, in British Columbia lakes, juvenile sockeye salmon (*Oncorhynchus nerka*) perform normal and reverse DVM in different lakes depending on predator densities or levels of competition with other planktivores (Levy 1990). Physico-biological influences in migration patterns are also apparent near the North Sea where the basking shark (*Cetorhinus maximus*) performs reverse DVM in shallow, inner-shelf areas while migrating normally near deep, stratified waters (Sims et al. 2005). While we observed changes in migration patterns for lakes with different available habitats, our analyses of competing models failed to provide a clear underlying mechanistic shift between migration patterns among lakes. This result was driven by strong risk taking behavior exhibited by smaller cisco in lakes with lower zooplankton densities.

While the mechanisms causing no DVM, reverse DVM, or normal DVM appear different in each inland lake, our modeling results indicated that movement patterns of cisco were related to their average size in each lake. The size of cisco was certainly associated with the amount of available food. As a consequence, differences in the amount of food available likely alters the importance of the various other niche

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dimensions including temperature/oxygen, foraging, growth, or predation risk concerns

for cisco in each lake. For example, when lower densities of zooplankton prey were

available in a lake, cisco maintained a smaller average size and migrated to areas of

optimal foraging (FRP model) and bioenergetic maximization (GRP model), in spite of

moving out of areas of ideal temperature/oxygen (T/O model) conditions and into areas

of higher predation risk (μ model). In Ten Mile Lake during 2010 and 2011, the majority

of the dwarf cisco population migrated up into shallow high predation risk areas ($\sim 5 - 10$

m below the surface) during the day, presumably to feed, while temperature conditions

approached $20 - 23°C$ at those depths. This temperature exceeds estimates of their

thermal optimum by several degrees (see Rudstam et al. 1993). Organisms migrating

into areas of higher predation risk and temperature conditions when food is limiting has

also been observed for zooplankton (Johnson and Jakobsen 1987), juvenile fishes

(Walters and Juanes 1993), amphibians (Anholt and Werner 1995), and large mammals

(Sinclair and Arcese 1995). Similar to studies on *Daphnia hyalina* (Gliwicz and

Pijanowska 1988), when more food was available cisco grew larger and had movement

patterns more consistent with behavioral thermoregulation and predator avoidance, and

did not migrate to areas of higher foraging or growth potential. These results suggest that

prey density may shift tradeoffs between temperature/oxygen, foraging, growth, and

predation risk concerns causing a range in potential vertical movement patterns of cisco.

If temperature and oxygen conditions or predation risk were driving the patterns in cisco

movements, we would not expect smaller sized cisco to migrate to areas above their

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thermal tolerance or into areas of highest predation risk in the water column as was observed.

Mehner and Kasprzak (2011) documented that only a portion of the *Coregonus* spp. population in Lake Stechlin, Germany, migrated while the other portion resided at similar depths during the day and night. Similarly, in a subset of our study lakes a portion of the cisco population migrated, while the other portion did not. Mehner and Kasprzak (2011) noted in their study that the proportion of non-migrants increased when foraging potential was lower deeper in the water column during the day. They also found that larger sized individuals tended to migrate while smaller individuals were often non-migrants. In our study, we found no relationship between the proportion of migrants and non-migrants compared to zooplankton densities in the water column. We also found no difference in the average size of migrants and non-migrants based on vertical gillnet catches of cisco at different depths in each lake. While the factors causing migrant and non-migrant behavior remain unclear, studies of individual fish and their behaviors using acoustic tags may yield additional insight. For example, it is possible that individuals may make more than one foray into shallow or deep water during a 24-hr period.

While the density and distribution of prey seems to play a large role in influencing cisco movements, the species composition of prey items consumed by cisco may also play a role in causing partial migrations or different DVM patterns. Cisco are known as generalists and are able to feed on a wide variety of prey items (Ahrenstorff et al. 2011; Dryer and Beil 1964). In the three lakes where cisco performed the most noticeable reverse DVM (i.e. Ten Mile, Trout, and Carlos) their diets were dominated by copepods

and small cladoceran species. Cisco also performed a reverse DVM in Manitowish Lake where they fed primarily upon *Chaoborus* spp.; however, a large portion of the population did not migrate perhaps because of the availability of this other prey resource. In the other seven lakes where cisco performed normal DVM or did not migrate, they consumed a much higher proportion of macro-zooplankton such as *Hexagenia* spp. and *Chaoborus* spp. both of which migrate off the bottom under low light conditions. Big Lake was the only exception where cisco consumed primarily *Daphnia* spp. but still performed normal DVM. Cisco may not perform a reverse DVM in these seven lakes because they are able to feed at high enough rates on macro-zooplankton higher in the water column at night to satisfy their energetic demands.

The average size of cisco was correlated with the amount of prey available among lakes and may be further confounded by the movements of different sized cisco. Cisco populations that were on average smaller were found in lakes with lower zooplankton densities and likely had higher metabolic costs by sometimes migrating to areas several degrees above their thermal preference in search of food. Cisco populations with a larger average size were present in lakes with higher densities of zooplankton and were more sedentary by staying near their temperature/oxygen preference instead of moving to find food. While there was some variability in cisco sizes within each lake, there was no apparent trend in different movement patterns of these different sized individuals. This suggests that despite the fact that a couple lakes contained a wider range in cisco size, average size was still a reasonable predictor of the mechanisms that influenced cisco movements. Additionally, the linear regressions between cisco average size and the

mechanisms influencing DVM behavior contained no outliers. While it is possible that a weak or strong year class of cisco may shift the migration behavior of the population slightly, we would expect their DVM pattern to shift according to the mechanisms we have identified, although we were unable to test this due to the short time series of data we collected in each lake. Low food availability and intraspecific competition due to overcrowding are both known to cause dwarfing of fish populations (Rask 1983; Sandheinrich and Hubert 1984). Density dependent competition does not seem to play a large role for these cisco populations, because cisco densities were not correlated with the average size of cisco. Instead, there was a gradient in the average size of cisco among lakes that was correlated with food availability and cisco movement patterns. The relatively continuous range of mean sizes of cisco, or more appropriately, the lack of a bimodal size distribution among most lakes, supports this view.

Although there is a rich history of studies examining DVM behavior, to the best of our knowledge there are no studies that have examined populations of a fish species that perform normal DVM, no DVM, and reverse DVM in different aquatic environments. Ultimately, the movement patterns of cisco (normal DVM, no DVM, or reverse DVM) could not be described by a particular set of mechanisms, because each lake had very different physical and biological conditions causing different movement patterns. Instead, average sizes and movement patterns of cisco were variable between lakes and were influenced by prey density. In lakes with lower prey densities, cisco maintained a smaller average size, and migrated to areas allowing for maximum foraging

and growth potential. In lakes with higher prey densities, cisco grew larger, and migrated

to optimal temperature/oxygen conditions where predation risk was minimized.

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Chapter 4

Seasonal changes in reverse diel vertical migrations of dwarf cisco (*Coregonus artedi*) in Ten Mile Lake, Minnesota

</div>

Introduction

The mechanisms driving diel vertical migrations (DVM) are becoming better understood through a large body of literature over the last century (Bohl 1980; Hays 2003; Hutchinson 1957). There is a general consensus that normal DVM patterns (i.e. morning descent and evening ascent in depth) are typically related to maximizing foraging or growth potential while minimizing predation risk (Mehner 2012). Comparatively, reverse DVM (i.e. morning ascent and evening descent in depth) is not well understood, especially for fishes, where only a few studies have documented the behavior. For example, young fishes in the San Francisco Estuary perform reverse DVM to facilitate retention in the estuary under different currents (Bennett et al. 2002), and the basking shark (*Cetorhinus maximus*) migrates reversely near inner shelf areas of the Clyde Sea to maximize consumption of reverse migrating *Calanus* species (Sims et al. 2005). Cisco (*Coregonus artedi*) perform reverse migrations in some inland lakes, while not in others, depending on the type of prey resources and the foraging, growth, and predation risk conditions in each lake (Ahrenstorff et al. In review). Other studies documenting reverse DVM of sockeye salmon (*Oncorhynchus nerka*) and Atlantic herring (*Clupea harengus*) conclude it to be a means of maximizing foraging potential higher in the water column during the day while avoiding predation risk of deeper

piscivores (Jensen et al. 2011; Levy 1990; Stockwell and Johnson 1999). For the majority of these studies, maximizing foraging or growth potential while minimizing predation risk (low risk, high reward) seems to drive the reverse DVM behavior. There are few, in any, examples in the literature where a planktivore performs different reverse DVM behaviors among seasons according to low risk, low reward or high risk, high reward strategies.

Foraging, growth, and predation risk models are methods used recently for determining the potential role of foraging, growth, and predation risk in influencing DVM behavior (Ahrenstorff et al. 2011; Jensen et al. 2011). Foraging models incorporate prey densities, prey and predator swimming speeds, and predator reaction distances to predict areas of highest foraging potential in the water column (Gerritsen and Strickler 1977). Growth, or bioenergetic, models use consumption rates, and temperature dependent rates of respiration, specific dynamic action, egestion, and excretion to predict areas of highest growth rate potential in the water column (Kitchell et al. 1977). The location of predators, or a risk model, is generally used to examine potential predation risk to a prey species (e.g. Mason and Patrick 1993). The results of most studies on normal or reverse DVM patterns that use these models describe situations where organisms migrate according to a low risk, high reward strategy. However, when that migration strategy is not possible, organisms may perform normal or reverse migrations according to high risk, high reward or low risk, low reward strategies (Ahrenstorff et al. In review; Jensen et al. 2006). In some situations, these different strategies can lead to

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partial migrations where a portion of a population migrates while the other portion does not (Jensen et al. 2011; Mehner and Kasprzak 2011).

Migration patterns would be expected to change as changes in water temperature, foraging or growth potential, and predation risk change among seasons. The majority of studies on reverse DVM behavior, however, have only examined one or two seasons. Jensen et al. (2011) and Ahrenstorff et al. (In review) examined data from August, Sims et al. (2005) used data from June, Bennett et al. (2002) analyzed data from April-June, Stockwell and Johnson (1999) used data from June-August, and Levy (1990) considered data from June and September. Given that other DVM strategies are known to change seasonally (Ahrenstorff et al. 2011), examinations of data on reverse migrating populations from spring, summer, fall, and winter may provide information to better explain how and why reverse migrations occur and whether they occur throughout the entire year.

DVM patterns exhibited by cisco, both reverse and normal, are becoming better understood in recent years. In Lake Superior, cisco perform normal diel vertical migrations primarily during summer, with distribution patterns being much more variable and potentially dependent on year to year variability in spring and fall (Ahrenstorff et al. 2011; Hrabik et al. 2006; Stockwell et al. 2010). In nearby smaller temperate lakes, cisco populations perform a range of DVM patterns including normal DVM, no DVM, and reverse DVM in different lakes during summer (Ahrenstorff et al. In review). The range in DVM patterns is apparently related to the size and growth of cisco in each lake. Lakes with less available food contained smaller cisco that exhibited lower growth and had

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DVM patterns consistent with maximizing foraging and growth potential, despite moving out of preferred temperature and oxygen conditions and into areas of highest predation risk. On the other hand, cisco populations in lakes with abundant food were composed of larger sized, faster growing, individuals that remained in areas of optimal temperature and oxygen conditions and avoided predation risk, instead of migrating to areas that would increase or maximize foraging and growth. Ten Mile Lake (Ahrenstorff et al. In review) had the smallest sized cisco of the 11 lakes studied (average of 124 mm total length) where they are often referred to as dwarf cisco. This population also had the most extensive reverse DVM pattern of cisco compared to the other lakes. Owing to the uniqueness of this lake (e.g. dwarf cisco and extensive reverse DVM), we conducted a more extensive set of surveys over multiple seasons and years to provide insight on variability in reverse DVM behavior in this unique population.

The purpose of this study was to examine changes in the reverse DVM pattern of dwarf cisco in Ten Mile Lake, Minnesota, in spring, summer, fall, and winter over multiple years. Our first objective sought to empirically document seasonal changes in the migration pattern of cisco by using hydroacoustics and vertical gillnetting. Our second objective used estimates of foraging, growth, and predation risk to evaluate the mechanisms causing different migrations during different seasons. We hypothesized that cisco would perform the most extensive reverse DVM during summer, when prey, thermal, and light gradients were most distinct (Ahrenstorff et al. In review). We predicted that reverse DVM patterns would be less extensive during spring and fall due to changes in light, temperature, prey availability, growth, and predation risk, the latter of

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which are temperature dependent. This result would also be similar to the less extensive

normal DVM patterns of cisco in Lake Superior observed during spring and fall

(Ahrenstorff et al. 2011). Lastly, we hypothesized that there would be no DVM during

the winter months because of low prey availability, and more uniform foraging, growth,

and predation risk conditions owing to pervasive low light and isothermal conditions.

Methods

Study Lake

We examined reverse DVM patterns of dwarf cisco in Ten Mile Lake, Minnesota

(N46°58'14" W94°34'21") (Figure 15) during the summer of 2010 and the spring,

summer, fall, and winter of 2011 and 2012. Ten Mile Lake has a surface area of 1,890 ha

and maximum depth of 63 m. The lake is considered oligotrophic and exhibits an

average Secchi disk transparency between 4 – 6 m during summer.

Physical sampling

We used vertical gillnets to determine the proportion of different pelagic species

present in Ten Mile Lake, the size distribution of cisco, and their diet composition. Each

gillnet was 3 m wide and set from the surface to the bottom of the lake at the same

deepwater location within the lake during each survey date (Figure 15). To establish the

proportion of different pelagic species present in Ten Mile Lake, we set five vertical

gillnets of different mesh sizes (10, 13, 19, 32, and 51 mm bar measure mesh) overnight

during the summer of 2010 and 2011. Because the majority of the catch was cisco during

those sampling events (97.5%), and cisco were almost exclusively captured in the 10 and

13 mm mesh nets (99.3%), we only set those two nets during the spring of 2011 and

summer of 2012. During winter, we set the 13 mm mesh net in 2011 and the 11 mm

mesh net in 2012 under the ice, in order to capture cisco for diet analyses across seasons.

We did not sample using gillnets during the spring of 2012 and the fall of 2011 and 2012

because catches were consistently dominated by cisco. All fishes that were captured in

the vertical gillnets were identified, counted, and measured to the nearest mm. Stomachs

were removed from a subset of up to 50 cisco from each survey date to determine their

diet composition. Within each individual stomach, all prey organisms were counted and

converted to mass estimates using length-weight regressions provided by the U.S.

Environmental Protection Agency (SOP-LG403 2003). These different combinations of

gillnetting surveys allowed us to determine the proportion of pelagic species present in

Ten Mile Lake, the size distribution of cisco, and their diet composition across seasons.

Hydroacoustic data were collected from Ten Mile Lake during the day and night

of each season and year to determine diel, seasonal, and yearly changes in vertical

distributions of cisco (Figure 15). We collected hydroacoustic data using a 70 kHz, split-

beam, DT-X hydroacoustic echosounder mounted on a Biofin tow-body which was towed

alongside the research vessel at a depth of 1 m from the surface at speeds of 2-3 m/s

(Biosonics, Inc., Seattle, WA). During the spring, summer, and fall we collected data

using a consistent systematic design with a sample density of 0.78 km/km^2 transect

distance to area ratio. In winter, we drilled holes through the ice and collected stationary

hydroacoustic data for 3-5 hours during the day and again at night at the deepest location

of the lake. Data collection and processing followed guidelines provided by the

Larentian Great Lakes standard operating procedure (Parker-Stetter et al. 2009; Rudstam

et al. 2009). Our hydroacoustic unit was calibrated during each survey using a 38 mm

tungsten carbide sphere and comparing its estimated acoustic strength to the known

value. Calibration offsets were applied during post processing when the observed sphere

target strength deviated from the theoretical target strength, according to the standard

operating procedure.

Hydroacoustic data were processed using Echoview software version

4.10.67.11651 (Myriax PTY LTD, Tasmania, Australia). Processing procedures included

removing echoes obviously not from fish, bottom dead zone echoes, and the near-field

exclusion zone. Data were analyzed in 200 m horizontal distance bins and 2 m depth

bins, from just below the near field exclusion zone to the maximum depth of each

horizontal bin. Within each of these bins, densities of cisco were calculated using the

echo-integration method and the following equation:

$$(1) \qquad P_{VS} = \frac{P_S}{\sum \left(P_S \times 10^{\left(\frac{\overline{TS_S}}{10} \right)} \right)} \times s_V$$

where P_S is the proportion of fish in size-class s, TS_S is the mean target strength for each

size-class, and s_V is the linear mean volume backscattering coefficient for each bin. P_S

was calculated using vertical gillnet catch data, and TS_S was estimated using single target

detection criteria provided in Rudstam et al. (2009). Day and night density estimates of

cisco were determined from each survey, in each 2 m depth bin, and analyzed in order to determine DVM tendencies.

Foraging, growth, and predation risk models

We used foraging, growth, and predation risk models to determine how these factors may influence DVM behavior of cisco in Ten Mile Lake. To determine the potential role of each of these factors, we first predicted the distribution of cisco based on each model during the day and night of each survey date, and then we compared those predictions to the actual distribution of cisco. The amount of overlap between the predicted and observed distribution of cisco indicates the amount of influence that factor may have on cisco distributions.

The foraging model was developed by Gerritson and Strickler (1977) and has been used to study the distributions of many species, including cisco (Ahrenstorff et al. In review; Ahrenstorff et al. 2011; Jensen et al. 2006). The model includes parameters such as the reaction distance of a predator and prey, their swimming speeds, and prey density. Reaction distance was based on light intensity by using a function created by Wright and O'Brien (1984) and modified for cisco (Jensen et al. 2006). We determined light levels during the day and night using a Li-Cor model LI-1400 light meter. Swimming speeds of cisco were estimated using an allometric equation developed by Rudstam et al. (1994), and zooplankton swimming speeds were estimated to be 1 mm/sec (Jensen et al. 2011). Prey density was determined by first analyzing which prey species were consumed by cisco, using stomach analyses, and then by determining the density of those prey species

in the water column using a Schindler-Patalas trap (1/2 m tall, 30 L, 63 µm mesh collecting cup). Zooplankton samples were collected with the Schindler-Patalas trap in 2 m increments from just below the surface to the bottom of the lake during each survey date.

The growth potential model for cisco was calculated based on foraging rates and temperature dependent bioenergetic equations from the generalized coregonine model (Rudstam et al. 1994). The growth model used in this study has been used for cisco in many other studies (Ahrenstorff et al. In review; Ahrenstorff et al. 2011; Jensen et al. 2006). Cisco consumption of zooplankton prey was estimated using the foraging model (encounter rate with prey) and capture probabilities of cisco consuming cladocerans (86.7%) and copepods (48.9%) from Link and Hoff (1998). Temperature was measured throughout the water column during each survey date using a YSI model 85 unit. Growth potential was estimated in 2 m intervals, from just below the surface to the bottom of the lake during each survey date.

Predation risk for cisco was estimated using the encounter rate model of Gerritson and Strickler (1977). It was similar to the foraging model, except the density term was excluded. This simulates where predation risk would be highest in the water column, based on reaction distance and swimming speed, assuming predators can move anywhere to maximize their foraging rate. Reaction distances for cisco and their predators were determined using the function by Wright and O'Brien (1984). Swimming speeds of cisco were the same as calculated previously, and predator swimming speeds were assumed to

be 3 m/min (Bahr 1977). Similar to the other models, predation risk was calculated in 2

m intervals from just below the surface to the bottom of the lake during each survey date.

Results

Physical sampling

In the vertical gillnets we captured a total of 487 cisco, 4 lake whitefish

(*Coregonus clupeaformis*), 2 northern pike (*Esox lucius*), and 2 walleye (*Sander vitreus*)

during all of the sampling dates. Length-frequency distributions for cisco were similar

across seasons and years, with the majority of cisco ranging between 75 – 157 mm

(Figure 16). Of the 487 cisco captured, only 2 individuals were somewhat larger at 178

and 243 mm. Cisco diets were generally dominated by copepods among seasons and

years, however, other prey proportions were more variable and seasonally dependent

(Figure 17). The primary prey items consumed by cisco in Ten Mile Lake included

copepods, *Daphnia* spp., *Bosmina longirostris*, and *Chydorus sphaericus*.

Cisco vertical distributions varied by season, but were relatively consistent among

years during the same season (Figure 18). Noticeable reverse DVM occurred during

spring, summer, and fall, but not winter, with some variability in magnitudes of the

migration among seasons. In spring, cisco densities were highest deeper in the water

column during the night of 2011 and 2012, and were slightly higher in the water column

during the day of 2011 and 2012. During the summer of 2010, 2011, and 2012, cisco

were consistently deeper during the night and had two different distributions during the

day. One peak was slightly higher in the water column during the day compared to night,

and the other peak was substantially higher in the water column during the day. During the fall of 2011 and 2012, cisco were deeper in the water column during the night and were slightly higher in the water column during the day. Lastly, during the winter of 2011 and 2012, cisco did not migrate considerably and were found deeper in the water column during the day and night.

Foraging, growth, and predation risk models

During the spring, summer, and fall of all years foraging potential was highest from just below the surface down to about 15 m during the day, while at night foraging potential was uniformly low throughout the water column (Figure 19). During winter, foraging potential was low throughout the water column during the day and night (Figure 19).

The growth model used foraging potential and temperature as inputs into the bioenergetic equations based on the depth specific values for each season and year. Temperature profiles indicated that during spring, fall, and winter of all years there was either a small temperature gradient or isothermal conditions present (Figure 20). During summer, Ten Mile Lake was stratified with surface temperatures near 25°C and the thermocline present at approximately 10 m depth (Figure 20). During spring, summer, and fall, growth model predictions were similar compared to the foraging model, with growth potential often near maximum consumption (0.70 g/g/day) in the upper 15 m of the water column during the day and near zero or negative growth predicted deeper in the water column during the day and throughout the water column at night (Figure 21). In

winter, growth rate potential was estimated to be negative throughout the water column during the day and night (Figure 21).

Predation risk was highest near the surface down to about 15 m during the day of the spring, summer, and fall, and was uniformly low at night (Figure 19). During winter, predation risk was low throughout the water column during the day and night (Figure 19).

Discussion

To the best of our knowledge, this is the first study to document how and why reverse DVM patterns of a fish species change throughout the year. In spring and fall, cisco reverse migrations were minimal, with their distributions being deeper in the water column at night and only slightly higher in the water column during the day. By migrating to slightly shallower depths during the day, cisco were able to increase foraging and growth potential, while simultaneously reducing predation risk, resulting in overall low risk and low reward. This strategy allowed cisco to avoid the negative growth they would have experienced under a normal DVM scenario. Cisco that perform normal DVM in Lake Superior during summer, also migrate less extensively during spring and fall, likely due to changes in foraging, growth, and predation risk (Ahrenstorff et al. 2011; Stockwell et al. 2010). During summer, a portion of the cisco population migrated according to the low risk, low reward strategy described above, while the other portion migrated according to a high risk, high reward strategy. The high risk, high reward strategy resulted in a portion of the cisco population migrating from deep water occupied at night, into the upper 15 m of the water column during the day. These

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shallow water areas had the highest foraging and growth potential, but also was the area with highest predation risk. It is possible that the low risk, low reward strategy does not provide enough growth for cisco to survive throughout the year, causing them to migrate according to the high risk, high reward strategy for at least part of the year. For example, during the summer of 2012 cisco distributions peaked at 10 m and 27 m during the day, which corresponded to an estimated growth rate over a one month period of approximately 2.43 g at 10 m during the day and 0.099 g at 27 m. Similar movements have been observed for reverse migrating Atlantic herring during summer, where they perform a low risk, low reward and high risk, high reward migration strategy (Jensen et al. 2011). In winter, cisco did not migrate vertically, likely because there were low risk, low reward conditions present throughout the water column due to darkness below the snow and ice cover. Other studies have found that the amount of light that penetrates through the ice influences DVM patterns of zooplankton and sockeye salmon due to changes in foraging, growth, and predation risk (Fortier et al. 2001; Steinhart and Wurtsbaugh 1999).

Our findings provide evidence that normal or reverse DVM patterns may not simply be driven by a low risk, high reward mechanism, as is commonly speculated (Mehner 2012). Alternatively, they may be driven by a low risk, low reward or high risk, high reward mechanism depending on growth potential and the amount and distribution of prey and predators in a lake. The amount and distribution of prey and predators may cause a shift in the importance of foraging, growth, and predation risk concerns. For example, when food availability is high throughout the water column *Daphnia* spp.

remain in the hypolimnion to avoid predation risk (Gliwicz and Pijanowska 1988), but

when it is low *Daphnia* spp. are known to feed near the surface despite the increased

predation risk (Johnson and Jakobsen 1987). Similar results were found by Ahrenstorff

et al. (In review), where lakes with less available food had smaller sized cisco that

migrated to areas of maximum foraging and growth potential, despite also increasing

their predation risk. These findings are consistent with laboratory studies on guppies

(*Poecilia reticulata*) (Abrahams and Dill 1989) and juvenile creek chubs (*Semotilus*

atromaculatus) (Gilliam and Fraser 1987), and field studies on coregonines (Jensen et al.

2006) and Atlantic herring (Jensen et al. 2011). Specifically, that if there are no low risk,

high reward areas in with which to forage, fishes will forage in low risk, low reward or

high risk, high reward areas depending on differences in potential growth rates. In this

study, slow growth in cisco was driven by the low amount of forage throughout Ten Mile

Lake, compared to similar lakes (Ahrenstorff et al. In review). To achieve adequate

growth for survival and reproduction, extensive reverse migrations of some cisco into

high predation risk areas is likely required for at least part of the summer. Ultimately, if

organisms cannot migrate in order to maximize foraging potential and minimize

predation risk, they may alternatively migrate according to a low risk, low reward or high

risk, high reward strategy.

The two migration trajectories observed during the summer for cisco in this study

resulted in what has recently been described as a partial migration, where a portion of the

population migrates while the other portion does not (Mehner and Kasprzak 2011).

Partial reverse migrations have recently been observed for Atlantic herring (Jensen et al.

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2011), and partial normal migrations for coregonines in Germany (Mehner and Kasprzak 2011). In our study, a portion of the population did not migrate extensively while the other portion performed an extensive reverse DVM during summer. It remains unclear if cisco alternate between strategies throughout the summer, or if the same fish always migrate according to the same strategy. Future studies should consider tagging individual fish to see if their migration strategies change throughout the summer. We observed no difference in the body size of migrating or non-migrating individuals, unlike coregonines in Lake Stechlin, where migrating individuals were often larger than non-migrating ones. Instead, the two migration trajectories observed here are more consistent with Jensen et al. (2011), and result from two different migrating strategies (low risk, low reward or high risk, high reward) to survive.

The results of this study allow us to speculate as to the causes of dwarf cisco being present in some lakes, such as Ten Mile Lake. It is likely a function of three primary factors, including, (1) the low availability of prey resources causing reduced growth potential, (2) the high risk, high reward migration strategy during summer which may increase size selective predation by piscivores, and (3) the ability of smaller individuals to feed in warmer surface waters (near 20°C), well above their thermal preference of 12°C (Rudstam and Magnuson 1985), compared to larger individuals. The density of prey resources in a lake have been shown to be positively correlated with the size of cisco present (Ahrenstorff et al. In review). When less food is available for cisco to consume, not only do they grow less, but they are likely to migrate according to a high risk, high reward strategy (Ahrenstorff et al. In review). This migration strategy may

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result in the largest sized cisco being consumed by predators, in accordance with optimal foraging theory (Breck 1993b), perpetuating smaller sized cisco being present in the lake. There may also be some evolutionary advantage to cisco maintaining a smaller size in Ten Mile Lake, because smaller individuals of a species are often thought to be better able to adapt to warmer water temperatures compared to larger individuals of the same species. For example, smaller individuals of 14 marine invertebrate species survived to higher temperatures than larger individuals of the same species when temperatures were incrementally increased in the lab (Peck et al. 2009). Similarly, smaller juvenile chinook salmon have significantly higher lethal temperature limits compared to adults (McCullough 2009). If larger cisco are not able to withstand warmer water temperatures near the surface, they will not be able to maximize their growth potential, resulting in lower growth rates. Overall, it is likely that low prey resources, size selective predation, and the ability of smaller fish to adapt to warmer water, all contribute to the result of dwarf cisco being present in Ten Mile Lake.

In summary, during spring and fall cisco performed minor reverse migrations according to a low risk, low reward strategy. In summer, a portion of the population performed the less extensive low risk, low reward migration while the other portion performed a more extensive reverse DVM which resulted in high risk and high reward. In winter, cisco did not migrate because there were only low risk, low reward conditions present at all depths. These results highlight an important point, that normal or reverse DVM patterns may not only be driven by a low risk, high reward migration strategy, but

instead a low risk, low reward or high risk, high reward strategy may yield similar DVM

patterns depending on the amount and distribution of predators and prey.

Chapter 5

Seasonally dynamic diel vertical migrations of mysis (*Mysis diluviana*), coregonines (*Coregonus* spp.), and siscowet lake trout (*Salvelinus namaycush*) in the pelagia of Western Lake Superior

Introduction

Understanding how and why diel vertical migration (DVM) patterns are dynamic between 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 including zooplankton (Gliwicz 1986; Worthington 1931), planktivores (Bohl 1980; Janssen and Brandt 1980), and piscivores (Hrabik et al. 2006; Weng and Block 2004). 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 (Boscarino et al. 2007; Gal et al. 2004). The mechanism underlying this migratory pattern is commonly attributed to optimizing foraging efficiency (Levy 1990; Narver 1970), or growth rates (Brett 1971; McLaren 1963; Wurtsbaugh and Neverman 1988), while avoiding predation risk (Lampert 1993; Zaret and Suffern 1976). Consequently, seasonal and annual variation in the abiotic and biotic environment 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 impact entire

aquatic ecosystems (Iwasa 1982; Steinberg et al. 2002).

In Lake Superior, the pelagic food web is composed of species known to perform,

and well adapted for, diel vertical migrations. The offshore pelagic community is

dominated by mysis *Mysis diluviana*, kiyi *Coregonus kiyi*, cisco *C. artedi*, and siscowet

lake trout *Salvelinus namaycush*, with shortjaw cisco *C. zenithicus*, bloater *C. hoyi*, and

rainbow smelt *Osmerus mordax* present at relatively low densities (Bronte et al. 2003;

Yule et al. 2009). Mysis vertical migrations are known to occur in many systems (Beeton

and Bowers 1982; Dakin and Latarche 1913), including Lake Superior (Bowers 1988;

Jensen et al. 2009). The DVM pattern of various coregonines has been documented in

Lake Michigan (TeWinkel and Fleischer 1999) and Lake Superior (Hrabik et al. 2006;

Stockwell et al. 2010; Yule et al. 2007). In addition, siscowet lake trout are known to

migrate vertically in Lake Superior (Hrabik et al. 2006; Stockwell et al. 2010).

Although vertical movements have been documented for mysis, kiyi, cisco, and

siscowet, 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 coregonines 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, concluding that they were related to growth potential and predation risk,

although the conclusions were based on limited field data and failed to incorporate a

seasonal component. Stockwell et al. (2010) added detail by examining DVM patterns of

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kiyi and cisco separately, finding that kiyi have more extensive vertical movements compared to cisco. In addition, Stockwell et al. (2010) observed that spring migrations were less pronounced for kiyi compared to summer and fall. It is clear that many of the important species in the Lake Superior pelagia migrate vertically, but it remains unclear how migrations change seasonally for each dominant species, how those movements are interrelated in a food web context, and 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, dictating how trophic levels interact (Hays 2003; Lampert 1993). For example, mysis have been found to migrate less extensively in spring and are found throughout the water column at night, likely because of isothermal conditions in the Great Lakes during that time period (Boscarino et al. 2009; Gal et al. 2004). For some fish species, such as juvenile kokanee salmon *Oncorhynchus nerka* and walleye pollock *Theragra chalcogramma*, DVM patterns are influenced by seasonal changes in water temperature, light, and prey/predator densities and distributions (Adams et al. 2009; Hardiman et al. 2004; Stockwell et al. 2010). However, for vendace *Coregonus albula* and Fontane cisco *C. fontanae*, 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.

Foraging, growth, and predation risk models have been used to explore factors influencing movement patterns of many species (Jensen et al. 2006; Wright and O'Brien

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1984). 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 of highest growth rate potential for a given organism based on fundamental bioenergetic principles (Kitchell et al. 1977). While foraging and growth models may provide explanations for the movement of top predators in aquatic ecosystems, they commonly fail to explain the movements of organisms in lower trophic levels where predation risk may be a driving factor (Iwasa 1982; Werner et al. 1983). Therefore, it is important to consider models that incorporate foraging opportunity, growth potential, and predation risk 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 sought to empirically characterize diel movement patterns of the three trophic levels simultaneously using hydroacoustics (fish) and an optical plankton counter (zooplankton) that collect data at a fine temporal resolutions. Our second objective explored the mechanisms driving movement patterns using a modeling approach, which was similar to Jensen et al. (2006), and used various abiotic (i.e. temperature and light) and biotic (i.e. predator-prey diets, distributions, and densities) inputs. Understanding how and why organisms migrate in Lake Superior is important because it will help elucidate nutrient and energy flow pathways through the system, and help clarify

predator-prey linkages which will aid fishery management decisions. Based on previous studies, we hypothesized that all four species would migrate during all seasons, with less extensive migrations during spring when the lake is isothermic and prey resources are dispersed throughout the water column (Gal et al. 2004; Hrabik et al. 2006; Stockwell et al. 2010). Alternatively, we hypothesized that cisco would exhibit less consistent migration patterns among seasons owing to their larger size and therefore lower risk to predation. In addition, we hypothesized that foraging or bioenergetic efficiency and predation risk would drive the movement patterns of mysis and kiyi, while predation risk would have a lesser influence on cisco movements due to their decreased vulnerability to predation (Jensen et al. 2006; Stockwell et al. 2010). Lastly, we hypothesized that siscowet would migrate concurrently with kiyi during all seasons, while also feeding upon deepwater sculpin *Myoxocephalus thompsonii* in bottom areas, to satisfy their energetic requirements as the top predator in the pelagia of Lake Superior.

Materials and Methods

Study site and sampling regime

This study was conducted in the western arm of Lake Superior (Figure 22). A 50 km long transect was sampled with hydroacoustics and an optical plankton counter 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 –

160 m. This location was selected because it represents a deep, pelagic area, typical of

offshore Lake Superior. Based on midwater trawl sampling along the study transect from

2005 – 2008, the fish community was comprised of coregonines (kiyi 70%, cisco 24%,

bloater 2%) and siscowet lake trout (<1%), with ninespine stickleback *Pungitius*

pungitius (<1%) and rainbow smelt (3%) also present ($n = 957$). DVM and diet analyses

focused only on kiyi, cisco, and the apex predator, siscowet, because bloater, ninespine

stickleback, and rainbow smelt were present at low densities. Research cruises were

scheduled during the spring isothermal (May), summer stratified (July), and fall

isothermal (October) periods. Sampling occurred during the summers of 2005 – 2006,

and in spring, summer, and fall of 2007 – 2008. Because moon phase influences

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 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

three days, allowing changes in vertical migrations over multiple day-night cycles to be

detected.

Fish sampling and diets

Day bottom trawls and night midwater trawls were used to determine the species

composition of demersal and pelagic fish along the study transect. Bottom trawls were

performed using a 3/4 Yankee bottom trawl (11.9 m head rope, 15.5 m footrope, and 2.2

m winglines) with a 13 mm mesh cod end liner. Trawl wingspread data was recorded using a NETMIND net mensuration system (Northstar Technical, Inc., St. John's, Newfoundland). Bottom trawls were fished for 30 minutes at two locations near the study transect (Figure 22) during each season in 2007 and 2008 (n = 12). Night midwater trawl tows were performed using a Gourock 20 m by 20 m box type midwater trawl with a 5 mm mesh cod end liner. The midwater trawl was monitored using an Imagenex trawl mensuration system (Imagenex Technology Corp., British Columbia, Canada) attached at the head rope which measured the trawl opening and depth. All midwater trawls targeted the primary scattering layer observed with hydroacoustics and were fished between 20 – 60 m at a constant head rope depth for 30 minutes to 1 hour during the summer of 2005 – 2006 and spring, summer, and fall of 2007 – 2008 (n = 8). Fish captured in bottom and midwater trawls were sorted by species, enumerated, and measured to the nearest millimeter total length.

Length-frequency distributions were constructed for kiyi, cisco, and siscowet captured in midwater trawls and for kiyi and siscowet captured in bottom trawls. A length-frequency distribution was not constructed for cisco captured in bottom trawls due to a low sample size (n = 1). Similarly, only one siscowet was captured in the eight midwater trawls. In order to get a better representation of the size distribution of particularly siscowet, but also kiyi and cisco, captured in midwater trawls, midwater trawl data collected from 2003 – 2009 in the western arm of Lake Superior was used, along with the data collected directly along the study transect (n = 91 total trawl tows). These ancillary trawls were performed using the same midwater trawl and methods as

described above for the trawls directly along the sampling transect. Of the midwater

trawls performed from 2003 – 2009, only those trawls located in the western arm of Lake

Superior which had a maximum depth greater than 120 m were used to avoid variability

in size distributions of fish found in other areas of the lake or nearshore.

Diet analyses were performed on up to 50 individual kiyi, cisco, and siscowet

collected from each research cruise along the study transect using the day bottom and

night midwater trawls. When analyzing an individual stomach, the contents were

subsampled when necessary (i.e. more than 100 individual prey items present), identified

to genus and species when possible, enumerated, and measured. Siscowet diet items

were dried and weighed in order to determine their dry mass, while length-weight

regressions used by the U.S. Environmental Protection Agency–Great Lakes National

Program Office (SOP-LG403, 2003) were applied to determine diet composition by prey

item (percent dry mass) for kiyi and cisco during each season and year from 2005 – 2008.

Zooplankton vertical migrations

To determine the extent of zooplankton vertical migrations an optical plankton

counter (OPC; Focal Technologies Corp., Dartmouth, N.S., Canada) was used and

mounted on a Triaxus tow body (MacArtney Offshore Inc., Houston, TX, USA). The

OPC uses a rectangular light beam to size and count zooplankton as they pass through the

aperture (Herman 1992). The Triaxus tow body, on which the OPC is mounted, 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 gathered about every 7 minutes (approximately 1 km horizontal distance).

Because the OPC provides only estimated sizes of objects, zooplankton net tow data was used to verify the size distribution and identify the species 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. At each site, a 0.5 m diameter, 250 μm conical mesh plankton net was lowered to a predetermined depth and retrieved at a speed of 1 m/s. Three replicate samples were collected from four different depths, including 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), providing diel, seasonal, and annual size distribution data for the zooplankton community.

Larger zooplankton species (e.g. *Bythotrephes longimanus*, *Daphnia* spp., and *Limnocalanus macrurus*) and mysis vertical distributions were analyzed using the OPC and net tow data because they were the primary prey resources consumed by cisco and kiyi, respectively. When the OPC collects data, it digitally records the size of each organism, 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) using an empirical equation (Herman 1992). However, most zooplankton are not spherical in shape, but more elliptical, with a major to minor axis ratio of approximately 1.33 (Sprules et al. 1998). For mysis, however, this ratio has been reported to be as high

as 4.5 (Jensen et al. 2009). Therefore, larger zooplankton species were considered to be 1.5 to 2.5 mm ESD (~ 1.7 to 2.9 mm actual length using ratio of 1.33:1), which encompasses the average size of zooplankton species found in cisco diets, including, *Bythotrephes longimanus*, *Daphnia* spp., and *Limnocalanus macrurus*. Anything over 2.5 mm ESD (~ 5.3 mm actual length using ratio of 4.5:1) was assumed to be a mysis target because they are the largest zooplankton species present in Lake Superior. This cutoff was based on net tow size distribution data and findings contained in Sprules (2000; 1998).

The movement patterns of zooplankton 1.5 to 2.5 mm ESD and mysis-sized targets greater than 2.5 mm ESD were determined in spring, summer, and fall of 2007 – 2008. Densities (number/m^3) of the larger zooplankton species were averaged based on the OPC data during the day and night in 5 m depth intervals from just below the surface to the bottom of the lake for each research cruise. Mysis densities at depth, as determined with the OPC, were averaged in 30 minute by 5 m depth bins up to the maximum depth for a 24 hour period. The DVM pattern for mysis was then evaluated statistically using a smoothing spline as described below. For zooplankton and mysis, average densities were determined based on the assumption that DVM trajectories did not vary over the short time scale (3 days) 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 was estimated using a DT-X scientific hydroacoustic echosounder

(Biosonics, Inc., Seattle, Washington), with a split beam, 70 kHz transducer, mounted on a Biosonics Inc. Biofin tow body. Hydroacoustic sampling, data collection, and calibration methods were analogous to Hrabik et al. (2006). During calibration, the measured target strength of the calibration sphere never varied significantly ($< \pm 1$ dB) from its expected target strength; 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 using Echoview software (version 4.0.73.6254, SonarData Pty Ltd., Tasmania). Single target detection parameters and methods described in Hrabik et al. (2006) were used for all data analyses. The data were analyzed in 30 minute 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 < TS < -35.6 dB), medium targets (-35.6 < TS < -32 dB), and large targets (TS > -32 dB), similar to Hrabik et al. (2006), Yule et al. (2006), and Stockwell et al. (2010). Using Love's (1977) equation, these target strengths correspond to 100 – 250 mm for small targets, 250 – 478 mm for medium targets, and > 478 mm for large targets. Although there are some targets that could be placed in the wrong size category if they are immature or significantly large, the midwater trawl data suggested that the majority of small targets were kiyi (94%), medium targets cisco (98%), and large targets siscowet (100%).

For each bin or cell, the volumetric fish density (P_{VS}; #/m³) of kiyi, cisco, and siscowet sized targets was calculated using the following equation:

$$(1) \qquad P_{VS} = \frac{P_S}{\Sigma \left(P_S \times 10^{\left(\frac{TS_S}{10}\right)} \right)} \times s_V$$

where P_S is the proportion and TS_S is the mean target strength for each of the three size classes (s) in each cell calculated 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 of the three size classes in each cell for the 3 day research cruise, average fish densities were calculated in the same depth and time cells over one 24 hour period for each size class.

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

Statistical analysis of vertical migration patterns

To estimate variability in vertical distributions for each species over a 24 hour period a weighted, penalized cubic smoothing spline (i.e. generalized additive mixed model – GAMM) was used with time as the predictor, densities the weights, and depth the response variable (Wood 2006; Wood and Augustin 2002). A cubic spline is a curve made up of sections of cubic polynomials joined together in sections (i.e. knots) so that they are continuous. The number and placement of knots controls 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 were chosen based on the data using generalized cross validation (Wood and Augustin 2002). A generalized additive mixed model was used with an autoregressing covariance structure, instead of simply a generalized additive model, to control for the effects of temporal autocorrelation present in the data. The statistical software package R was used to model the depth distribution data for each species during each research cruise (GAMM using mgcv package v1.6-2 for R v2.11.1). A 95% point-wise confidence interval was then fit to each modeled distribution to allow an easier comparison of vertical migrations among species, seasons, and years. In addition, the coefficient of determination (R^2) was reported, which describes 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 that predict the distribution of organisms were considered. First, a foraging rate

potential (FRP) model was considered for kiyi and cisco using an encounter rate model

developed by Gerritsen and Strickler (1977), as applied by Mason and Patrick (1993) and

Jensen et al. (2006):

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

where R_{ij} is the reaction distance (m) of predator j (kiyi or cisco) to prey i (mysis or other

zooplankton), v_j and v_i are the swimming speeds (m/min) of predator and prey, and d_i is

the prey density (#/m^3).

Reaction distance was determined using the reaction distance model developed by

Wright and O'Brien (1984), as used by Jensen et al. (2006) for coregonines:

$$(3) \qquad R_{ij} = \left(1.44\beta(l - 0.2)\right)/1000$$

where R_{ij} is the reaction distance (m), l is the average length (mm) of prey (mysis or

zooplankton, respectively), and the β parameter is defined as a function of light at depth

(I_x; lux) and turbidity (τ; Nephelometric turbidity units):

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

When light levels were 0 lux, a reaction distance of 2 cm was used for coregonines

similar to Jensen et al. (2006), because coregonines are known to feed in the dark

(TeWinkel and Fleischer 1999). To determine light level at depth (I_x), surface light

intensity data gathered in Duluth, Minnesota, was used for all seasons during 2005 from

the National Solar Radiation Data Base (NSRDB). Average irradiance (W/m^2) was

converted to visible light (lux) using a conversion factor of 1 W/m² to 120 lux (Lampert and Sommer 1997). Light intensity at depth x was then modeled using the Beer-Lambert equation (Hutchinson 1957):

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

where k is the extinction coefficient (m⁻¹) as obtained from Koenings and Edmundson (1991).

Because the swimming speed of kiyi and cisco is unknown, their swimming speed was estimated using an allometric equation developed by Rudstam et al. (1994) for bloater, a closely related coregonine species in Lake Michigan:

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

where v_j is the swimming speed (cm/s) and W is the average weight (g) of an individual organism. Negligible zooplankton swimming speed was assumed relative to planktivore swimming speed and mysis swimming speed was assumed to be 0.6 m/min which has been used in similar modeling studies (Jensen et al. 2006; Mason and Patrick 1993) and is reasonable based on measured values (Ramcharan and Sprules 1986).

Prey density (d_i) was determined for zooplankton and mysis using the optical plankton counter, as described previously. For cisco modeling prey inputs, 1.5 – 2.5 mm ESD zooplankton densities were used from all seasons in 2007 – 2008, which corresponded to the size range of organisms found in cisco diets. For kiyi modeling, mysis densities were calculated for each research cruise in 2007 – 2008, except in the spring of 2007. Therefore, data from the spring of 2008 was used as the prey model input for 2007.

A growth rate potential (GRP) model was also evaluated in the 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 dependant consumption, respiration, specific dynamic action, egestion, and excretion (Kitchell et al. 1977). The fundamental bioenergetic equations were obtained from Hanson et al. (1997). Many model parameters are physiological constants, which were acquired from the generalized coregonine model derived by Rudstam et al. (1994). Other model inputs are 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 using a bathyothermograph (ABT-1, Alec Electronics Co. Ltd., Kobe, Japan). Preferred prey items were determined by performing diet analyses, as described previously. Lastly, consumption rates were estimated from the foraging potential model, where 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 foraging and growth rate model predictions were estimated in spring, summer, and fall, of 2007 – 2008 during the day and night for kiyi and cisco in 5 m depth bins up to the maximum depth.

Predation risk (μ) was also incorporated into the foraging and growth models because predation risk is known to influence the movement patterns of organisms (Dill and Fraser 1984; Werner and Hall 1988). Predation risk to the planktivores (kiyi or cisco) was defined as the encounter rate with predators (siscowet), similar to Mason and Patrick (1993). Therefore, predation risk can be modeled with an equation analogous to

equation (2), by substituting predator density (d_v) for prey density (d_i). While kiyi and cisco swimming speeds were the same as calculated before, siscowet reaction distance and swimming speed were also calculated. Reaction distance for lake trout was determined using a function developed by Vogel and Beauchamp (1999) for light intensities less than and greater than the saturation intensity threshold of 17.83 lux:

(7) < 17.83 lux

$$R = 26.84 + 2.81 I_x - 6.09 \ln(\tau) - 0.025 \ln(\tau) I_x$$

(8) ≥ 17.83 lux

$$R = 77.79 + 0.046 I_x - 6.09 \ln(\tau) - 0.025 \ln(\tau) I_x$$

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

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

where W is weight (g) and T is temperature (°C).

Four models (FRP, FRP/μ, GRP, GRP/μ) were considered in evaluating the factors influencing movement patterns of kiyi and cisco. All of the parameter inputs for each of the models are outlined in Table 3. The performance of each model was evaluated by comparing the percent overlap among the observed and predicted depth distributions of each species using Schoener's (1970) index. The calculated percent overlaps were then averaged (across time of day, season, and year) for each of the four models and comparisons were made using a Wilcoxon Rank Sum test with a Bonferroni

correction (i.e. $P_\alpha = 0.05/4 = 0.0125$) to determine if any model performed significantly better when compared to others for predicting depth distributions of kiyi and cisco.

Results

Species and length frequency

Day bottom trawls performed along the study transect during the spring, summer, and fall of 2007 – 2008 captured 21,965 individual fish ($n = 12$ trawls). Of those, deepwater sculpin were the most abundant (19,654 individuals), followed by kiyi (2,167 individuals), and siscowet (120 individuals). Other species captured at low densities included 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). Kiyi were the most abundant (670 individuals) followed by cisco (226 individuals). Other species included bloater, ninespine stickleback, rainbow smelt, and siscowet.

Length-frequency distributions were constructed for kiyi and siscowet using bottom and midwater trawl data, and for cisco using only midwater trawl data because only one cisco was captured in bottom trawls (Figure 23). Kiyi sizes ranged between 111 – 229 mm (mean = 167 mm) in bottom trawls and 61 – 275 mm (mean = 155 mm) in midwater trawls, with two distinct modes for each distribution. Cisco sizes ranged between 203 – 451 mm (mean = 324 mm) for the midwater trawls with only one noticeable mode. Siscowet length-frequency distributions, which were broader with no

distinct modes, ranged between 209 – 610 mm (mean = 386 mm) in bottom trawls and 70
– 740 mm (mean = 402 mm) in midwater trawls.

Diet composition

Kiyi captured in midwater and bottom trawls primarily consumed mysis (~ 98%
by mass) regardless of season and year (*n* = 656 stomachs analyzed; Figure 24A). Cisco
diets were more variable among seasons and years, consuming primarily cladocerans,
such as *Bythotrephes longimanus* and *Daphnia* spp., as well as copepods (*n* = 253
stomachs analyzed; Figure 24B). Other prey items found in cisco stomachs at less than
1% of the total biomass included *Bosmina* spp., chironomid larvae, *Daphnia* resting eggs,
Diporeia, oligochaetes, ostracods, *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 24C). Deepwater sculpin were the
primary prey resource consumed by biomass, followed by coregonines, and unknown
fish. Other prey items consumed by siscowet included mysis, terrestrial invertebrates,
and parts of birds.

DVM patterns of three trophic levels

Mysis, kiyi, cisco, and siscowet all displayed DVM during at least part of the year
(Figure 25). Weighted, penalized regression spline fits using density as weights and time
as the predictor accounted for 17 – 98% of the variability in the depth distribution of
organisms (Table 4). Mysis showed vertical migrations, from near the bottom (about 140

– 160 m) during the day to shallower depths at night, during all seasons. However, in spring, mysis did not migrate as high into the water column at night (~ 60 m), when compared to summer and fall (~ 30 m). Kiyi underwent migrations similar in magnitude when compared to mysis, with a less extensive upward migration at night during spring (up to approximately 60 m in depth) compared to summer and fall (~ 40 m in depth). Variations in DVM patterns were consistent among years for mysis during summer and fall and for kiyi during the spring, summer, and fall. Cisco movement patterns varied between seasons, and to some extent, within seasons among years. During spring, variable vertical movements were observed with the majority of the cisco population migrating between 60 m at night during 2007 to 100 m during the day. Diel differences in cisco distributions were negligible during the spring of 2008. During summer, cisco migrated from shallower depths at night (~ 30 m) to deeper areas during the day (~ 130 m), with some variation among years. During fall, cisco were found near 30 m during the day and night in 2007 and 2008. Siscowet migrated vertically during all seasons. Spring migrations brought siscowet up to 45 m on average at night compared to summer and fall when they rose to 30 m, which was consistent in depth with the upper depths occupied by mysis and kiyi at night.

Empirical estimates of biological and physical modeling parameters

Based on the results of the diet analyses, the density and distribution data calculated with the OPC for 1.5 – 2.5 mm ESD zooplankton was used as the prey input for the cisco model (Figure 26). This size range 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 = 2.03 mm). Densities of

zooplankton calculated with the OPC and zooplankton net tows have been shown to be

similar (Sprules et al. 1998). For kiyi prey inputs, seasonal mysis density and distribution

data (Figure 25) were used, as determined with the OPC. For mysis, whole water column

density estimates with the OPC and zooplankton net tows were not significantly different

during each season and year (two-tailed *t*-test, all $P - values > 0.05$).

Light at depth, used to calculate reaction distance, varied slightly among seasons,

while water temperature, used to calculate swimming speeds and growth potential, varied

by season and to a lesser extent by year (Figure 27). Maximum depth of light penetration

reached approximately 35 m in spring, 45 m during summer, and 30 m during fall. Most

organisms began migrating downward in the morning as surface light levels began

increasing past 5 lux. Upward migrations in the evening began just after sunset, once

light levels were approaching 0 lux throughout the water column. During 2007 – 2008,

water temperatures were isothermal in spring, stratified in summer, and gradually

decreasing with depth in fall. Spring temperatures were approximately 2.5°C throughout

the water column in 2007 – 2008. In summer 2007, the thermocline was found at 5 m,

and only slightly deeper (6 m) during the summer of 2008. Fall water temperatures

varied from 9°C at the surface to about 3°C at 160 m during 2007 – 2008, but never

changed more than 1°C over a 1 m depth interval.

Modeling results

Kiyi movement patterns were best predicted with the FRP and the FRP/µ models, with highest predicted daytime foraging rate potential between 125 – 175 m and highest nighttime predictions between 15 – 50 m during all seasons and years (Figure 28). Percent overlap between the observed depth distribution of kiyi and the predicted distribution averaged 56.7% for the FRP model and 56.3% for the FRP/µ model, with no significant difference detected among models. The GRP and GRP/µ models also performed similarly well, with calculated percent overlaps of 45.1% and 44.7%, with no detectable difference between models. Both foraging models performed better when compared to the growth rate potential models, but these results were not significantly different after Bonferroni correction ($P_\alpha = 0.0125$) (FRP vs. GRP, $P = 0.03$; FRP vs. GRP/µ, $P = 0.02$; FRP/µ vs. GRP, $P = 0.05$; FRP/µ vs. GRP/µ, $P = 0.04$).

For cisco, movement patterns were best predicted by the FRP/µ model (average percent overlap 41.8%), with most predictions placing cisco between 5 – 50 m during the day and night (Figure 29). The FRP (31.7%), GRP (38.2%), and GRP/µ (37.9%) models only performed slightly worse. No significant difference was observed among calculated percent overlaps for any of the model predictions for cisco.

Discussion

Mysis vertical distributions varied seasonally, as has been observed in other studies (Boscarino et al. 2007; Gal et al. 2004), and seems to be driven by the location of predators and prey. For example, in Lake Ontario, highest mysis densities were deeper and broader at night in the spring and fall (both ~ 50 m), compared to a shallower and

more distinct mysis layer at approximately 10 m in the summer (Gal et al. 2004). In our

study, mysis vertical migrations were deeper at night in the spring (~ 60 m) compared to

summer and fall (~ 30 m). The lower magnitude of migration in spring is likely

attributable to a lake in a state of mixing and isothermic conditions, causing their prey to

disperse more evenly throughout the water column (Bowers 1988; Gal et al. 2004).

Spring diatom blooms and subsequent death/sinking may also provide a source of prey to

mysis 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 mysis diet in May in

Lake Ontario, which was much higher compared to other seasons. In summer and fall,

mysis migrations were more extensive extending to shallower depths at night, where

highest phytoplankton and zooplankton resources were located (Yurista et al. 2009;

present study). The movement patterns of mysis are likely driven by their prey as well as

predation risk, although we were unable to quantitatively test this with modeling because

mysis are omnivorous (Johannsson et al. 2001) and have many potential predators (A.

Gamble, University of Minnesota-Duluth, unpublished data). Our findings are consistent

with both Gal et al. (2004) and Boscarino et al. (2007) who conclude that mysis migrate

to maximize feeding rates and minimize predation risk. Foraging opportunity alone

cannot explain the movements of mysis in Lake Superior because most plankton

resources are located in the upper 30 m of the water column during thermally stratified

periods (Bowers 1988). In addition, Bowers (1988) noted that mysis rarely migrate

above 50 m at night. Our results show that mysis migrate to approximately 20 m at night

during the summer and fall, indicating that there are differences in the current migration

pattern of mysis relative to that observed in the 1980's in Lake Superior. The observed

differences in the magnitude of migration could be attributed to different sampling

techniques (staged net tows versus OPC, respectively), and changes in predation risk,

food availability or other factors. In both studies, most mysis migrated to near the

bottom, instead of simply to a safe depth where predation risk is low, likely because the

bottom affords greater foraging opportunities (e.g. detritus) compared to staying in a deep

pelagic layer (Scavia and Fahnenstiel 1987). However, not all mysis migrate to the

bottom because of increased predation risk from deepwater sculpin or increased energetic

costs of deep migrations (McLaren 1963). Overall, mysis movements appear to be

consistent with risk-sensitive foraging (McNamara and Houston 1992) that exemplifies a

tradeoff between foraging and predation risk.

Kiyi vertical migrations closely followed mysis migrations while simultaneously

avoiding areas of highest predation risk throughout the year. This pattern suggests the

importance of both prey and predators in driving the movements of kiyi. Consistent with

findings in Stockwell et al. (2010), kiyi migrated less extensively in spring compared to

summer and fall. Our empirical and modeling results suggest that mysis are important in

driving the movements of kiyi in Lake Superior. This finding is important when

considering nutrient transport and energy flow between trophic levels and habitats (e.g.

benthic and pelagic). While foraging and growth were important in predicting kiyi

movements, it was more difficult to assess the influence of predation risk because kiyi

distributions following mysis prey coincided directly with areas of lowest predation risk

from siscowet. As a result, incorporating predation risk (i.e. FRP/μ and GRP/μ models)

did not significantly improve predictions of vertical movement patterns. Because predation risk was confounded with prey, it was difficult to determine the complete influence of predation risk on kiyi movements. We believe that predation risk from siscowet does influence kiyi distributions, but were unable to assess the relative importance of predation to foraging. Thus, a model that includes a predation risk component and a foraging model component would likely be more accurate if predator risk/foraging opportunities decouple. Future changes to the food web of Lake Superior may provide additional information that could help assess the overall importance of predation risk to kiyi.

Comparing multiple competing models is often useful for identifying mechanisms important to observed dynamics. However, we could not determine whether FRP or GRP models were more effective at predicting the distribution of kiyi. The foraging models were better at describing the movements of kiyi when compared to the growth potential models, but the differences were not significant. Given the minimal temperature gradient ($\sim 2°$ C) experienced by kiyi during vertical movements, and the fact that the primary data input difference between the models is temperature, it is not surprising that the models predicted similar distribution patterns. Our results were similar to studies on alewife and bloater movements in Lake Michigan, where the location of potential prey items, such as mysis, *Daphnia* spp., and *Diporeia* were identified as drivers of movement patterns (Eshenroder and Burnham-Curtis 1999; Eshenroder and Burnham-Curtis 2001; Janssen and Brandt 1980; TeWinkel and Fleischer 1999).

Cisco are a large bodied coregonine with a diverse diet that are less susceptible

than kiyi to predation by siscowet (Stockwell et al. 2010). However, cisco vertical

migrations were driven by the location of prey resources and to a lesser extent predation

pressure. While the migration pattern of cisco was less pronounced than kiyi, their

response to each source of variability resulted in shallower migrations during the day,

compared to mysis and kiyi, regardless of season. The FRP/μ model appeared to be the

best for predicting the distribution of cisco. However, the results of the model could not

be differentiated statistically from the performance of the FRP, GRP, and GRP/μ models.

It is possible that foraging, growth, and predation risk all play a role in determining the

movements of cisco, or that some other factors are also important. Previous research by

Stockwell et al. (2010) suggested that predation pressure on adult cisco is low in offshore

areas of Lake Superior, and may have little effect on DVM patterns primarily because

cisco have relatively large body sizes. Based on the large size of cisco relative to

siscowet, and diet information gathered here and in other studies (Harvey et al. 2003;

Negus et al. 2008), the vulnerability of large cisco to predation by siscowet is likely low.

However, it is difficult to completely discount predation risk because predation does

occur on smaller cisco and there may be a perceived predation risk from the largest

siscowet (>600 mm) predators. There also may be some lasting effect of dealing with

predation risk from lean lake trout in nearshore areas where juvenile cisco spend most of

their time (Stockwell et al. 2010). Cisco were regularly found in deeper water, below

areas of highest foraging potential during the day, suggesting that they avoid areas of

high light where large siscowet search volumes would be high. Even very low predator

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density or a perceived predation risk is capable of influencing habitat use of prey species in other systems (He et al. 1993; Werner et al. 1983). A drastic reduction of siscowet densities would yield insight into the overall influences of predation risk on cisco movements (Hrabik et al. 2006). Studying DVM patterns of cisco in years with very different siscowet densities would allow a more thorough understanding of the role of predation.

Coregonine DVM patterns were thought to be driven by predation risk and mysis prey resources during the summer (Jensen et al. 2006); however, we now know that the DVM pattern for kiyi and cisco is driven by predators and the location of mysis or zooplankton prey, respectively, throughout the spring, summer, and fall. Specifically, our study is unique when compared to other studies in that we separated coregonines by species, considered data from multiple seasons and years, and collected concurrent mysis and plankton information. Jensen et al. (2006) concluded that coregonines migrate to minimize the ratio of predation risk to growth, which cannot be refuted by our results. They observed two migration trajectories that minimized the risk to growth ratio, when using mysis as the prey input for their modeling exercises. One trajectory was relatively shallow, starting just below the thermocline (~ 25 m) at night and following low light levels down to 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 (> 150 m) during the day that tracked highest mysis densities. Our modeling results never predicted this shallow high-risk, high-growth trajectory when using measured mysis densities as the prey input because we never observed mysis higher in the water column during the day. Jensen et

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al. (2006) suggested that low densities of mysis present just below the thermocline during the day could lead to this result. However, the low densities of mysis used in the Jensen et al. (2006) modeling were from only a few samples collected in 1986 (Bowers 1988). Cisco were predicted to follow, and generally did follow, the shallow high-risk, high-growth trajectory when using 1.5 – 2.5 mm ESD zooplankton as the modeling prey input for cisco. The two migration trajectories predicted by Jensen et al. (2006) were consistent with our findings. However, the differences were likely attributable to separating the distributions of kiyi and cisco and considering them independently as in Stockwell et al. (2010). However, unlike Stockwell et al. (2010), our study incorporated direct measures of the preferred prey of cisco and kiyi and measured the distribution patterns over an entire 24 hr cycle.

Previous findings indicate a possible change in the participation of siscowet in vertical migration behavior in recent years. Hrabik et al. (2006) and Jensen et al. (2006), suggested the shallow high-risk, high-growth trajectory was observed for coregonines in 2001 and the deeper low-risk, low-growth trajectory in 2004. This change in migration trajectories among years was attributed to a higher density of siscowet participating in DVM in 2004, thus increasing predation risk causing organisms to migrate deeper. Conversely, Stockwell et al. (2010) found no relationship between the migration amplitude of coregonines with various siscowet densities. Our results were consistent with Stockwell et al. (2010) in that we could not identify a relationship between kiyi or cisco migration patterns and siscowet densities. However, this was likely because

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siscowet densities and their vertical movements did not vary significantly along our study transect across years.

Previous studies have shown that siscowet 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 likely driven by prey resources. It is likely that siscowet feed on coregonines higher in the water column at night and on coregonines and sculpin near the bottom during the day (Conner et al. 1993). Although coregonines were found in siscowet diets at lower proportions than deepwater sculpin, the greater nutritional value of coregonines (cisco = 6,922 J/g, bloater = 9,879 J/g) to sculpin (sculpin = 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 their modeled search volume could be as much as 500 times greater in the upper water column (27.0 m^3/min) compared to the bottom (0.056 m^3/min). However, the lack of prey observed near the thermocline during the day likely drives siscowet migrations to the bottom, where densities of sculpin and kiyi are considerably higher. Because capture efficiencies of different prey on the bottom likely vary due to differences in habitat use and predator avoidance, a foraging and growth model was not used for this species (Breck 1993a; Mason and Brandt 1996). It is unlikely that capture rates would be accurately described by the encounter rate model we used. Further research investigating siscowet capture efficiencies of 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 likely important determinants of species distributions under certain conditions (e.g. Beeton and Bowers 1982; Bevelhimer and Adams 1993; Jensen et al. 2006; Magnuson et al. 1979; Mason and Patrick 1993). In Lake Superior, the upper extent of vertical migrations seems to be limited by temperature. Mysis, kiyi, cisco, and siscowet all remained below the thermocline during evening ascents and occupied approximately 5°C water at night. Other studies have reported that mysis avoid strong thermal gradients, generally preferring water temperatures between 6 – 8°C, and rarely moving into water temperatures exceeding 15°C (Boscarino et al. 2007; Mauchline 1980; Rudstam et al. 1999). Pelagic fishes in Lake Superior prefer cold temperatures as well, generally avoiding water greater than 10 – 12°C (Negus 1995; Wismer and Christie 1987; Yule et al. 2007). Vertical migration patterns were also closely related to changing light levels over the day-night cycle in our study and others (Gal et al. 1999; Van Gool and Ringelberg 2003). In addition, light was clearly a factor dictating the timing of upward and downward migrations. While it was difficult to determine exact light levels preferred or avoided by organisms in our study, previous studies have reported that mysis prefer light not exceeding 10^{-2} to 10^{-4} lux (Moen and Langeland 1989; Teraguchi et al. 1975). Coregonines generally remain at light levels below 10^{-3} lux (Yule et al. 2007), with reaction distances decreasing significantly below 10^{-2} lux (Link and Edsall 1996; Vogel and Beauchamp 1999). Overall, our results and past studies indicate that daily and seasonal changes in temperature and light appear to be important factors in modifying vertical migrations of organisms, but are not the primary mechanisms driving DVM

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behavior in Lake Superior where the distribution of food resources and risk of predation seem more important. DVM 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 are not known as driving factors of vertical migrations and therefore were not analyzed here.

In summary, mysis, kiyi, and siscowet all underwent vertical migrations during the seasons studied. Cisco 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 (mysis, kiyi, and cisco). Overall, our results are unique in that they provide a clearer picture of seasonal and annual DVM patterns in three trophic levels of organisms. Our findings highlight the importance of mysis in driving the distribution of kiyi. However, under the current food web configuration, we are unable to determine the overall influence of predation risk from siscowet 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, through increased harvest, could have significant population impacts on lower trophic levels in the food web. Recent findings suggest that vertically moving organisms including *Limnocalanus macrurus*, mysis, kiyi and siscowet all 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

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of Minnesota-Duluth, unpublished data). Alterations of fishing regulations that decreased

densities of predatory siscowet in the open water areas would likely have a cascading

effect that would increase the density of kiyi and other planktivores in the pelagia and

reduce the net flux of nutrients by mysis and other zooplankton, which represent the bulk

of the transport. Effective ecosystem scale management should consider the overall

ramifications of increasing fishing effort on long-lived pelagic predators such as the

siscowet on nutrient regeneration and energy flow throughout the lower trophic levels.

The fact that the majority of the pelagic food web in Lake Superior performs vertical

migrations suggests a need for research to track nutrient cycling between benthic and

pelagic habitats and the role migrations play in energy flow throughout the aquatic food

web.

Chapter 6

Conclusions

The objective of this dissertation was to examine how abiotic and biotic conditions within lakes influence how and why diel vertical migration (DVM) patterns change for different species, across ecosystems, seasons, and years. Chapter 2 examined normal DVM patterns, among other things, of Hovsgol grayling (*Thymallus nigrescens*) in Lake Hovsgol, Mongolia, during the summer of 2009. Chapter 3 studied normal DVM, no DVM, and reverse DVM of cisco (*Coregonus artedi*) in 11 inland lakes throughout Minnesota and northern Wisconsin during the summers of 1996-1997 and 2010-2011. Chapter 4 documented reverse DVM patterns of cisco in Ten Mile Lake, Minnesota, during the summer of 2010 and the spring, summer, fall, and winter of 2011 and 2012. Lastly, Chapter 5 investigated normal DVM patterns of *Mysis diluviana*, kiyi (*Coregonus kiyi*), cisco (*C. artedi*), and siscowet lake trout (*Salvelinus namaycush*) in the pelagic areas of Lake Superior during the summer of 2005 and 2006, and the spring, summer, and fall of 2007 and 2008. In addition to the novel results provided by each study independently, a discussion summarizing of all of these studies collectively provides a synthesis of information on how and why DVM patterns change between species, ecosystems, seasons, and years. While an abundance of literature exists about differences in DVM behavior, this discussion will only include those studies presented above. References to the results of other studies can be found in the previous chapters.

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Each species has different physiological requirements; therefore we would expect DVM patterns of different species to differ accordingly. DVM patterns were certainly different for some of the species we studied. In Lake Superior, normal DVM patterns of kiyi were considerably higher in magnitude compared to normal DVM patterns of cisco, which is likely related to physiological adaptations in kiyi that promote their deeper water existence compared to cisco. In Lake Hovsgol, normal DVM patterns of Hovsgol grayling were small in comparison to reverse DVM patterns of cisco in Ten Mile Lake. However, DVM patterns were also similar for some species in the same ecosystem. For example, in Lake Superior *Mysis diluviana*, kiyi, and siscowet lake trout performed a similar normal DVM. This result was driven by the fact that *Mysis diluviana* and kiyi could maximize foraging and growth potential, while minimizing predation risk, by migrating similarly. Siscowet lake trout, on the other hand, are likely making similar migrations to maximize foraging and growth potential, because they are not vulnerable to predation once they reach large enough sizes. We might predict that DVM patterns for the same species should be similar between ecosystems, due to the same physiological requirements of the species. However, in Lake Superior and in smaller inland lakes we observed cisco populations that performed a variety of normal DVM, no DVM, and reverse DVM in the different lakes. While the physiological requirements of cisco were likely similar between lakes, the physical and biological conditions of each lake were significantly different, causing the variable movements.

Different ecosystems have different abiotic and biotic conditions which causes differences in movement patterns of species. Many factors may influence the physical

and biological conditions present in a lake (e.g. lake size, morphometry, productivity, and species composition). For example, lake size and morphometry may influence lake mixing which may change the temperature and oxygen conditions in the lake and also the distribution of prey and predators. Productivity and species composition may also influence the density and types of prey and predators found in a lake. We observed that changes in temperature, oxygen, prey, and predators caused variable DVM patterns of species in all of our studies. Cisco migrations provide a good example of this because we can examine how movements changed between ecosystems for the same species. We found cisco populations that performed normal DVM, no DVM, and reverse DVM in Lake Superior and smaller inland lakes in Minnesota and northern Wisconsin. In general, cisco movement patterns were related to prey density. When prey density was lower, cisco grew slower, and had movement patterns consistent with maximizing foraging and growth potential, despite moving out of preferred temperature/oxygen conditions and into areas of higher predation risk. When prey density was higher cisco grew larger, and stayed in areas near their temperature/oxygen preference and avoided predation, while experiencing less than maximum foraging and growth potential. Overall, differences between ecosystems can cause diverse DVM patterns which are driven by the physical and biological conditions of each lake.

Seasonal changes in temperature, light, prey availability, and predator distributions likely alter the DVM pattern of species across seasons. We observed different reverse DVM patterns of cisco in Ten Mile Lake during the spring, summer, fall, and winter. Additionally, normal DVM patterns of *Mysis diluviana*, kiyi, cisco, and

siscowet lake trout changed between the spring, summer, and fall. In both examples, the

mechanisms causing the shift in migration strategies were similar. During spring and

fall, the diel movements of species in both studies were of a smaller magnitude

(compared to summer) and more variable. This was likely a result of a mixing lake,

causing variable changes in temperature, prey availability, growth, and predation risk, the

latter of which are temperature dependent. Furthermore, changes in the angle of the sun

and day length cause decreases in light penetration and longer periods of darkness during

these seasons. During summer, the DVM patterns of species in both studies were more

consistent, likely due to more distinct light, thermal, prey, and predator gradients. In

winter, cisco did not migrate in Ten Mile Lake likely because of low prey availability,

and more uniform foraging, growth, and predation risk conditions owing to pervasive low

light and isothermal conditions. While we did not sample during the winter in Lake

Superior, the lack of ice and constant mixing likely makes the lake conditions more

similar to spring and fall, therefore it would be expected that the movements of the Lake

Superior species would be consistent with their spring and fall migrations.

While DVM patterns change between species, ecosystems, and seasons, few

studies have examined how DVM patterns change yearly. Three of our four studies

contained more than one year of data. Of those studies, there were very minimal

differences in DVM patterns for the same species from one year to the next in each study

lake. For example, cisco performed the same normal DVM, no DVM, or reverse DVM

pattern among different years in the 11 inland lakes we studied (2 years of data). In Lake

Superior, despite changing DVM patterns between seasons, movement patterns were

consistent between years for all of the dominant pelagic species in each season (4 years of data). Additionally, cisco movement patterns were consistent from one year to the next during the spring, summer, fall, and winter in Ten Mile Lake, Minnesota (3 years of data). The lack of significant changes in DVM patterns of these species over multiple years in the same ecosystem indicates that the physical and biological conditions in each lake were likely relatively consistent over time. If one of the lakes were to undergo drastic environmental changes, the DVM patterns of the species present in that lake would likely change accordingly, although we were unable to test this due to the limited time scale and consistent environmental conditions observed during these studies. Additional data collected over a longer time period may provide useful information about how DVM patterns change over time.

Overall, understanding that DVM patterns of organisms change among species, ecosystems, and seasons, but that organisms show similar patterns within a season among years, is intriguing. This result is likely due to the fact that the majority of DVM patterns are driven by temperature, oxygen, foraging/growth potential, and predation risk in each lake. These factors differ in importance for different species, and change in different ecosystems and seasons, but they are likely more consistent from one year to the next for the same species in the same ecosystem and the same season. Each individual study in this dissertation is unique and novel, providing results ranging from the first publication in the English literature on the Hovsgol grayling to the first study that documented normal DVM, no DVM, and reverse DVM for a single fish species in different lakes. Collectively, these studies have improved and advanced our understanding of how and

why organisms perform DVM. Consistent patterns include: (1) that a diversity of DVM behavior can be exhibited by a single species at similar latitudes, among lakes, among seasons, (2) lakes that lack a significant predation risk to predators consistently have populations that exhibit patterns of distribution consistent with optimal foraging hypotheses, (3) that populations in low food environments are likely to exhibit risk taking strategies to obtain food, and (4) that seasonal changes in DVM are often as strong in magnitude as changes in distribution among lakes.

Tables

Table 1. Physical and biological characteristics of the hydroacoustic transects sampled. Juvenile grayling are considered to be 100 – 170 mm, while adult grayling are > 170 mm.

Transect	Day/ Night	Time sampled (min)	Minimum depth (m)	Maximum depth (m)	Juvenile density (ind.·ha^{-1})	Adult density (ind.·ha^{-1})
2	D	160	103	123	10.8	10.9
2	N	140	40	130	17.5	25.5
3	D	60	145	207	5.8	3.0
4	N	170	32	119	5.1	9.0
5	D	180	62	175	17.9	14.9
5	N	120	67	78	23.7	22.4
6	N	300	53	152	9.5	14.0
7	D	110	41	112	18.5	22.8
7	N	150	51	95	23.6	34.4
8	D	30	26	51	3.2	6.8
8	N	140	65	131	5.3	5.5
9	D	130	26	95	11.3	12.1
9	N	170	65	222	21.0	22.6

Table 2. Physical and biological attributes of the study lakes. Sizes of cisco and density estimates were averaged across years when more than one year of data were available.

Lake	Date(s) sampled	Location	Surface area (ha)	Maximum depth (m)	Secchi depth (m)	DVM pattern	Average size of cisco (mm)	Range in cisco size (mm)	Average cisco density (# ha^{-1})
Big	25-June-1997	46°09'22" 89°13'06"	335	19	4.5	Normal	256	164-330	2462
Carlos	9-Aug-2010 3-Aug-2011	45°57'51" 95°21'21"	1020	50	3	Reverse	180	80-420	1458
Clear	5-July-1996 1-July-1997	46°08'47" 89°48'39"	208	14	3.5	None	274	197-339	2852
Dead Pike	15-July-1996	46°06'06" 89°53'57"	125	24	2.5	Normal	178	159-202	168
Elk	3-Aug-2010 25-July-2011	47°11'18" 95°13'06"	110	28	3.5	None	208	77-322	466
Little Star	25-June-1996	46°06'55" 89°51'38"	105	21	6	Normal	276	251-299	633
Manitowish	18-June-1996	46°06'26" 89°50'30"	201	19	5	Reverse	246	192-314	199
Papoose	25-June-1997	46°11'04" 89°48'08"	171	20	5	None	300	131-354	4214
Ten Mile	18-July-2010 2-Aug-2011	46°58'14" 94°34'21"	2042	63	4.5	Reverse	124	88-243	3270
Trout	4-June-1996	46°02'46" 89°40'31"	1564	36	6	Reverse	152	115-192	385
White Iron	28-July-2010	47°52'21"	1388	14	2	None	162	69-367	1083

Table 3. Biological and physical parameters used in the foraging, growth, and predation risk models.

Parameter	Symbol	Value	Unit	Source
Density (zooplankton)	d_i		$\#/m^3$	Measured
Density (mysis)	d_i		$\#/m^3$	Measured
Density (lake trout)	d_j		$\#/m^3$	Measured
Extinction coefficient	k	0.15	m^{-1}	Koenings and Edmundson 1991
Foraging rate potential (encounter rate with prey)	FRP		$\#{\cdot}m^{-3}{\cdot}min^{-1}$	Gerritsen and Strickler 1977
Growth rate potential	GRP		$g{\cdot}g^{-1}{\cdot}d^{-1}$	Hanson et al. 1997
Length (zooplankton)	l	2.5	mm	Measured
Length (mysis)	l	15	mm	Measured
Light level at depth x	I_x		lux	Hutchinson 1957
Light level at surface	I_0	$0 - 5{\times}10^{-4}$	lux	NSRDB
Predation risk (encounter rate with predator)	μ		$\#{\cdot}m^{-3}{\cdot}min^{-1}$	Gerritsen and Strickler 1977
Reaction distance	R_{ij}		m	Wright and O'Brian 1984
Swimming speed (mysis)	v_i	0.6	m/min	Mason and Patrick 1993
Swimming speed (kiyi)	v_i or v_j	10.2	m/min	Rudstam et al. 1994
Swimming speed (cisco)	v_i or v_j	16.3	m/min	Rudstam et al. 1994
Swimming speed (lake trout)	v_j	18 – 26	m/min	Stewart et al. 1983
Temperature	T	3 – 12	°C	Measured
Turbidity	τ	0.5	NTU	Koenings and Edmundson 1991
Weight (kiyi)	W	30	g	Measured
Weight (cisco)	W	200	g	Measured
Weight (lake trout)	W	675	g	Jensen et al. 2006

Table 4. Weighted, penalized regression spline fits predicting mysis (*Mysis diluviana*), kiyi (*Coregonus kiyi*), cisco (*C. artedi*), and siscowet lake trout (*Salvelinus namaycush*) depths based on time of day for spring, summer, and fall from 2005 – 2008. N is the number of 5 m by 30 minute intervals where data were available, df are the model degrees of freedom, and R^2 values express the proportion of depth variability explained by the model.

		Mysis			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
	2008	238	6.8	0.97	634	7.7	0.94	196	6.2	0.85	150	4.2	0.17
Fall	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

Figures
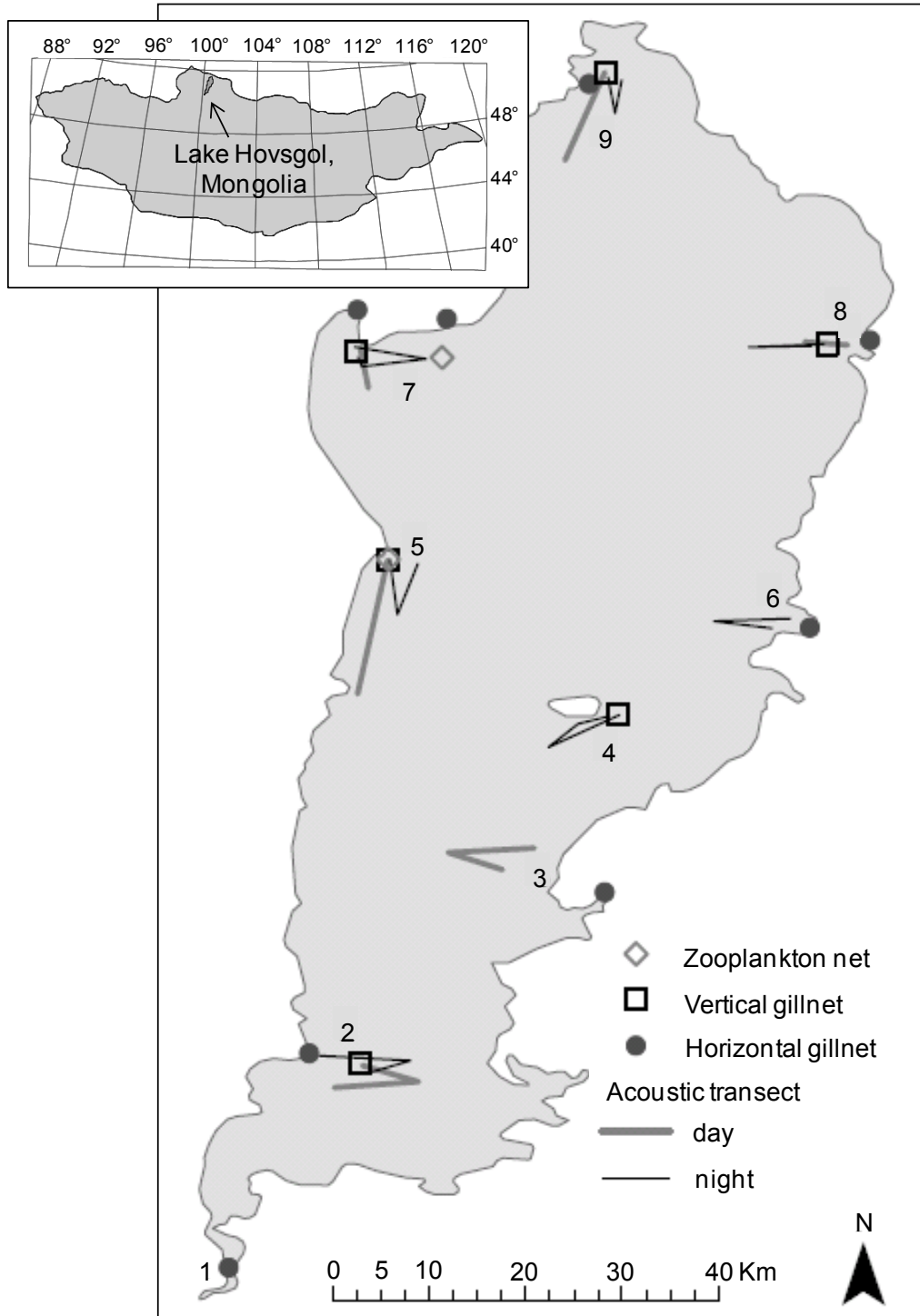
Fig. 1. Areas of Lake Hovsgol, Mongolia, sampled using hydroacoustics, vertical and horizontal gillnetting, and zooplankton net tows.

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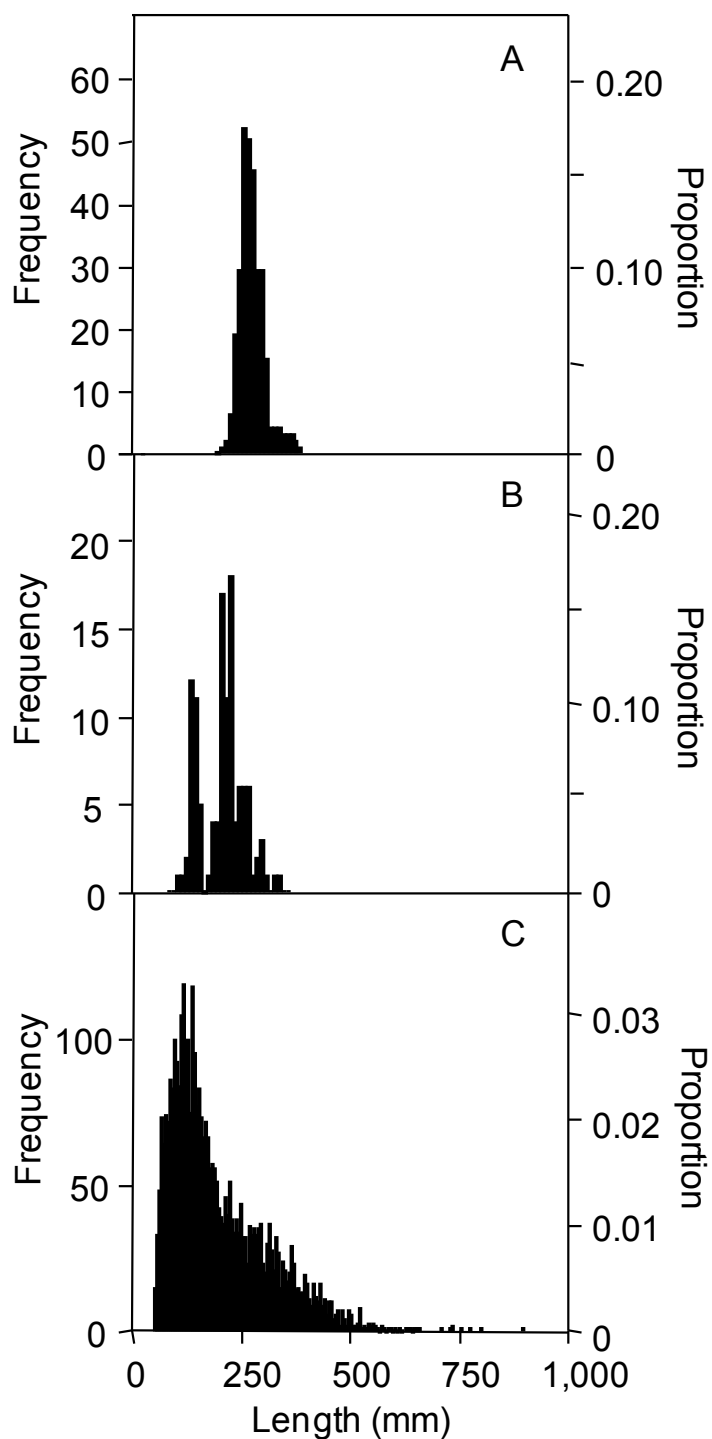
Fig. 2. Length-frequency distributions for Hovsgol grayling (*Thymallus nigrescens*) sampled with A) horizontal gillnets (*N* = 301), B) vertical gillnets (*N* = 118), and C) hydroacoustics (*N* = 3,618).

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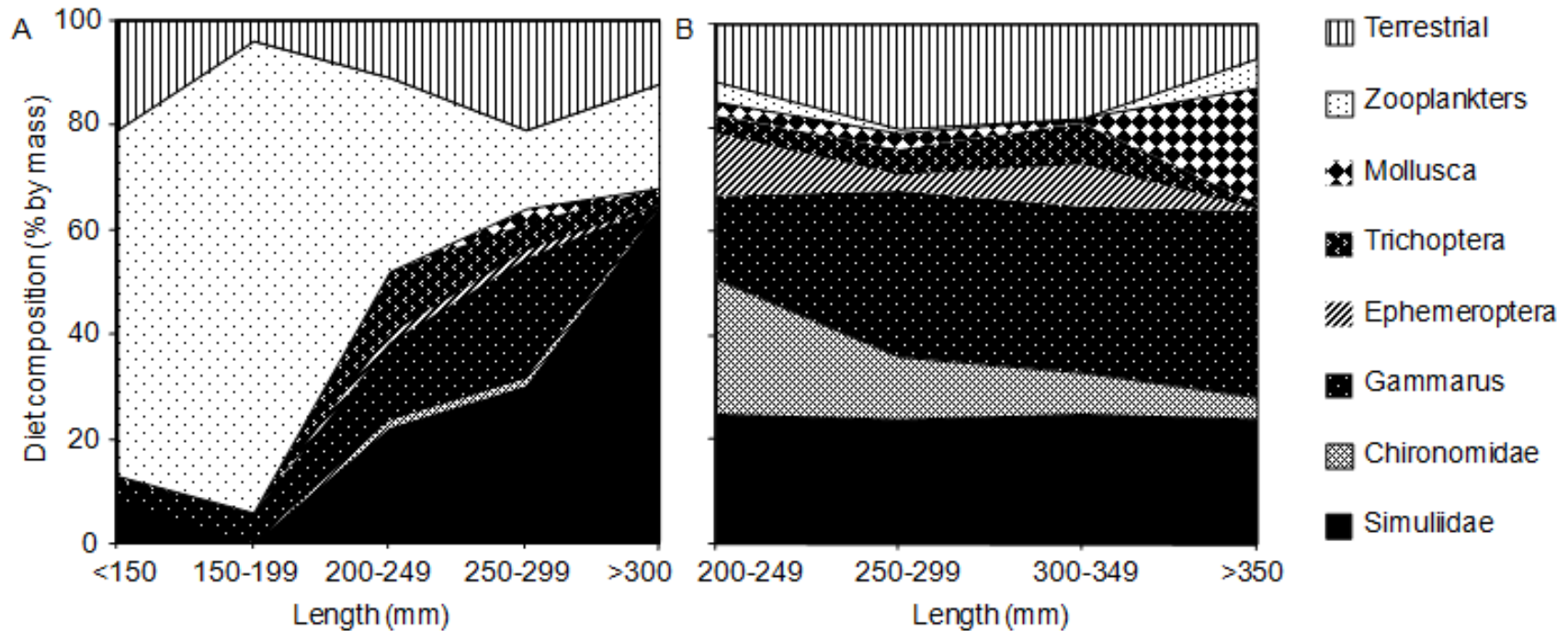
Fig. 3. Diet composition (% by mass) of Hovsgol grayling (*Thymallus nigrescens*) caught in A) pelagic vertical gillnets and B) littoral horizontal gillnets. Diet items present at less than 5% of the total biomass are not shown.
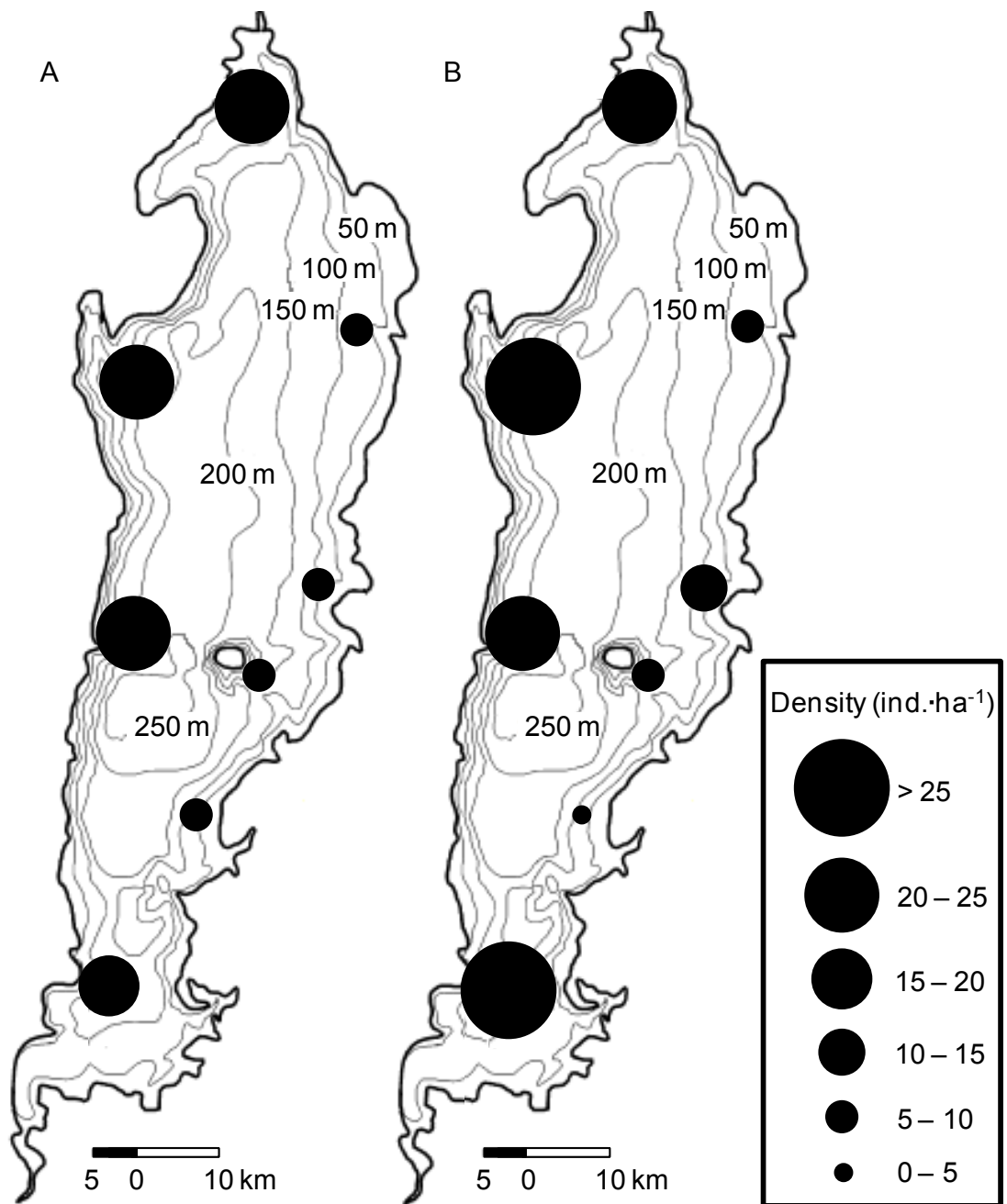
Fig. 4. Transect mean density estimates (ind.·ha^{-1}) of A) smaller (100 – 170 mm) and B) larger (> 170 mm) Hovsgol grayling (*Thymallus nigrescens*) in Lake Hovsgol, Mongolia.
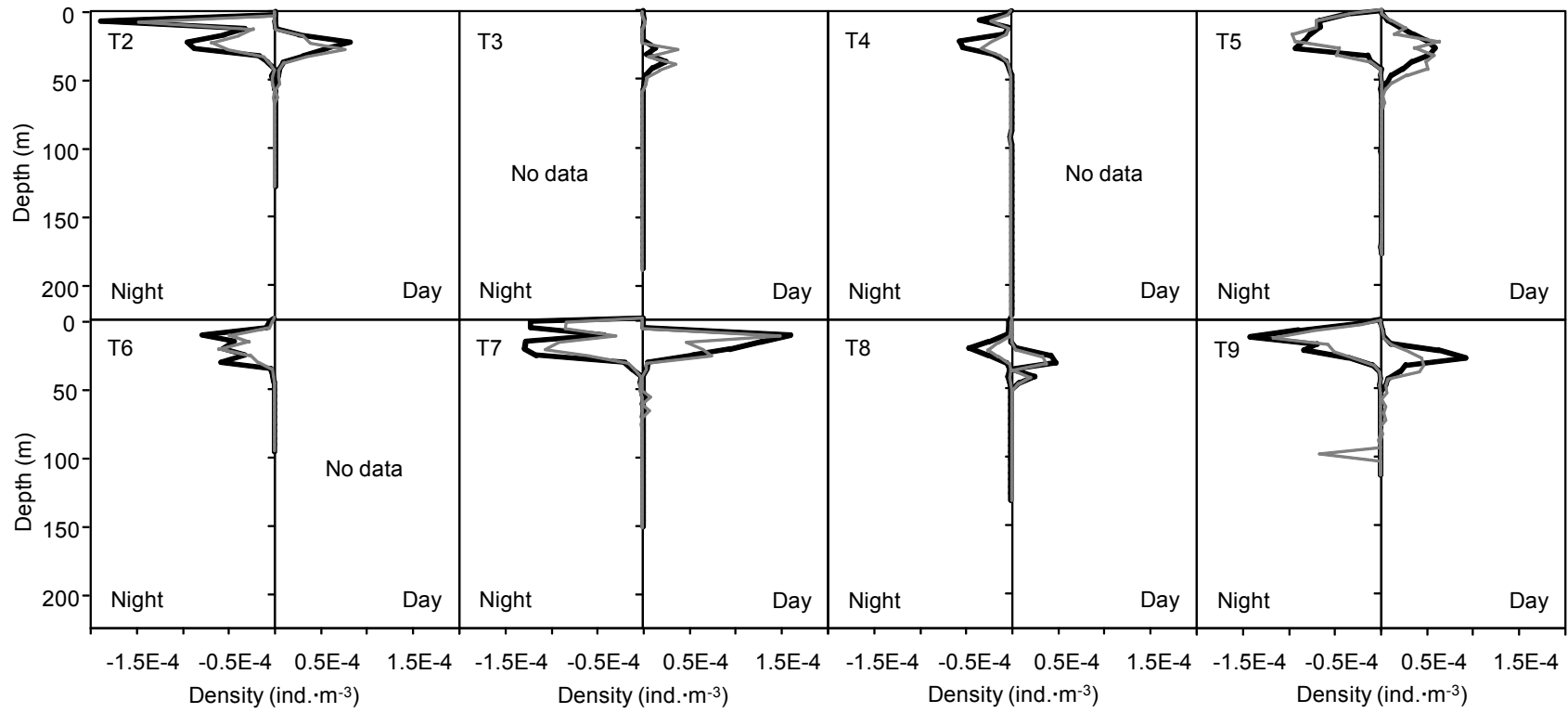
Fig. 5. Day and night vertical distributions of smaller Hovsgol grayling (gray line; 100 – 170 mm; *Thymallus nigrescens*) and larger Hovgsol grayling (black line; > 170 mm) at 8 transects (e.g. T2, T3, etc.) throughout Lake Hovsgol, Mongolia. No acoustic collections were made for those dates and times noted as "No data" in the figure.

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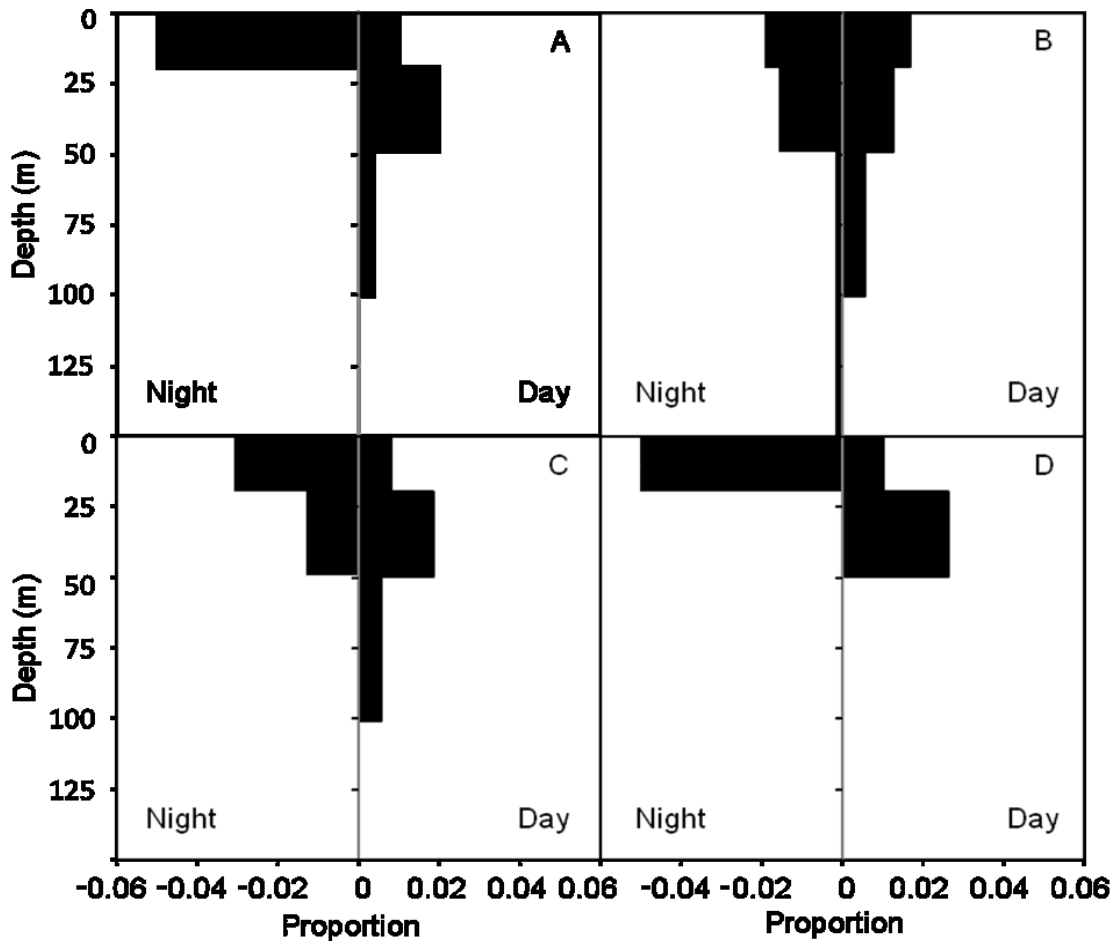
Fig. 6. Day and night vertical migrations, by proportion in each meter of the water column, of the zooplankton community consisting of A) calanoid copepods, B) cyclopoid copepods, C) *Daphnia* spp., and D) *Bosmina* spp.

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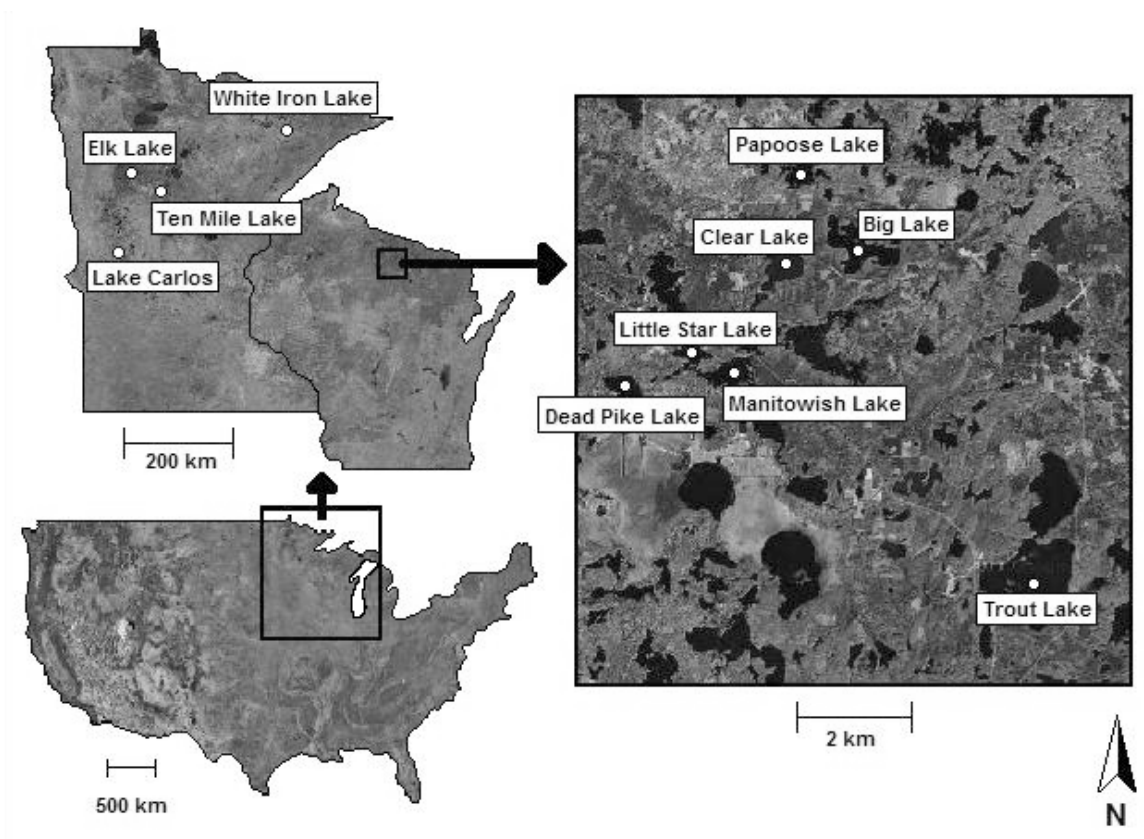
Fig. 7. Study lakes sampled in Wisconsin, USA (*n*=7), and in Minnesota, USA (*n*=4).
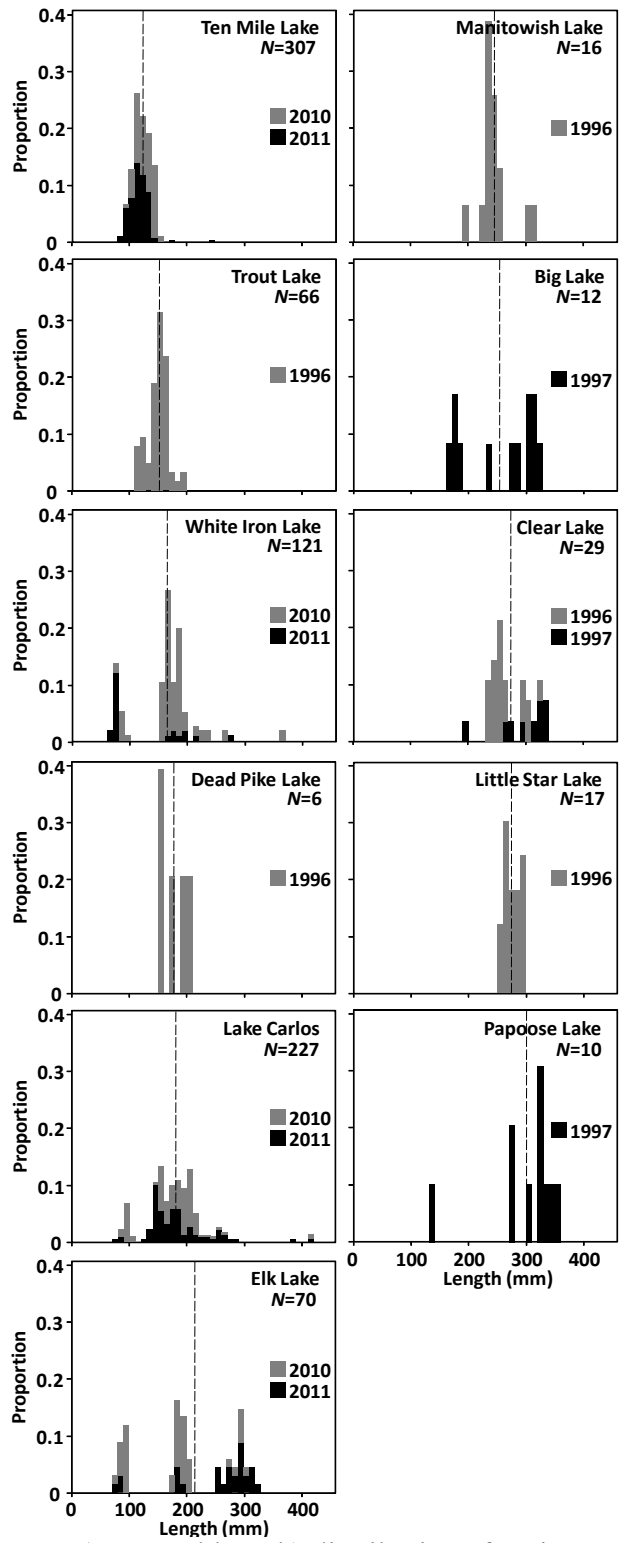
Fig. 8. Length-frequency (mm total length) distributions for cisco captured in each lake. The vertical dashed lines represent the average size of cisco present in each lake.

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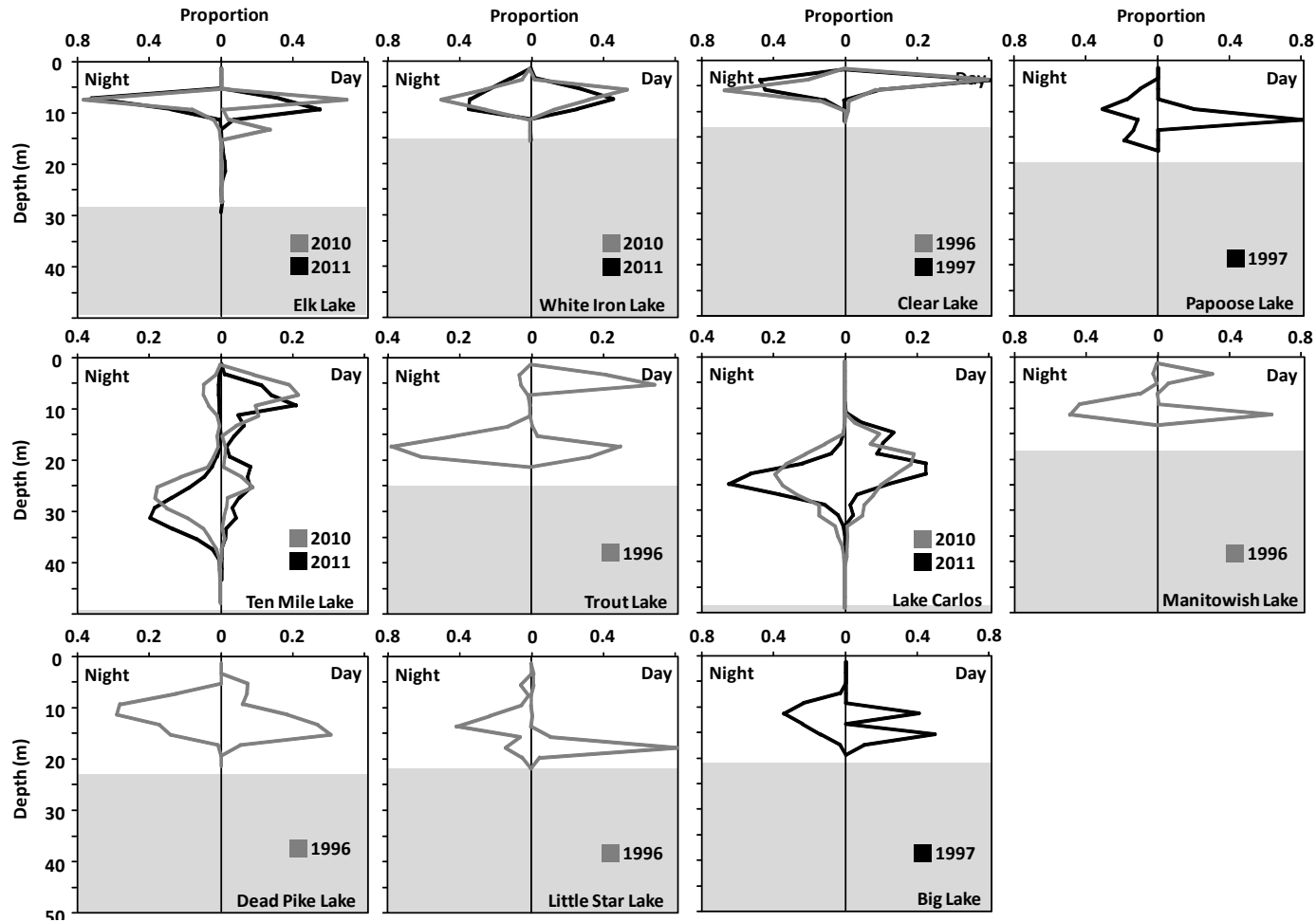
Fig. 9. Cisco vertical distributions during the day and night in each study lake during different years showing no diel vertical migrations (top row), reverse diel vertical migrations (middle row), and normal diel vertical migrations (bottom row). The light grey shaded area represents the bottom area for each lake.

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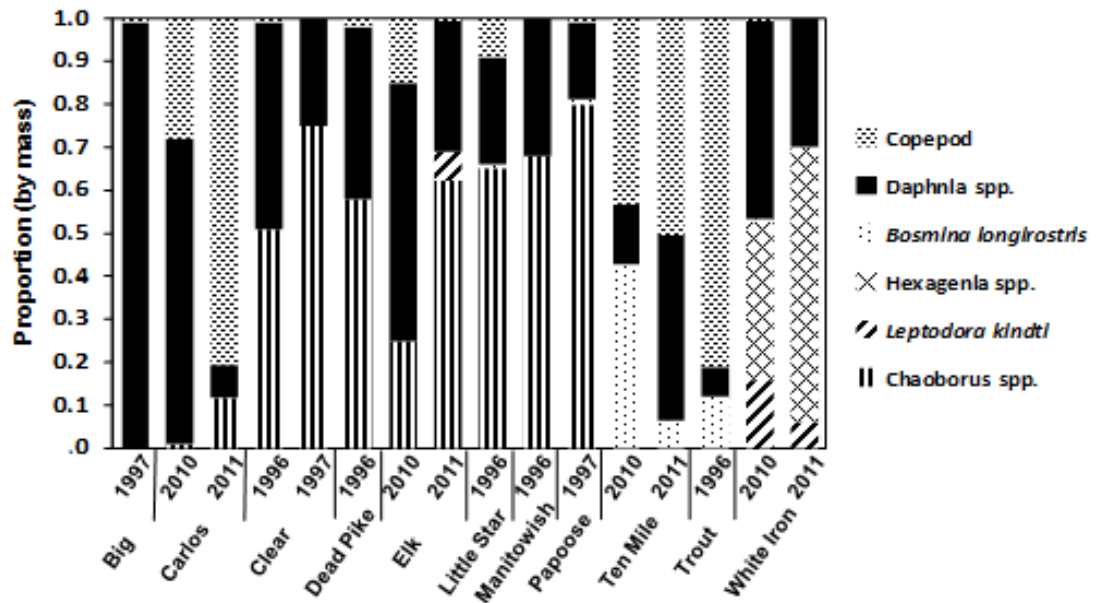
Fig. 10. Taxonomic composition of the diet (proportion by mass) for cisco in each study lake during each year sampled. Diet items that represented <5% of the biomass were not included.
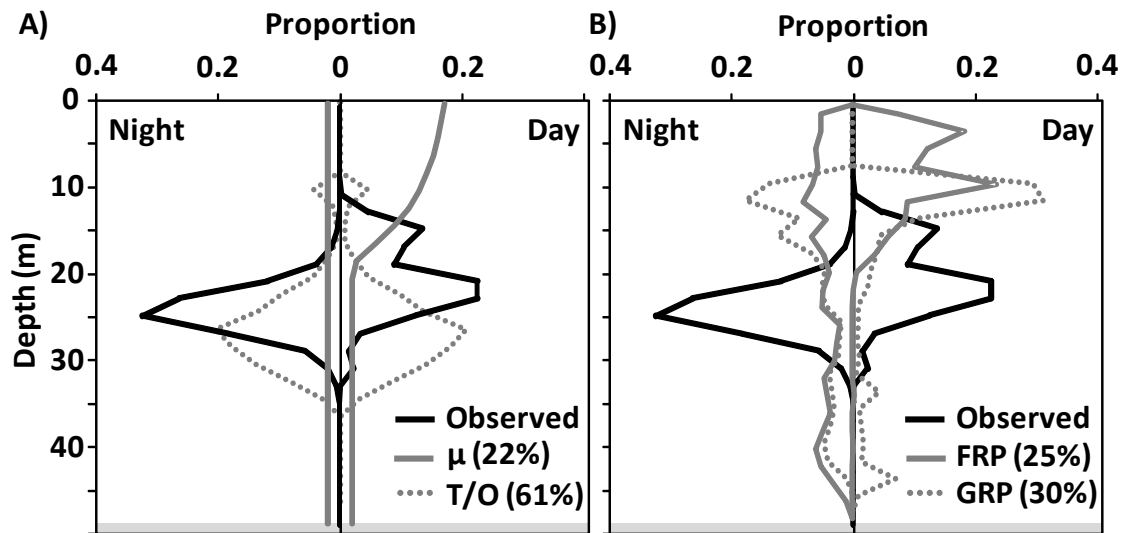
Fig. 11. Comparison between the observed distribution of cisco in Lake Carlos in 2011 and their predicted distribution based on the A) predation risk (μ) and temperature/oxygen (T/O) model, and B) foraging rate potential (FRP) and growth rate potential (GRP) model. The percentages represent the calculated percent overlap between the observed and each predicted distribution.
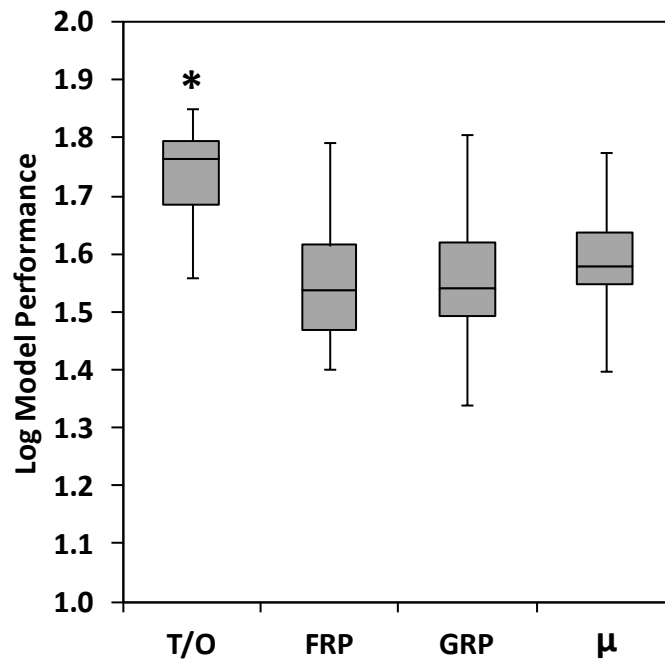
Fig. 12. Box and whisker plots showing the average percent overlap for the temperature/oxygen (T/O), foraging rate potential (FRP), growth rate potential (GRP), and predation risk (μ) models. The T/O model was significantly different from the others.
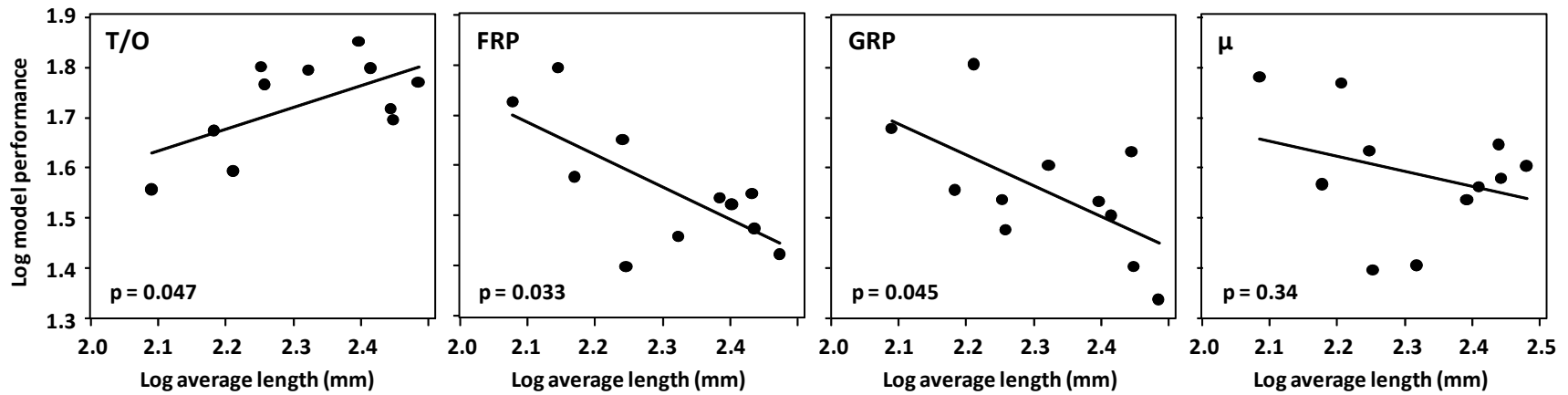
Fig. 13. Model performance (% overlap) between the observed and predicted distributions of cisco based on models of temperature/oxygen (T/O), foraging potential (FRP), growth potential (GRP), and predation risk (μ) plotted against the average size of cisco (mm) in each inland lake.
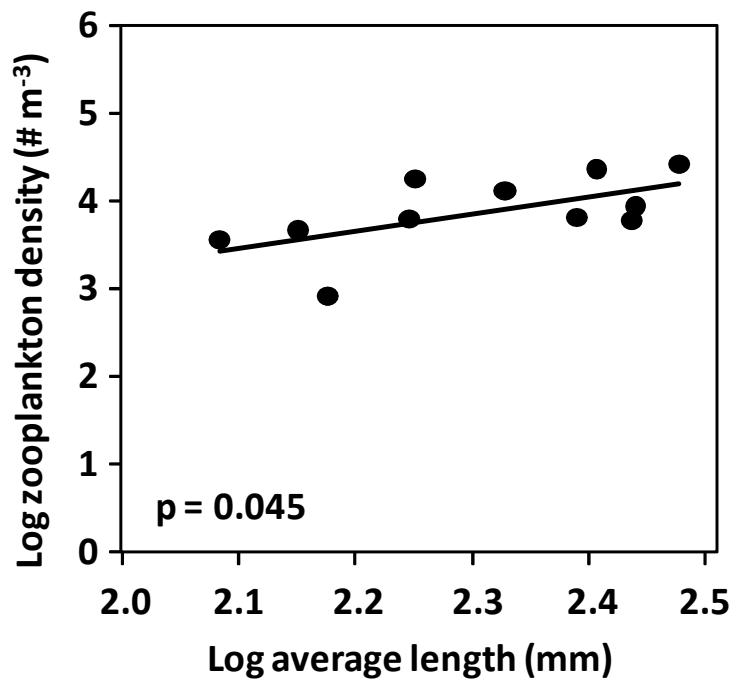
Fig. 14. The relationship between zooplankton density (# m^{-3}) and the average size of cisco (mm) in each inland lake.
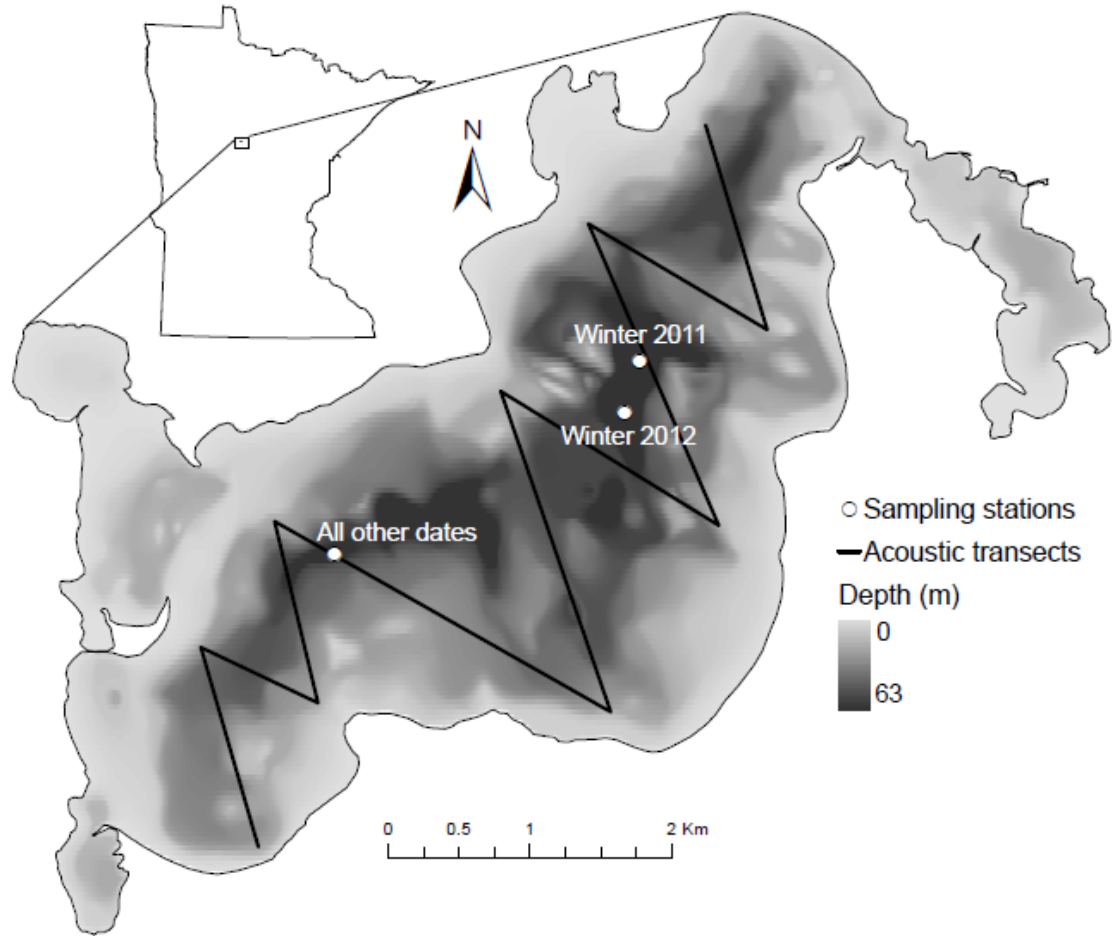
Fig. 15. Locations of stationary sampling sites and hydroacoustic transects sampled during the summer of 2010 and the spring, summer, fall, and winter of 2011 and 2012 in Ten Mile Lake, Minnesota.
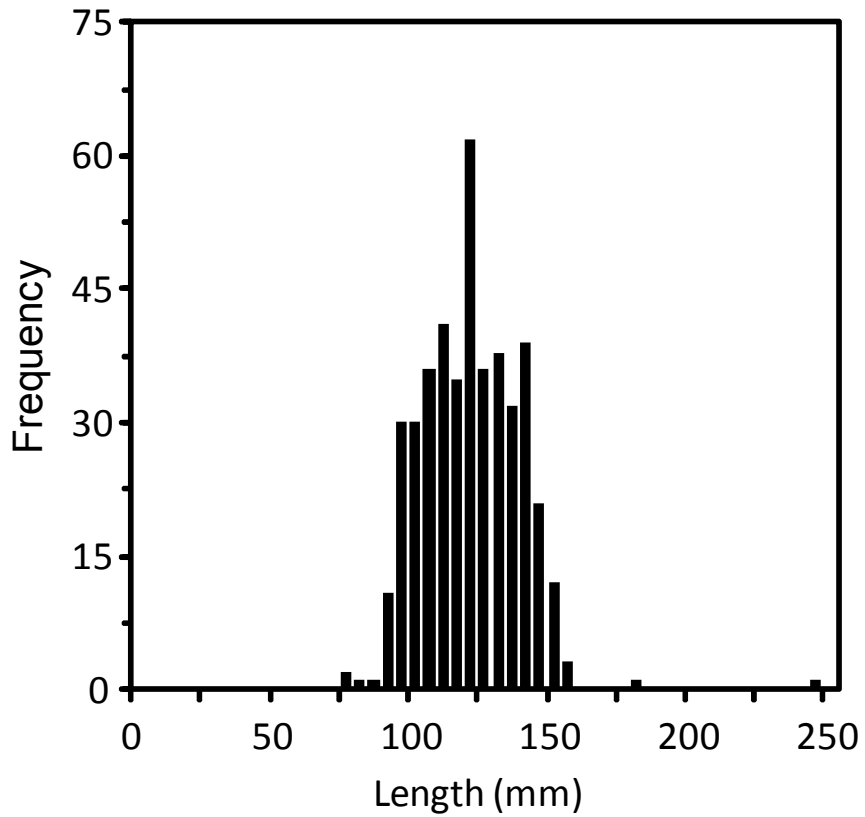
Fig. 16. Length-frequency (mm total length) distribution of cisco (*Coregonus artedi*) in Ten Mile Lake caught using vertical gillnets during the spring of 2011, summer of 2010, 2011, and 2012, and the winter of 2011 and 2012. Cisco lengths did not vary between seasons or years.

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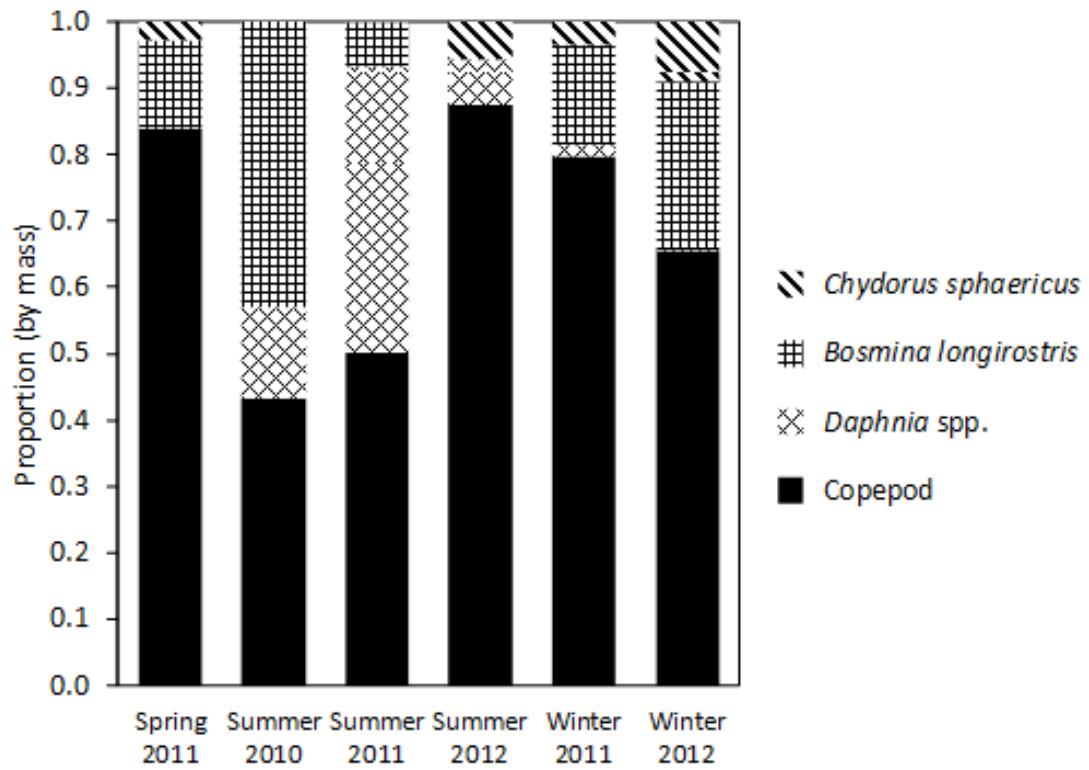
Fig. 17. Diet composition (proportion by mass) of cisco (*Coregonus artedi*) during different seasons and years in Ten Mile Lake, MN.
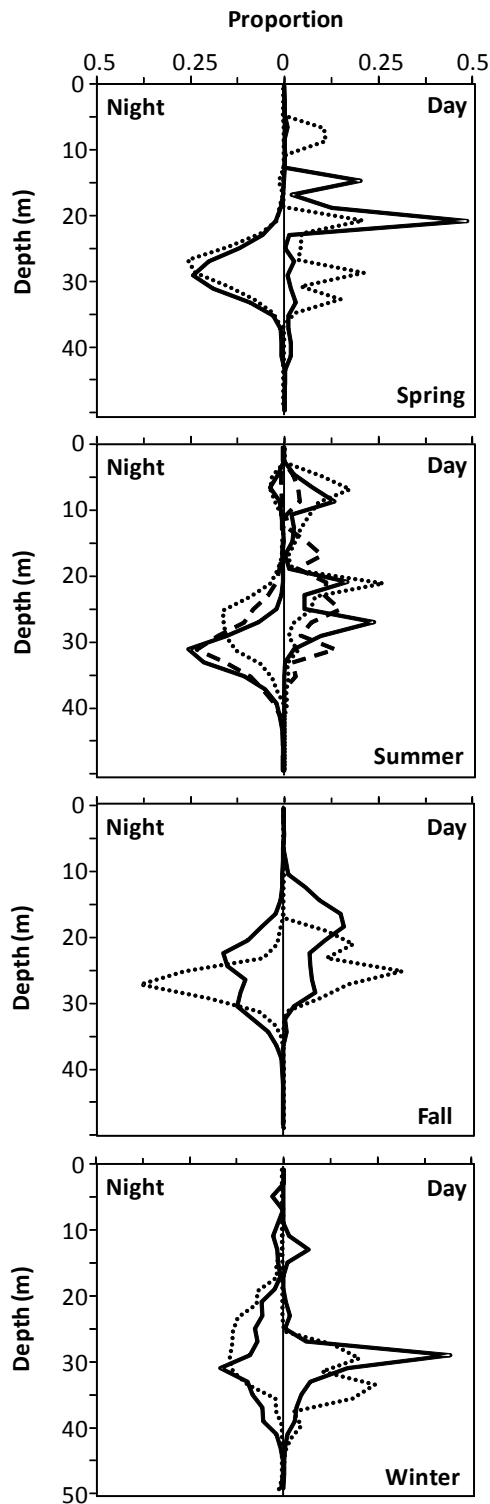
Fig. 18. Day and night vertical distributions of cisco (*Coregonus artedi*) in Ten Mile Lake during the spring, summer, fall, and winter of 2010 (dashed line), 2011 (dotted line), and 2012 (solid line).

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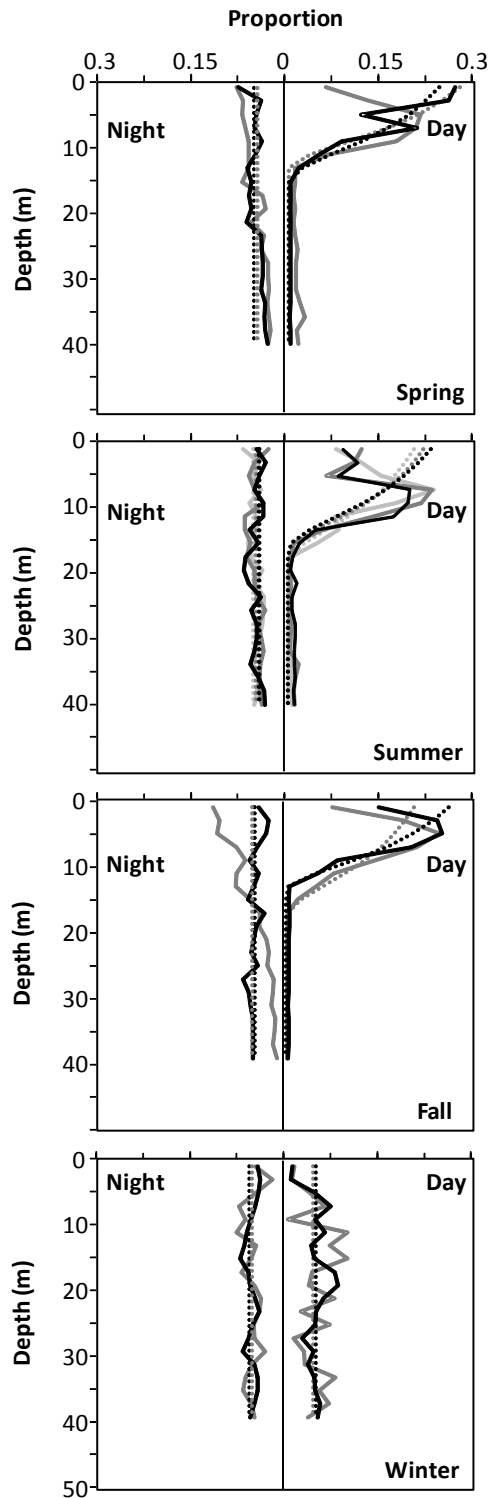
Fig. 19. Foraging (solid line) and predation risk (dotted line) model predictions for cisco (*Coregonus artedi*) in Ten Mile Lake during the spring, summer, fall, and winter of 2010 (light gray line), 2011 (dark gray line), and 2012 (black line).

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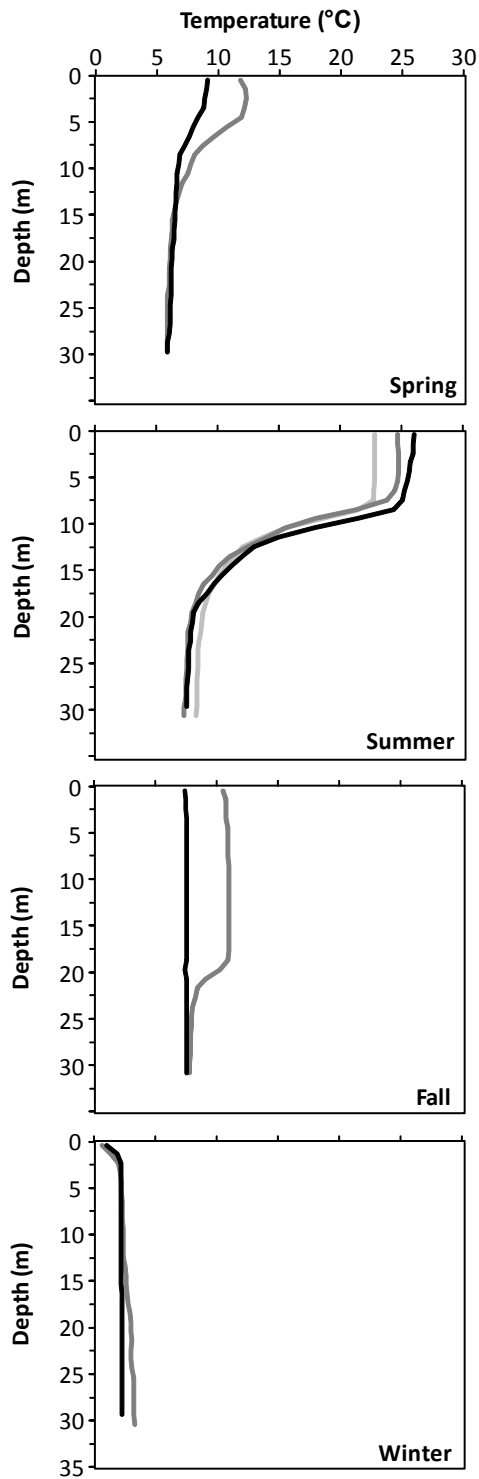
Fig. 20. Temperature (°C) conditions in Ten Mile Lake during the spring, summer, fall, and winter of 2010 (light gray line), 2011 (dark gray line), and 2012 (black line).
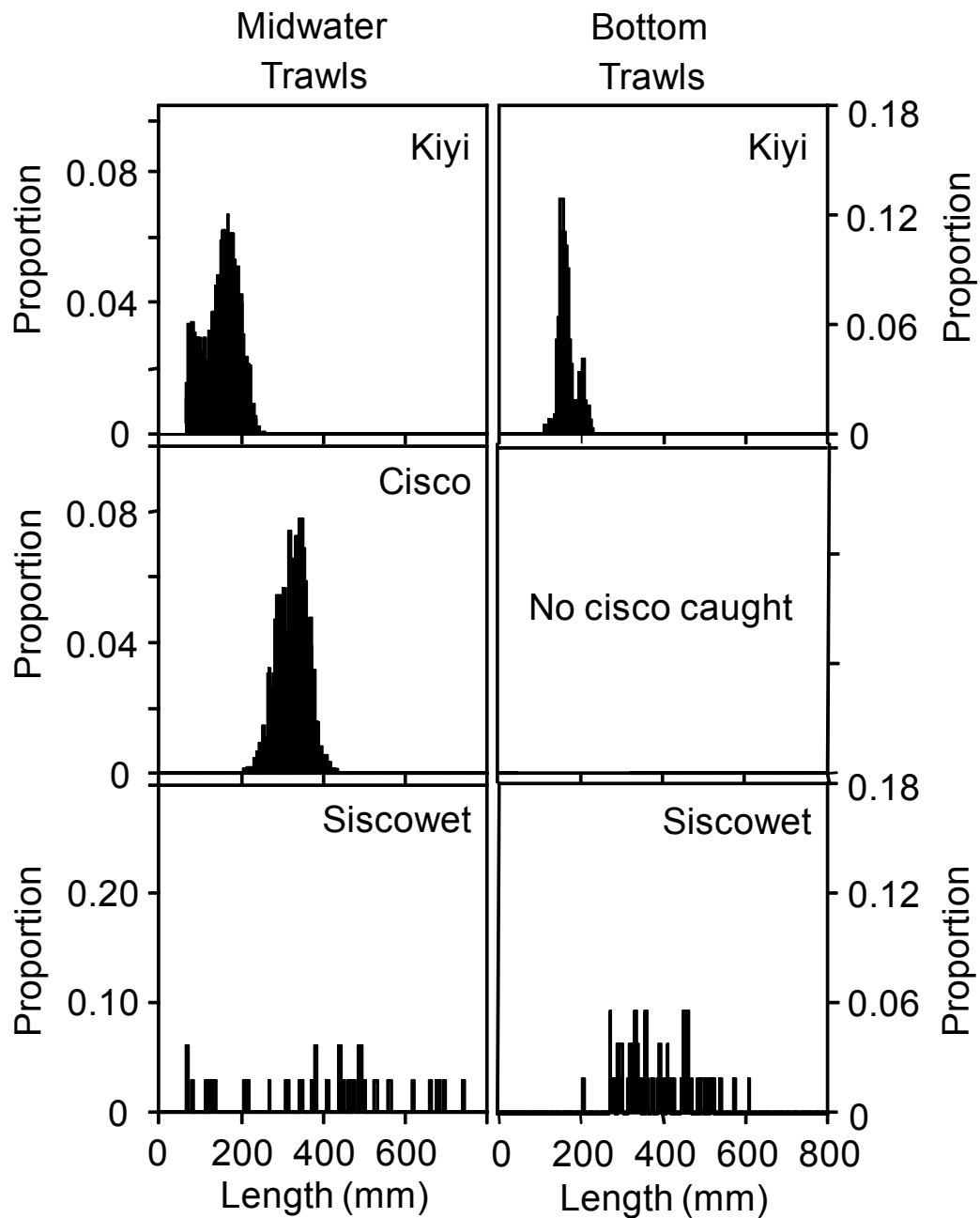
122
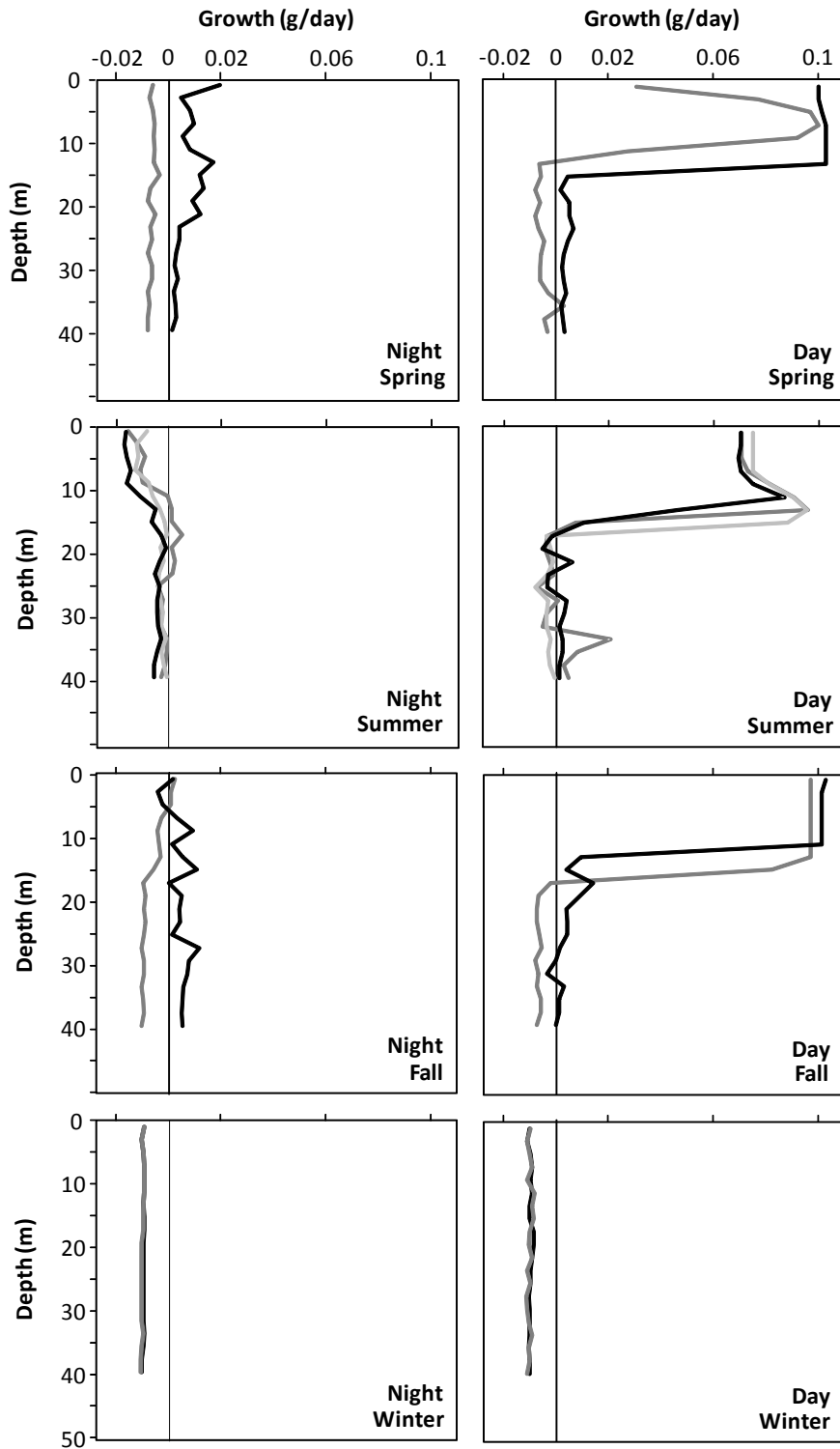
Fig. 21. Day and night growth model predictions (g/day) of cisco in Ten Mile Lake during the spring, summer, fall, and winter of 2010 (light gray line), 2011 (dark gray line), and 2012 (black line).
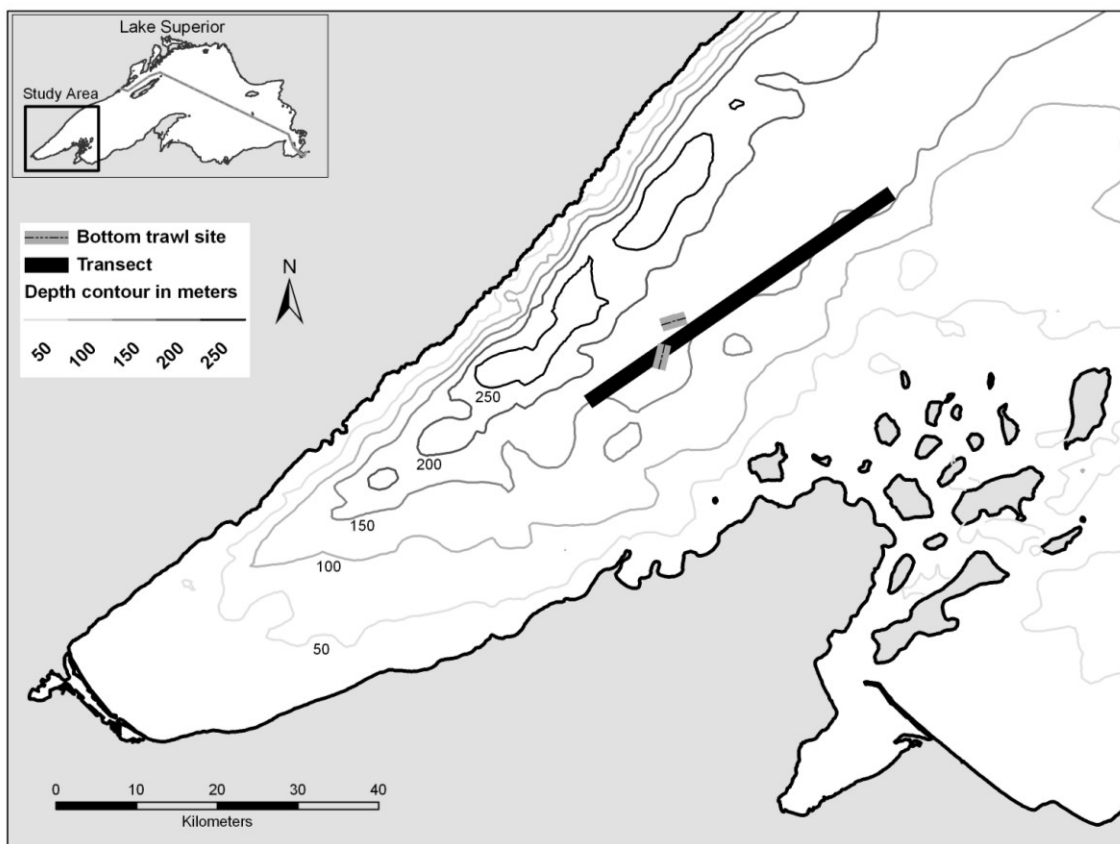
Fig. 22. The survey transect sampled seasonally from 2005-2008 in the western arm of Lake Superior. The study transect was approximately 50 km long, with depths ranging from 140 – 160 m.

Fig. 23. Length-frequency distributions for kiyi (*Coregonus kiyi*), cisco (*C. artedi*), and siscowet lake trout (*Salvelinus namaycush*) captured during all seasons in midwater (from 2003 – 2009) and bottom trawls (from 2007 – 2008).
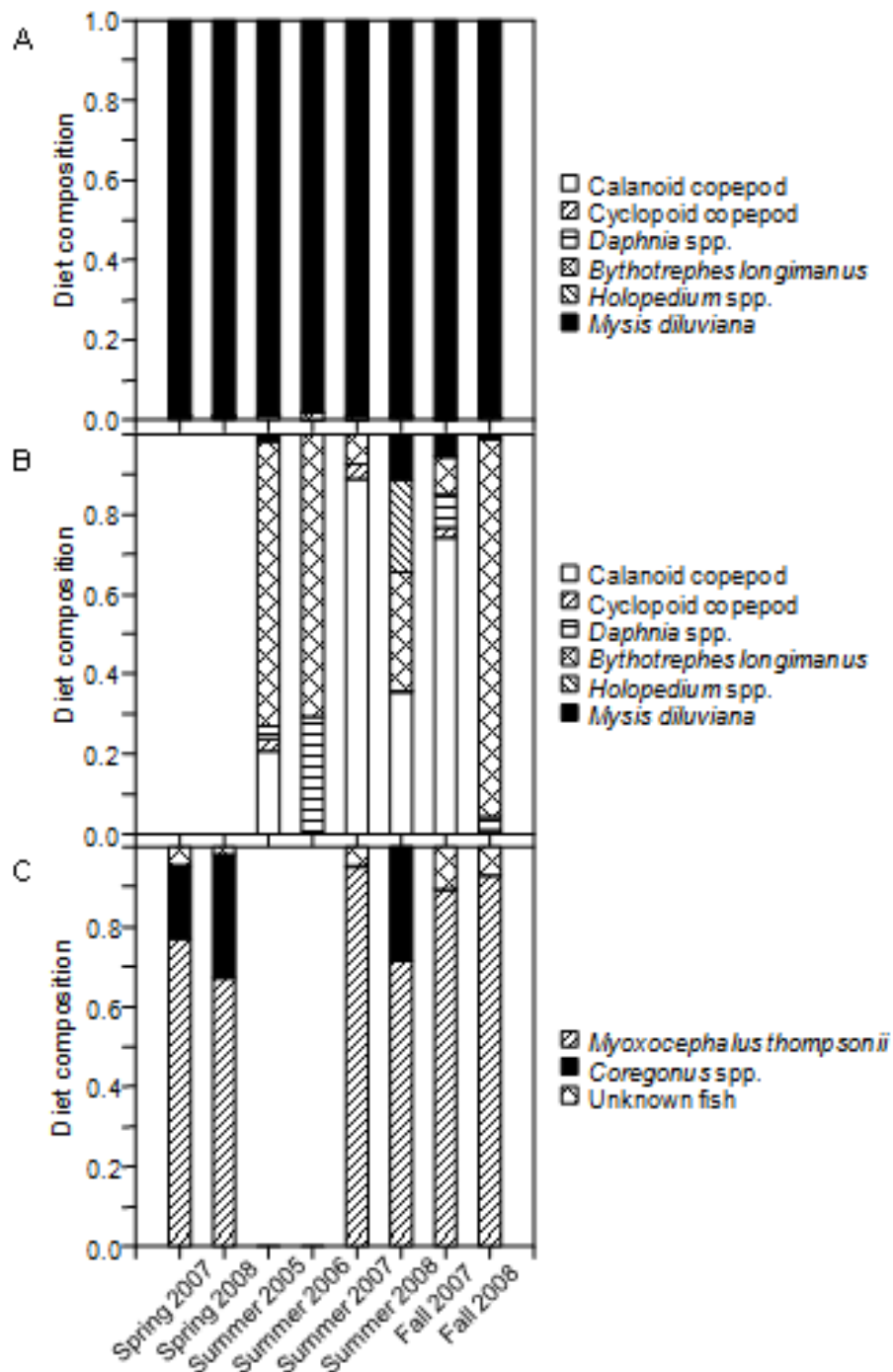
Fig. 24. Diet proportions calculated by mass for (A) kiyi (*Coregonus kiyi*) (*n* = 656), (B) cisco (*C. artedi*) (*n* = 253), and (C) siscowet lake trout (*Salvelinus namaycush*) (*n* = 111) captured in midwater and bottom trawls along the study transect from 2005 – 2008 during each season. Diet items present at less than 1% of the total biomass were not included.
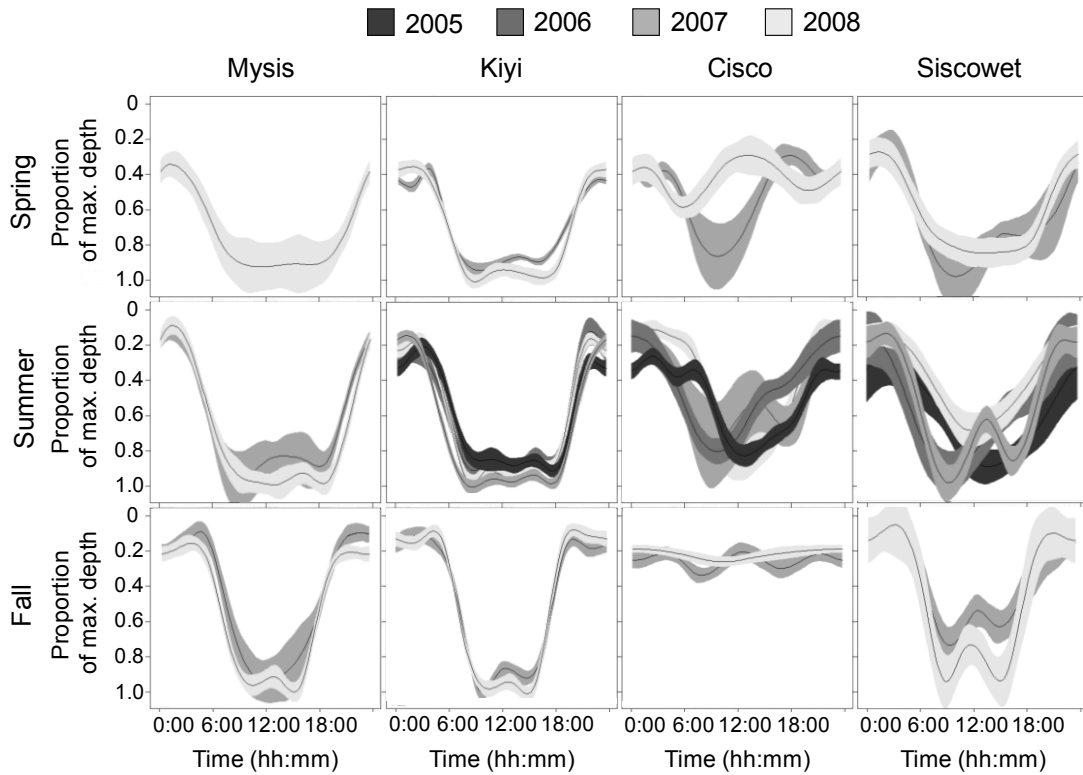
Fig. 25. Weighted, penalized regression splines (GAMM using mgcv v1.6-2 for R v2.11.1) modeling diel vertical migration behavior with time as the predictor, depth the response, and weighted by density during all seasons from 2005 – 2008. Each species is shown in columns, rows show the seasons, and different shades of gray represent different years. A 95% point-wise confidence interval band is associated with each species and year.

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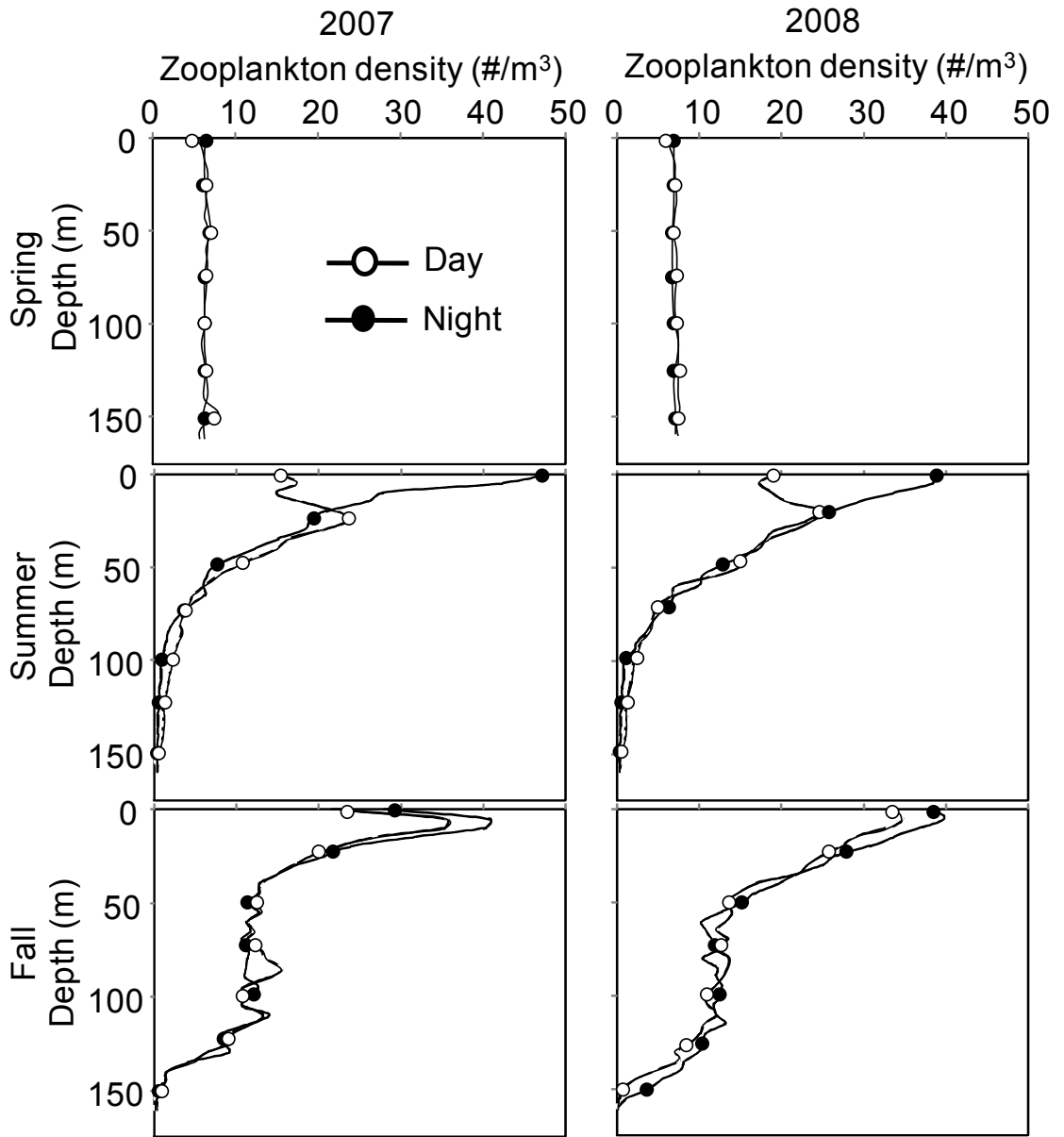
Fig. 26. Zooplankton density (#/m^3) estimates, in 5 m depth bins, for organisms between 1.5 – 2.5 mm ESD during the day and night in three seasons during 2007 – 2008.
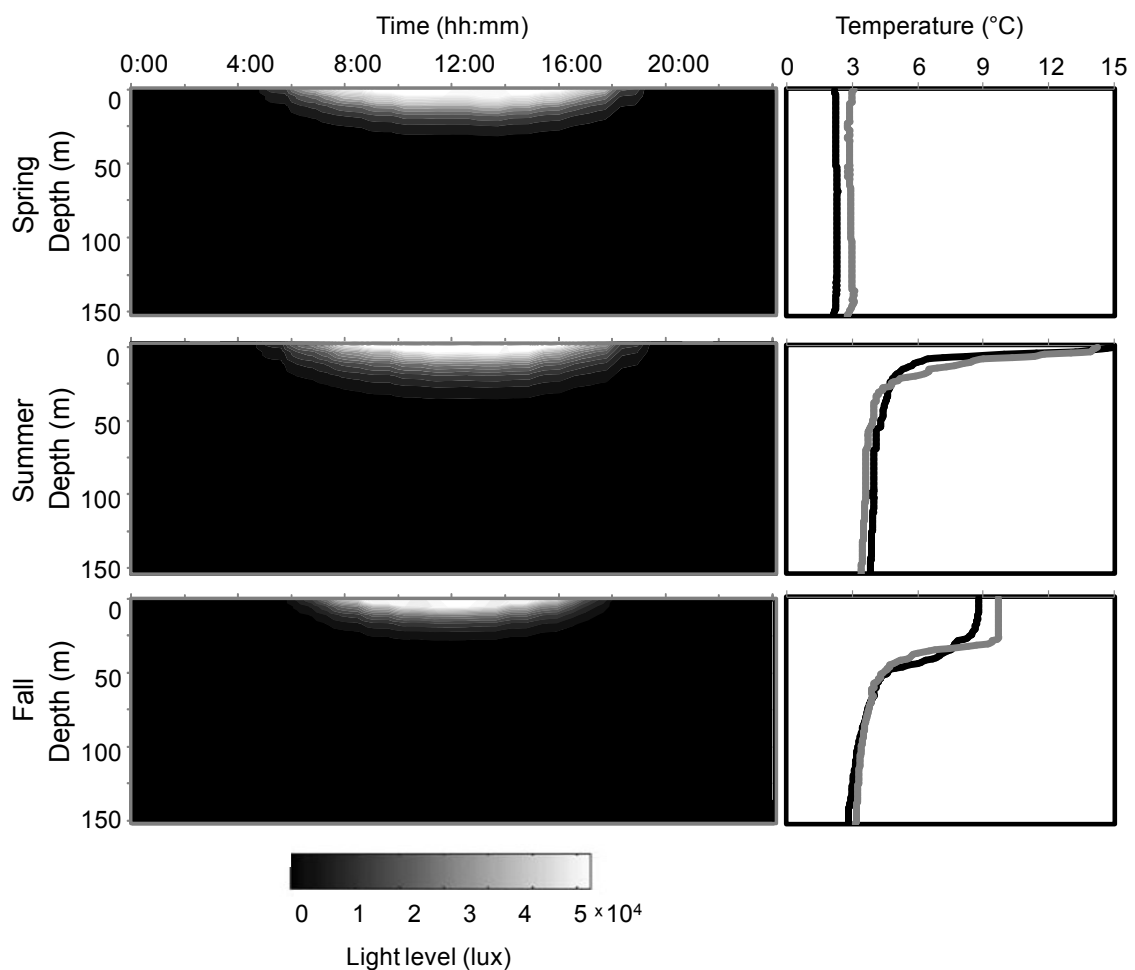
Fig. 27. Seasonal light levels (lux) and water temperature (°C) by depth. Light levels were based on surface light intensity data from Duluth, Minnesota, recorded in 2005 (NSRBD). Water temperatures were collected in 2007 (black line) and 2008 (grey line) during each season.
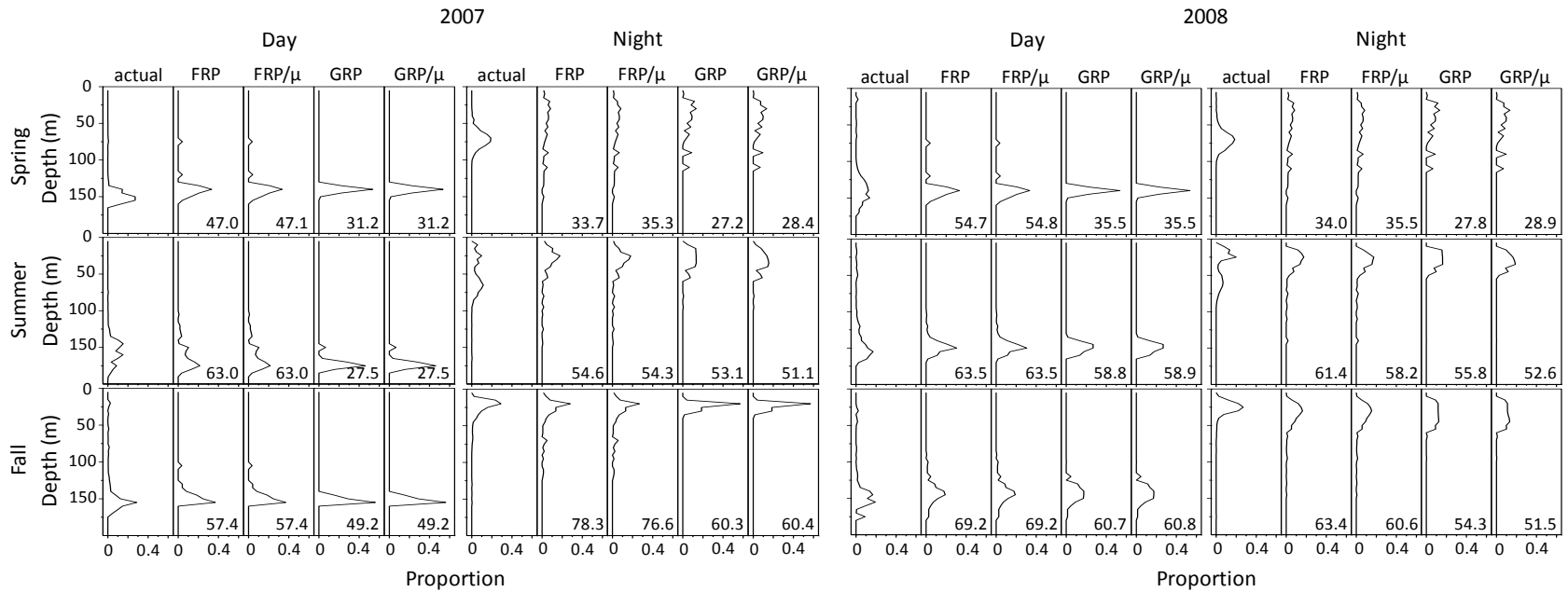
Fig. 28. Kiyi (*Coregonus kiyi*) observed and predicted depth distributions from the day and night during all seasons in 2007 – 2008. Models include FRP = foraging rate potential, FRP/μ = foraging potential – predation risk ratio, GRP = growth rate potential, and GRP/μ = growth rate potential – predation risk ratio. Percent overlap of the modeled distribution with the observed distribution is reported in the lower right of each box.
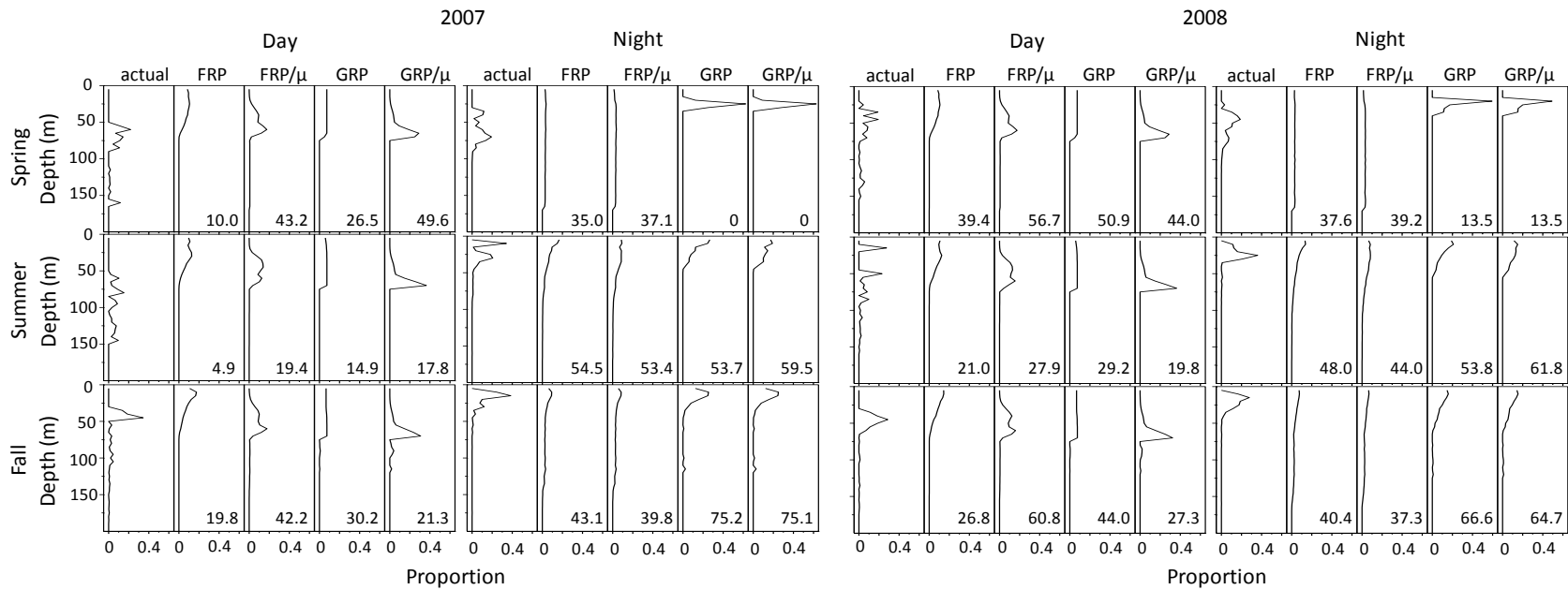
Fig. 29. Cisco (*Coregonus artedi*) observed and predicted depth distributions from the day and night during all seasons in 2007 – 2008. Models include FRP = foraging rate potential, FRP/μ = foraging potential – predation risk ratio, GRP = growth rate potential, and GRP/μ = growth rate potential – predation risk ratio. Percent overlap of the modeled distribution with the observed distribution is reported in the lower right of each box.

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