

# Food resource effects on diel movements and body size of cisco in north-temperate lakes

Tyler D. Ahrenstorff · Thomas R. Hrabik ·  
Peter C. Jacobson · Donald L. Pereira

Received: 10 October 2012 / Accepted: 17 June 2013 / Published online: 29 June 2013  
© Springer-Verlag Berlin Heidelberg 2013

**Abstract** The movement patterns and body size of fishes are influenced by a host of physical and biological conditions, including temperature and oxygen, prey densities and foraging potential, growth optimization, and predation risk. Our objectives were to (1) investigate variability in vertical movement patterns of cisco (*Coregonus artedii*) in a variety of inland lakes using hydroacoustics, (2) explore the causal mechanisms influencing movements through the use of temperature/oxygen, foraging, growth, and predation risk models, and (3) examine factors that may contribute to variations in cisco body size by considering all available information. Our results show that cisco vertical movements vary substantially, with different populations performing normal diel vertical migrations (DVM), no DVM, and reverse DVM in lakes throughout Minnesota

and northern Wisconsin, USA. Cisco populations with the smallest body size were found in lakes with lower zooplankton densities. These smaller fish showed movements to areas of highest foraging or growth potential during the day and night, despite moving out of preferred temperature and oxygen conditions and into areas of highest predation risk. In lakes with higher zooplankton densities, cisco grew larger and had movements more consistent with behavioral thermoregulation and predator avoidance, while remaining in areas with less than maximum foraging and growth potential. Furthermore, the composition of potential prey items present in each lake was also important. Cisco that performed reverse DVM consumed mostly copepods and cladocerans, while cisco that exhibited normal DVM or no migration consumed proportionally more macro-zooplankton species. Overall, our results show previously undocumented variation in migration patterns of a fish species, the mechanisms underlying those movements, and the potential impact on their growth potential.

---

Communicated by Øyvind Fiksen.

---

T. D. Ahrenstorff (✉) · T. R. Hrabik  
Department of Biology, University of Minnesota-Duluth,  
207 Swenson Science Building, 1035 Kirby Drive,  
Duluth, MN 55812, USA  
e-mail: ahre0051@d.umn.edu

T. R. Hrabik  
e-mail: thrabik@d.umn.edu

*Present Address:*  
T. D. Ahrenstorff  
Minnesota Department of Natural Resources, 1601 Minnesota  
Drive, Brainerd, MN 56401, USA

P. C. Jacobson  
Minnesota Department of Natural Resources, 27841 Forest Lane,  
Park Rapids, MN 56470, USA

D. L. Pereira  
Minnesota Department of Natural Resources, 500 Lafayette  
Road, St. Paul, MN 55155, USA

**Keywords** Vertical migration · Reverse · Dwarf · Growth · Predation risk

## 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 (Levy 1990; Sims et al. 2005; Jensen et al. 2011). 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 (Sims et al. 2005; Ahrenstorff et al. 2012). 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 (Johnson and Jakobsen 1987; Gliwicz and Pijanowska 1988). While considerable variability in movement patterns of species has been observed, no studies have examined a variety of 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 (Forward 1988; Appenzeller and Leggett 1995). 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 (Werner and Mittelbach 1981; Ahrenstorff et al. 2011). 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 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.

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 food availability and water temperatures, 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 artedii*) 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 1, 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 which 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. These lakes varied considerably in their physical conditions in terms of surface area (105–2,042 ha), maximum depth (14–63 m), and Secchi depth (2–6 m) (Table 1). The lakes also varied in biological conditions. 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 kindtii*), 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 1). 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 over a single night (6–20 h) 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 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 were 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) by using a coefficient of variation of 25 %. 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) DT-X hydroacoustic echosounder was used in 2010 and 2011. We collected data with a ping rate of 3 pings  $s^{-1}$  at a pulse length of 0.4 ms for all lakes. 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 ( $\pm 1$  dB).

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 ve.4.10, SonarData, Tasmania, Australia), 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 set 6 dB below the minimum target strength of cisco (−52 dB) for all lakes (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

**Table 1** Physical and biological attributes of the study lakes

Lake	Date(s) sampled	Location	Surface area (ha)	Maximum depth (m)	Secchi depth (m)	DVM pattern	Cisco stomachs analyzed	Average size of cisco (mm)	Range in cisco size (mm)	Average cisco density (# m <sup>-3</sup> )	Average cisco density (# ha <sup>-1</sup> )
Big	25 June 1997	46°09'22"N 89°13'06"W	335	19	4.5	Normal	12	256	164–330	0.012	2,462
Carlos	9 Aug 2010 3 Aug 2011	45°57'51"N 95°21'21"W	1,020	50	3	Reverse	102	180	80–420	0.0039	1,458
Clear	5 July 1996 1 July 1997	46°08'47"N 89°48'39"W	208	14	3.5	None	29	274	197–339	0.024	2,852
Dead pike	15 July 1996	46°06'06"N 89°53'57"W	125	24	2.5	Normal	6	178	159–202	0.00076	168
Elk	3 Aug 2010 25 July 2011	47°11'18"N 95°13'06"W	110	28	3.5	None	69	208	77–322	0.0015	466
Little star	25 June 1996	46°06'55"N 89°51'38"W	105	21	6	Normal	17	276	251–299	0.0029	633
Manitowish	18 June 1996	46°06'26"N 89°50'30"W	201	19	5	Reverse	16	246	192–314	0.0014	199
Papoose	25 June 1997	46°11'04"N 89°48'08"W	171	20	5	None	10	300	131–354	0.022	4,214
Ten mile	18 July 2010 2 Aug 2011	46°58'14"N 94°34'21"W	2,042	63	4.5	Reverse	135	124	88–243	0.0067	3,270
Trout	4 June 1996	46°02'46"N 89°40'31"W	1,564	36	6	Reverse	66	152	115–192	0.0016	385
White iron	28 July 2010 28 July 2011	47°52'21"N 91°47'36"W	1,388	14	2	None	69	162	69–367	0.0065	1,083

Sizes of cisco and density estimates were averaged across years when more than 1 year of data were available

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). To examine diel movements, day and night hydroacoustic density estimates (fish  $\text{m}^{-3}$ ) were averaged across all time bins in 2-m depth bins for each lake. We then plotted these average densities of cisco in the 2-m depth bins during the day and night for each lake to determine diel movement patterns for cisco between lakes.

#### 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 (1970) index. This index calculates a percent overlap between the observed and predicted distribution of animals:

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

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, 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), and for an interaction effect between model type and DVM type ( $\alpha = 0.05$ ). Lastly, we used a 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 dataset 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  $\text{mg L}^{-1}$ , and have a

lower lethal limit of 1.9  $\text{mg L}^{-1}$ . 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:

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

where  $R_{ij}$  is the reaction distance (m) of a predator  $j$  (cisco) to prey  $i$  (zooplankton),  $v_j$  and  $v_i$  are the swimming speeds ( $\text{m min}^{-1}$ ) of predator and prey, and  $d_i$  is the prey density ( $\# \text{m}^{-3}$ ). 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- $\mu\text{m}$  mesh collecting cup. In the Minnesota lakes, a 0.5-m-tall, 30-L trap was used with a 63- $\mu\text{m}$  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 ( $\mu$ ) for cisco in the water column was determined using an equation similar to Eq. (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 Eq. (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  $3 \text{ m min}^{-1}$  (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. The predation risk ( $\mu$ ) model can be more intuitively thought of as a predator avoidance ( $1 - \mu$ ) model, so that cisco should choose to inhabit areas where predator avoidance is maximized, similar to how cisco should choose to live where T/O, FRP, and GRP are maximized.

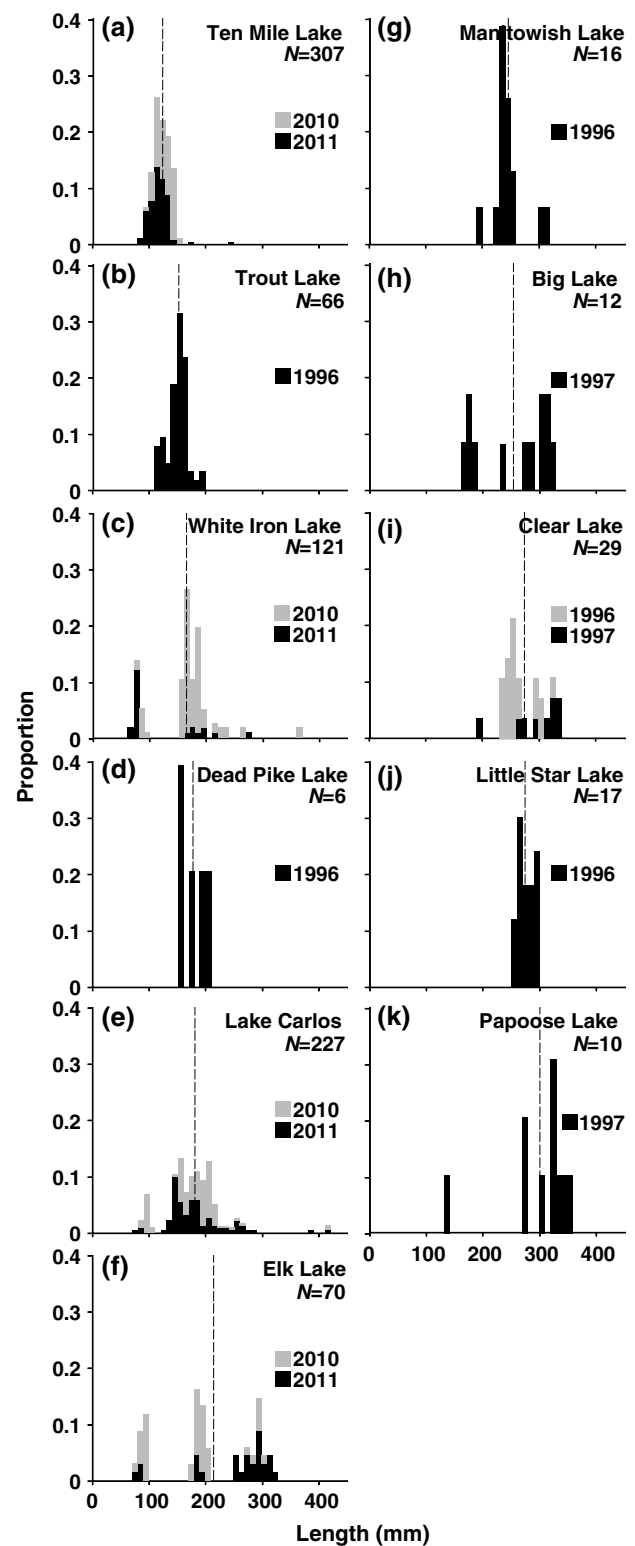
#### Determinants of cisco size

We used multiple regression to compare the average size of cisco to cisco density ( $\# \text{ ha}^{-1}$ ) across all lakes, with zooplankton density as a covariate, to test for the influence of density dependence on the average size of cisco ( $\alpha = 0.05$ ). We then tested for the influence of resource limitation on cisco sizes, by comparing the average and maximum sizes of cisco to zooplankton densities across all lakes using linear regression ( $\alpha = 0.05$ ). All values were log-transformed to normalize the dataset.

## Results

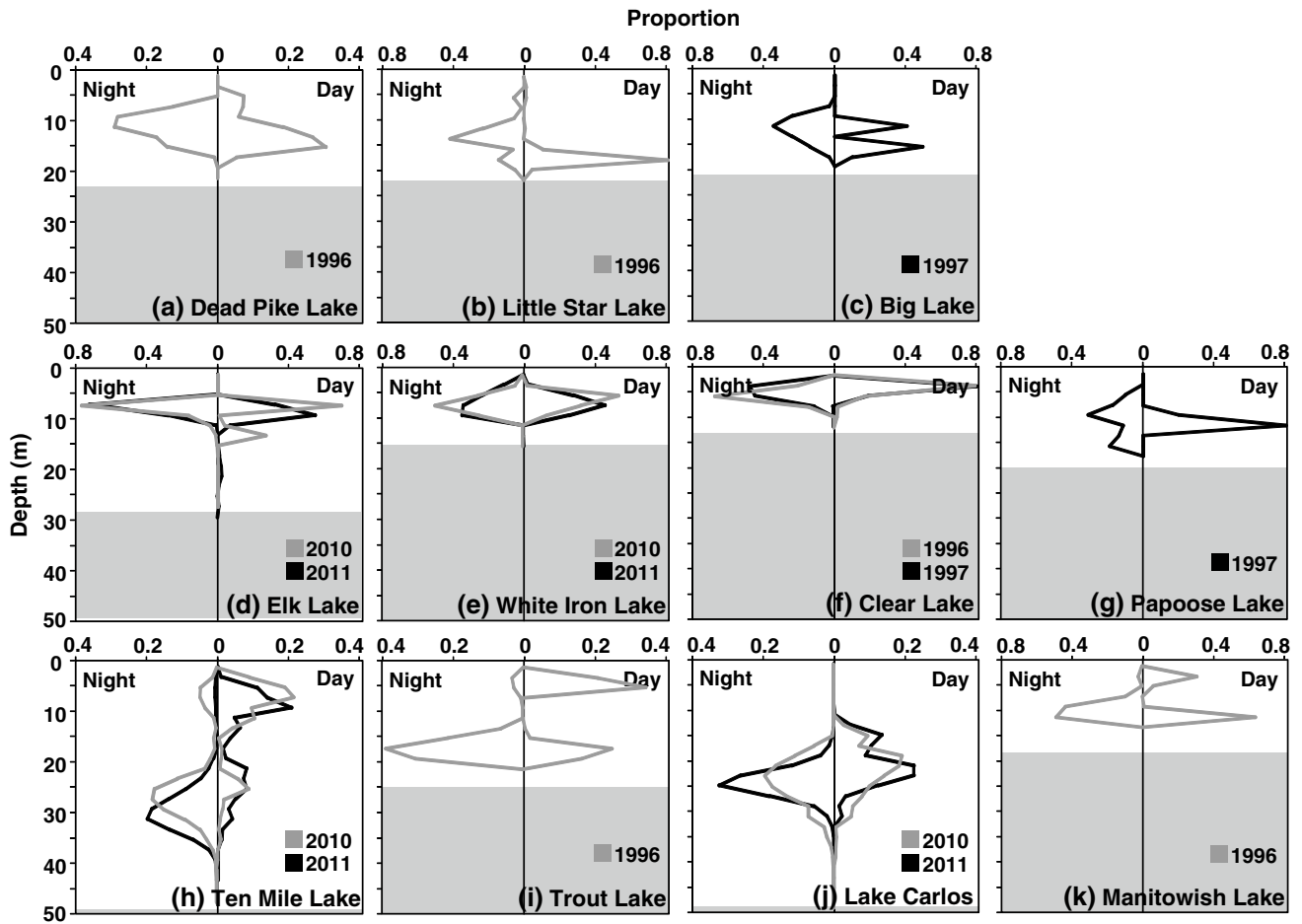
#### Fish communities

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 lucius*;  $n = 5$ ), 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 (Fig. 1). There was a gradient in the average size of cisco caught in the study lakes



**Fig. 1** Frequency distribution for cisco (*Coregonus artedii*) based on total length (mm) of fish captured in 11 study lakes in Minnesota and Wisconsin, USA, during different years. The average size of cisco present in each lake is indicated by vertical dashed lines. Sampling used a continuum of vertical gillnet mesh sizes; sample size ( $N$ ) represents the total number of fish sampled in each lake





**Fig. 2** Cisco vertical distributions, calculated in 2-m depth bins using hydroacoustic estimates of average density, during the night and day in each study lake during different years showing normal diel verti-

cal migrations (*top row*), no diel vertical migrations (*middle row*), and reverse diel vertical migrations (*bottom row*). The light gray shaded area represents the bottom area for each lake

(Table 1), 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**

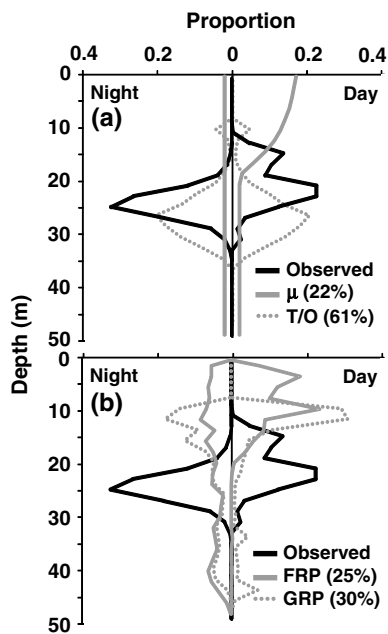
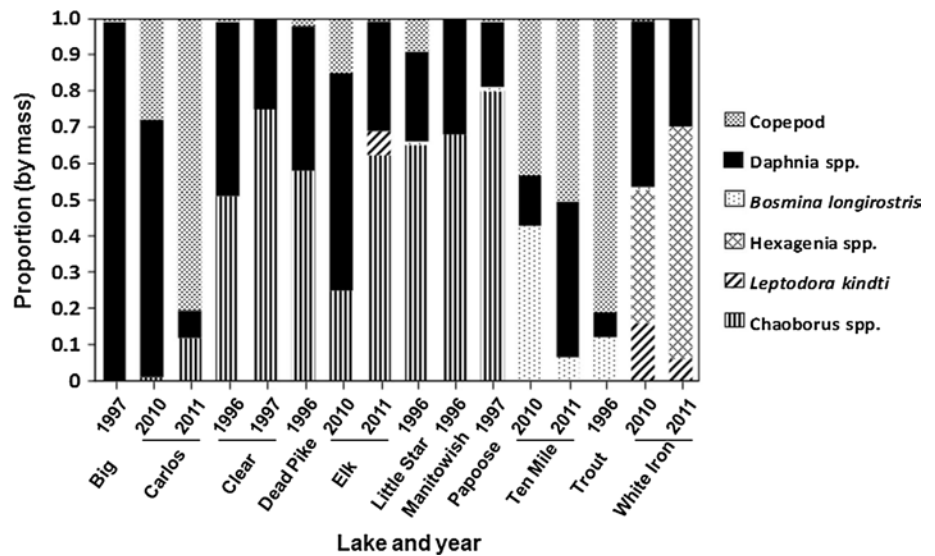
Cisco density estimates calculated using hydroacoustics at night averaged between 168 and 4,214 fish ha<sup>-1</sup> in the study lakes (Table 1). Cisco vertical migrations were variable in the study lakes (Fig. 2). No discernible DVM pattern of cisco was observed in Clear, Elk, Papoose, or White Iron Lakes (~0 m average change in depth between the 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**

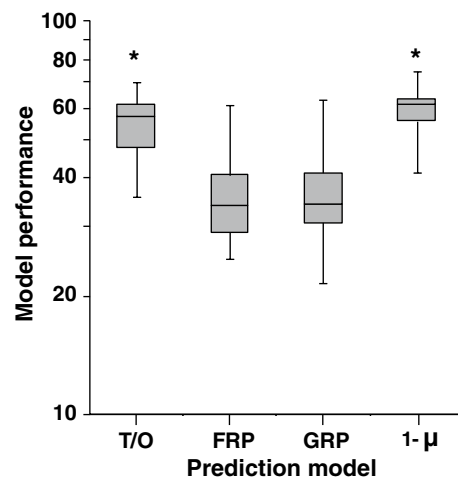
The T/O, FRP, GRP, and (1 - μ) models require empirical inputs including the temperature and oxygen conditions of each lake, the composition of prey items in cisco diets (Fig. 3), and the location and density of those prey items in the water column. In many of the lakes, water temperatures were either too warm near the surface (>17 °C) or oxygen levels were too low near the bottom of the lake (<1.9 mg L<sup>-1</sup>) 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. Generally, cisco populations that performed reverse DVM consumed proportionally more

**Fig. 3** Taxonomic composition of the diet (proportion by mass) for cisco in each study lake during each year sampled (the sample size of cisco stomachs analyzed in each lake is located in Table 1). Diet items that represented <5 % of the total biomass are not included



**Fig. 4** Comparison between the observed distribution of cisco in Lake Carlos in 2011 and their predicted distribution based on the **a** predation risk ( $\mu$ ) and temperature/oxygen (*T/O*) models, and **b** foraging rate potential (*FRP*) and growth rate potential (*GRP*) models. For each predicted distribution, the calculated percent overlap with the observed distribution is shown in parentheses

copepods and smaller cladocerans, while cisco populations that performed normal or no DVM consumed a higher proportion of macro-zooplankton species. 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



**Fig. 5** Performance of 4 prediction models: *box* and *whisker* plots showing the log<sub>10</sub>-transformed average percent overlap for the 11 lakes between the observed and temperature/oxygen (*T/O*), foraging rate potential (*FRP*), growth rate potential (*GRP*), and predator avoidance ( $1 - \mu$ ) model predictions. The *boxes* represent the difference between the 25th and 75th percentiles while the *whiskers* represent the end points. The *asterisk* indicates that the *T/O* and ( $1 - \mu$ ) models were significantly different from the *FRP* and *GRP* models ( $\alpha = 0.05$ )

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 observed and predicted distribution of cisco for each of the models (for example, see Fig. 4) across all lakes, the *T/O* and predator avoidance ( $1 - \mu$ ) model performed significantly better than the *FRP* and *GRP* models ( $P = 3.4 \times 10^{-5}$ ; Fig. 5; Table 2). By splitting the lakes into categories defined



**Table 2** Results of a two-factorial ANOVA to test for differences in the performance among models across all lakes (i.e. T/O, FRP, GRP, and  $1 - \mu$ ), 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), and for an interaction effect between model type and DVM type

Source	Type III SS	df	Mean squares	F ratio	P value
Model	0.45	3	0.15	11.22	$3.4 \times 10^{-5}$
DVM	0.001	2	0.0005	0.035	0.97
Interaction (Model X DVM)	0.029	6	0.0048	0.37	0.89
Error	0.43	32	0.013		

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  $(1 - \mu)$  models among each group of lakes ( $P = 0.97$ ; Table 2). The interaction effect between model type and DVM type also indicated no significant differences ( $P = 0.89$ ; Table 2).

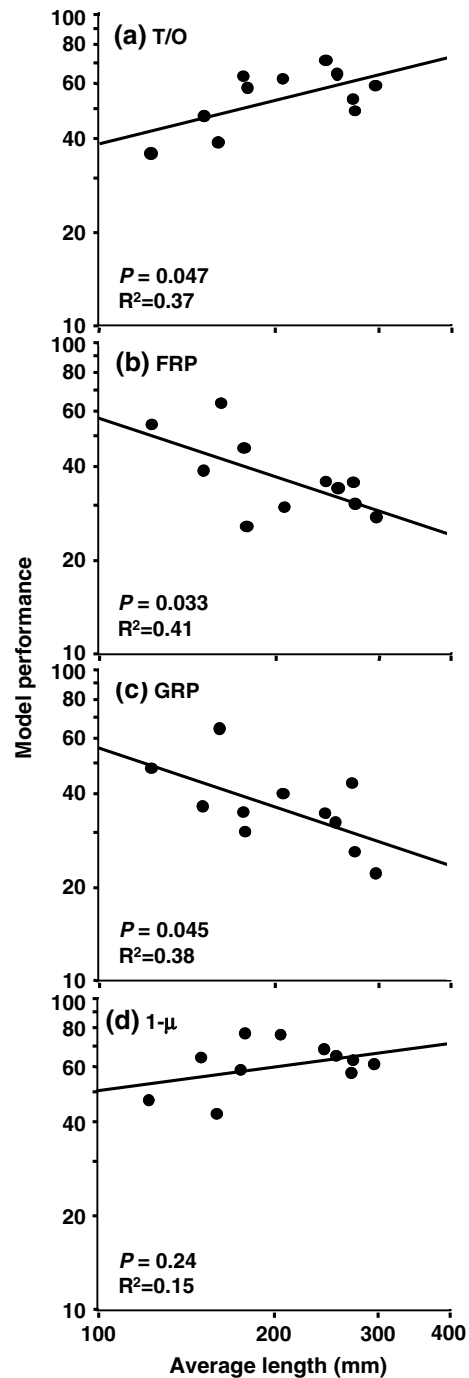
Model performance for each of the four models varied with changes in the average size of cisco present in each lake. For the T/O model, model performance was lowest for lakes with the smallest-sized cisco and model performance increased significantly as the average size of cisco increased in each lake ( $F_{1,9} = 5.28$ ;  $P = 0.047$ ) (Fig. 6). 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 (Fig. 6). For the  $(1 - \mu)$  model there was a general, albeit non-significant, trend where lakes with the smallest sized cisco were located in areas of lowest predator avoidance, and model performance increased as the average size of cisco increased in each lake ( $F_{1,9} = 1.58$ ;  $P = 0.24$ ; Fig. 6).

**Determinants of cisco size**

There was no significant effect between the average size of cisco and cisco density (# ha<sup>-1</sup>) in the study lakes, with zooplankton density as a covariate identified using multiple regression ( $F_{2,8} = 2.41$ ;  $P = 0.15$ ). However, zooplankton density was positively correlated with the average size of cisco ( $F_{1,9} = 5.41$ ;  $P = 0.045$ ; Fig. 7) and maximum size of cisco ( $F_{1,9} = 9.33$ ;  $P = 0.014$ ) in all inland lakes when examined independently.

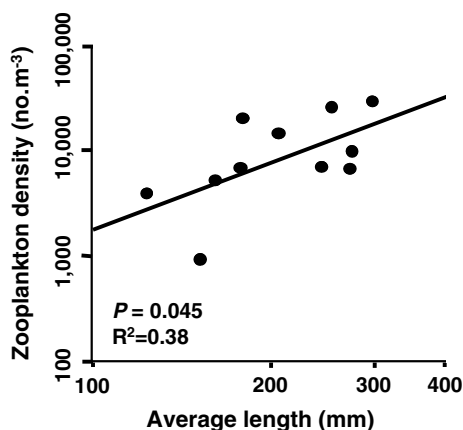
**Discussion**

Our findings are consistent with other studies in that we observed different vertical movement patterns of a



**Fig. 6** Log10-transformed model performance (percent overlap) between the observed and predicted distributions of cisco based on models of **a** temperature/oxygen (T/O), **b** foraging potential (FRP), **c** growth potential (GRP), and **d** predator avoidance ( $1 - \mu$ ) versus the log10-transformed average size of cisco (mm) in each inland lake. The diagonal line and statistics in each plot represent the results of a linear regression

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



**Fig. 7** The relationship between log<sub>10</sub>-transformed zooplankton density (number per cubic meter) and the average size of cisco (mm) in each inland lake. The diagonal line and statistics represent the results of a linear regression

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 dimensions including temperature/oxygen, foraging, growth, or predator avoidance 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 ( $\mu$  model). In Ten Mile Lake during 2010 and 2011, the majority of the dwarf cisco population migrated up into shallow high predation risk areas (~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 have 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 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-h 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 (Dryer and Beil 1964; Ahrenstorff et al. 2011). 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 of 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 avoidance was maximized. Our most significant finding was that prey density appeared to dictate the importance of the other ultimate factors known to influence DVM behavior and mediate the range of behaviors exhibited by different populations of cisco. Additional work examining the role of prey density, particularly low prey density, and prey distribution on behavior may yield new insight into proximate and ultimate controlling factors.

**Acknowledgments** Donn Branstrator, Stephanie Guildford, Robert Hecky, John Pastor, and several anonymous reviewers deserve thanks for providing comments on the proposal and earlier versions of this manuscript. We thank Andy Carlson, Allison Gamble, Kyle Gilles, Logan Jacobson, Tyler Kaspar, Jiethyl Piersak, Cindy Tomcko, and numerous Minnesota Department of Natural Resource interns for field assistance. This work was funded by the Legislative-Citizen Commission on Natural Resources, through the Minnesota Department of Natural Resources, and by a University of Minnesota Doctoral Dissertation Fellowship awarded to T.D. Ahrenstorff.

## References

- Aglen A (1983) Random errors of acoustic fish abundance estimates in relation to the survey grid density applied. *FAO Fish Rep* 300:293–297
- Ahrenstorff TD, Hrabik TR, Stockwell JD, Yule DL, Sass GG (2011) Seasonally dynamic diel vertical migrations of *Mysis diluviana*, coregonine fishes, and siscowet lake trout in the pelagia of western Lake Superior. *Trans Am Fish Soc* 140:1504–1520
- Ahrenstorff TD, Jensen OP, Weidel BC, Mendsaikhan B, Hrabik TR (2012) Abundance, spatial distribution, and diet of endangered Hovsgol grayling (*Thymallus nigrescens*). *Environ Biol Fish* 94:465–476
- Anholt BR, Werner EE (1995) Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* 76:2230–2234
- Appenzeller AR, Leggett WC (1992) Bias in hydro acoustic estimates of fish abundance due to acoustic shadowing: evidence from day-night surveys of vertically migrating fish. *Can J Fish Aquat Sci* 49:2179–2189
- Appenzeller AR, Leggett WC (1995) An evaluation of light-mediated vertical migration of fish based on hydro acoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*). *Can J Fish Aquat Sci* 52:504–511

- Bahr DM (1977) Homing, swimming behavior, range, activity patterns and reaction to increasing water levels of walleyes (*Stizostedion vitreum vitreum*) as determined by radio-telemetry in navigational pools 7 and 8 of the upper Mississippi River during spring, 1976. Master thesis, University of Wisconsin-Madison, Madison
- Bohl E (1980) Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia* 44:368–375
- Brandt SB, Mason DM, Patrick EV (1992) Spatially-explicit models of fish growth rate. *Fisheries* 17:23–33
- Clark CW, Levy DA (1988) Diel vertical migrations by juvenile sockeye salmon and the ant predation window. *Am Nat* 131:271–290
- Dryer WR, Beil J (1964) Life history of lake herring in Lake Superior. *Fish Bull* 63:493–529
- Forward RB (1988) Diel vertical migration: zooplankton photobiology and behaviour. *Oceanogr Mar Biol Annu Rev* 26:361–393
- Gerritsen J, Strickler JR (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. *J Fish Res Board Can* 37:73–82
- Gliwicz MZ, Pijanowska J (1988) Effect of predation and resource depth distribution on vertical migration of zooplankton. *Bull Mar Sci* 43:695–709
- Haney JF (1988) Diel patterns of zooplankton behavior. *Bull Mar Sci* 43:583–603
- Hile R (1938) Morphometry of the cisco, *Leucichthys artedi* (LeSueur), in the lakes in the northeastern highlands, Wisconsin. *Int Rev Ges Hydrobio* 36:57–130
- Hutchinson GE (1957) A treatise on limnology, vol 1. Wiley, New York
- Iwasa Y (1982) Vertical migration of zooplankton: a game between predator and prey. *Am Nat* 120:171–180
- Jensen OP, Hansson S, Didrikas T, Stockwell JD, Hrabik TR, Axenrot T, Kitchell JF (2011) Foraging, bioenergetic and predation constraints on diel vertical migration: field observations and modeling of reverse migration by young-of-the-year herring *Clupea harengus*. *J Fish Biol* 78:449–465
- Johnson GH, Jakobsen PJ (1987) The effect of food limitation on vertical migration in *Daphnia longispina*. *Limnol Oceanogr* 32:873–880
- Levy DA (1990) Reciprocal diel vertical migration behaviour in planktivores and zooplankton in British Columbia Lakes. *Can J Fish Aquat Sci* 47:1755–1764
- Loch JS (1974) Phenotypic variation in the lake whitefish, *Coregonus clupeaformis*, induced by introduction into a new environment. *J Fish Res Board Can* 31:55–62
- Love RH (1977) Target strength of an individual fish at any aspect. *J Acoust Soc Am* 62:1397–1403
- Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. *Am Zool* 19:331–343
- Mason DM, Brandt SB (1996) Effects of spatial scale and foraging efficiency on the predictions made by spatially-explicit models of fish growth rate potential. *Environ Biol Fish* 45:283–298
- Mehner T (2012) Diel vertical migration of freshwater fishes: proximate triggers, ultimate causes and research perspectives. *Freshw Biol* 57:1342–1359
- Mehner T, Kasprzak P (2011) Partial diel vertical migrations in pelagic fish. *J Anim Ecol* 80:761–770
- Parker-Stetter SL, Rudstam LG, Sullivan PJ, Warner DM (2009) Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Great Lakes Fishery Commission Special Publication, Michigan
- Rask M (1983) Differences in growth of perch (*Perca fluviatilis* L.) in two small forest lakes. *Hydrobiologia* 101:139–144
- Rudstam LG, Magnuson JJ (1985) Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedi*, and yellow perch, *Perca flavescens*. *Can J Fish Aquat Sci* 42:1178–1188
- Rudstam LG, Lathrop RC, Carpenter SR (1993) The rise and fall of a dominant planktivore: direct and indirect effects on zooplankton. *Ecology* 74:303–319
- Rudstam LG, Binkowski FP, Miller MA (1994) A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. *Trans Am Fish Soc* 123:344–357
- Rudstam LG, Parker-Stetter SL, Sullivan PJ, Warner DM (2009) Towards a standard operating procedure for fishery acoustic surveys in the Laurentian Great Lakes, North America. *ICES J Mar Sci* 66:1391–1397
- Sandheinrich MB, Hubert WA (1984) Intraspecific resource partitioning by yellow perch, *Perca flavescens*, in a stratified lake. *Can J Fish Aquat Sci* 41:1745–1752
- Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418
- Shields BA, Underhill JC (1993) Phenotypic plasticity of a transplanted population of dwarf cisco, *Coregonus artedii*. *Environ Biol Fish* 37:9–23
- Sims DW, Southall EJ, Tarling GA, Metcalfe JD (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *J Anim Ecol* 74:755–761
- Sinclair ARE, Arcese P (1995) Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* 76:882–891
- SOP-LG403 (2003) U.S. Environmental Protection Agency's Great Lakes National Program Office. Available: [www.epa.gov/greatlakes/monitoring/sop/chapter\\_4/LG403.pdf](http://www.epa.gov/greatlakes/monitoring/sop/chapter_4/LG403.pdf)
- Todd TN, Smith GR, Cable LE (1981) Environmental and genetic contributions to morphological differentiation in ciscoes (*Coregoninae*) of the Great Lakes. *Can J Fish Aquat Sci* 38:59–67
- von Siebold CT (1863) Die Subwasserfische von Mitteleuropa. Engelmann, Leipzig
- Walters CJ, Juanes F (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can J Fish Aquat Sci* 50:2058–2070
- Werner EE, Mittelbach GG (1981) Optimal foraging: field tests of diet choice and habitat switching. *Am Zool* 21:813–829
- Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An experimental test of the effects of predation risk in habitat use in fish. *Ecology* 64:1540–1548
- Wright DI, O'Brien WJ (1984) The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis annularis*). *Ecol Monogr* 54:65–98