Empirical evaluation of predator-driven diel vertical migration in Lake Superior

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Abstract: Recent studies on Lake Superior suggest that diel vertical migration (DVM) of prey (generalized *Coregonus* spp.) may be influenced by the density of predatory siscowet (*Salvelinus namaycush*). We empirically evaluated this hypothesis using data from acoustic, midwater trawl, and bottom trawl sampling at eight Lake Superior sites during three seasons in 2005 and a subset of sites in 2006. We expected the larger-bodied cisco (*Coregonus artedi*) to exhibit a shallower DVM compared with the smaller-bodied kiyi (*Coregonus kiyi*). Although DVM of kiyi and cisco were consistent with expectations of DVM as a size-dependent, predator-mediated process, we found no relationship between siscowet density and the magnitude of DVM of either coregonid. Cisco appear to have a size refuge from siscowet predation. Kiyi and siscowet co-occur in demersal habitat > 150 m during the day, where visual predation is unlikely, suggesting predator avoidance is not a factor in the daytime distribution of kiyi. Seasonal patterns of kiyi DVM were consistent with reported DVM of their primary prey *Mysis relicta*. Our results suggest that consideration of nonvisual foraging, rather than light-based foraging theory (i.e., the antipredation window), is necessary to understand the processes driving DVM in deepwater systems.

Résumé : Des études récentes sur le lac Supérieur laissent croire que la migration verticale journalière (DVM) des proies (les *Coregonus* spp. en général) est influencée par la densité du prédateur, le touladi siscowet (*Salvelinus namaycush*). Nous évaluons cette hypothèse de manière empirique à l'aide de données provenant d'échantillonnages acoustiques et de prélèvements aux chaluts pélagique et benthique dans huit sites au lac Supérieur durant trois saisons en 2005 et dans un sous-ensemble de sites en 2006. Nous nous attendions à ce que le cisco de lac (*Coregonus artedi*) de plus grande taille ait une DVM moins profonde que le cisco kiyi (*Coregonus kiyi*) plus petit. Bien que les DVM du cisco kiyi et du cisco de lac soient en accord avec les attentes relatives à la DVM comme processus relié à la taille et géré par le prédateur, il n'existe aucune relation entre la densité du siscowet et l'importance de la DVM chez les deux corégonidés. Les ciscos semblent posséder un refuge relié à la taille contre la prédation du siscowet. Le cisco kiyi et le cisco de lac se retrouvent ensemble dans l'habitat benthique > 150 m durant le jour où la prédation visuelle est peu probable, ce qui indique que l'évitement des prédateurs n'est pas un facteur explicatif de la répartition du cisco kiyi durant la journée. Les patrons saisonniers de DVM du cisco kiyi correspondent aux patrons de DVM signalés chez leur proie principale *Mysis relicta*. Nos résultats indiquent qu'il faut tenir compte de la recherche non visuelle de nourriture plutôt que de la recherche basée sur la lumière (c'est-à-dire, la fenêtre antiprédation) pour comprendre les processus explicatifs de la DVM dans les systèmes d'eau profonde.

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Introduction

Diel vertical migration (DVM) is a common feature in aquatic systems, occurring over multiple trophic levels including primary producers (e.g., James et al. 1992), herbivores (e.g., Stich and Lampert 1981; Frost and Bollens 1992; Thomson and Allen 2000), planktivores (e.g., Janssen and Brandt 1980; Levy 1987, Scheuerell and Schindler 2003), piscivores (e.g., Kitagawa et al. 2000; Hrabik et al. 2006; Sims et al. 2006), and omnivores (e.g., Beeton 1960). A number of mechanisms have been proposed to explain DVM behavior. These mechanisms include maximizing for-

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aging opportunities (e.g., Narver 1970; Schoener 1971; Eshenroder and Burnham-Curtis 1999), optimizing bioenergetic efficiency (e.g., Brett 1971; Bevelhimer and Adams 1993), and minimizing predation risk (e.g., Eggers 1978; Levy 1987; Clark and Levy 1988). Clark and Levy (1988) synthesized these mechanisms into a behavioral model predicting that movement to shallower depths for feeding should occur at intermediate light levels (i.e., the antipredation window) minimizing the ratio of predation risk to feeding (or growth) rate. Evidence in support of the antipredation window hypothesis has grown in recent years (e.g., Kaartvedt et al. 1996; Scheuerell and Schindler 2003; Hardiman et al. 2004).

Recent research on Lake Superior suggests that predator density impacts the DVM behavior of forage fishes in offshore regions. Observations obtained from acoustics suggest that the magnitude of DVM in *Coregonus* spp. was positively related to the density of siscowet (*Salvelinus namaycush*; Hrabik et al. 2006), a deepwater morphotype of lake trout that preys largely on coregonids and deepwater sculpin (*Myoxocephalus thompsonii*; Conner et al. 1993; Harvey and Kitchell 2000; Ray et al. 2007) and also appears to undergo DVM (Hrabik et al. 2006). Jensen et al. (2006) developed a model to examine the mechanisms underlying coregonid DVM behavior and found strategies that minimized the ratio of predation risk (μ) to potential growth rate (*G*) best explained their vertical distribution. Their model suggested two DVM strategies that coregonids might follow: a low risk – low growth trajectory characterized by a deeper DVM and a high risk – high growth trajectory characterized by a shallower DVM. Jensen et al. (2006) suggested that the deeper trajectory would be advantageous when predator density is high and the shallower trajectory more advantageous when predator densities are low or coregonid densities are high (i.e., greater potential for intraspecific competition). Empirical observations of coregonid vertical distribution reported by Hrabik et al. (2006) were consistent with these modeling predictions, but were limited to three sampling occasions across two years and did not include sampling of demersal habitat.

Two coregonid species are common in offshore waters of Lake Superior — kiyi (*Coregonus kiyi*) and adult cisco (*Coregonus artedi*; Hrabik et al. 2006; Stockwell et al. 2006; Yule et al. 2009). Other coregonid species exist in Lake Superior, including shortjaw cisco (*Coregonus zenithicus*) and bloater (*Coregonus hoyi*), but the former is rare (Hoff and Todd 2004; Gorman and Todd 2007) and the latter is largely confined to where bathymetric depths are less than 140 m (Adams et al. 2006). Adult cisco differ from kiyi in several basic attributes (Table 1). First, cisco reach larger sizes than kiyi as adults (Bersamin 1958; Smith 1964; Stockwell et al. 2006) and thus may be less susceptible to predation. Second, cisco feed on different prey (copepods and cladocerans) than kiyi (*Mysis relicta*). Finally, cisco are not associated with the bottom during daylight (Stockwell et al. 2006) but kiyi are (Yule et al. 2007). Based on these differences, divergent DVM behavior between the two species should be expected whereby the larger-bodied cisco will likely undergo less pronounced DVM than the smaller-bodied kiyi. The Hrabik et al. (2006) and Jensen et

al. (2006) studies did not explore DVM as a species-specific process.

In this study, we use complementary sampling techniques in offshore demersal (bottom trawls) and pelagic (midwater trawls and acoustics) habitats to empirically test several hypotheses about coregonid DVM in Lake Superior. First, we compare day and night bottom trawl catches to test Hrabik et al.'s (2006) acoustic observations of DVM in siscowets and coregonids. If siscowet and their coregonid prey perform DVM, we would expect day bottom trawl catches to be higher than night bottom trawl catches (e.g., TeWinkel and Fleischer 1999). Second, Hrabik et al.'s (2006) interannual comparisons suggest that the magnitude of DVM of coregonids may be higher in years when siscowet density is high. We therefore expected a positive correlation across sample sites between the magnitude of coregonid DVM (i.e., the difference between daytime and nighttime median depths) and siscowet density. Third, we expect the larger-bodied cisco to undergo less pronounced DVM than the smaller-bodied kiyi because of diet preferences, observed daytime habitat usage differences, and likely differences in vulnerability to siscowet predation (Table 1). Consequently, we expect a strong relationship between the magnitude of kiyi DVM and siscowet density compared with adult cisco. Such a finding would suggest that species differences influence DVM behavior and may account for the two most effective strategies modeled for a generalized coregonid by Jensen et al. (2006).

Materials and methods

General sampling design

We sampled a total of eight stations distributed across Lake Superior (Fig. 1) in spring (May and June), summer (July and August), and fall (October) of 2005. Two of the sites were sampled again in 2006 during spring, summer, and fall (Table 2). Stations included in this study had bathymetric depths ranging from 147 m to 327 m (Table 2). Stations were sampled with bottom (day and night) and midwater (night) trawls and acoustic gear (day and night) using the US Geological Survey's R/V *Kiyi*. Acoustic data were collected concurrently with each trawl tow. Day samples were collected after sunrise and before sunset. Night samples were collected between 0.5 h after nautical twilight in the evening and 0.5 h before nautical twilight in the morning. In 2005, day and night sampling at each station were performed within the same 24-h period (median difference, 6 h; range, 5–19 h). In 2006, time between day and night sampling at each station was greater because of logistical constraints (median difference, 54 h; range, 4–336 h). Only two sites were sampled in 2006 because of budget shortcomings (Table 2).

Biological sampling

We sampled demersal fishes using a 3/4 Yankee bottom trawl (11.9 m headrope, 15.5 m footrope, and 2.2 m wing lines) with 89 and 64 mm trammel mesh and 13 mm cod end mesh (all mesh sizes were stretch measure). Bottom trawls were fished for 30 min tows at each station at 3–4 km·h⁻¹. Bottom trawl wingspread data were recorded at roughly 10 s intervals using a NETMIND net mensuration

Table 1. Contrast in basic attributes between kiyi (*Coregonus kiyi*) and adult cisco (*Coregonus artedi*) suggesting different expectations for DVM behavior.

	Adult cisco	Kiyi	Source
Maximum size	495 mm	300 mm	Bersamin 1958; Smith 1964; Stockwell et al. 2006; Negus et al. 2008
Siscowet predation	Size refuge	Vulnerable	Damsgård 1995; Keeley and Grant 2001
Diet	Copepods and cladocerans	*Mysis relicta*	Anderson and Smith 1971; Johnson et al. 2004
Demersal behavior	No	Yes	Stockwell et al. 2006; Yule et al. 2007

Fig. 1. Location of eight stations sampled in Lake Superior in 2005 and 2006. See Table 2 for sampling details.
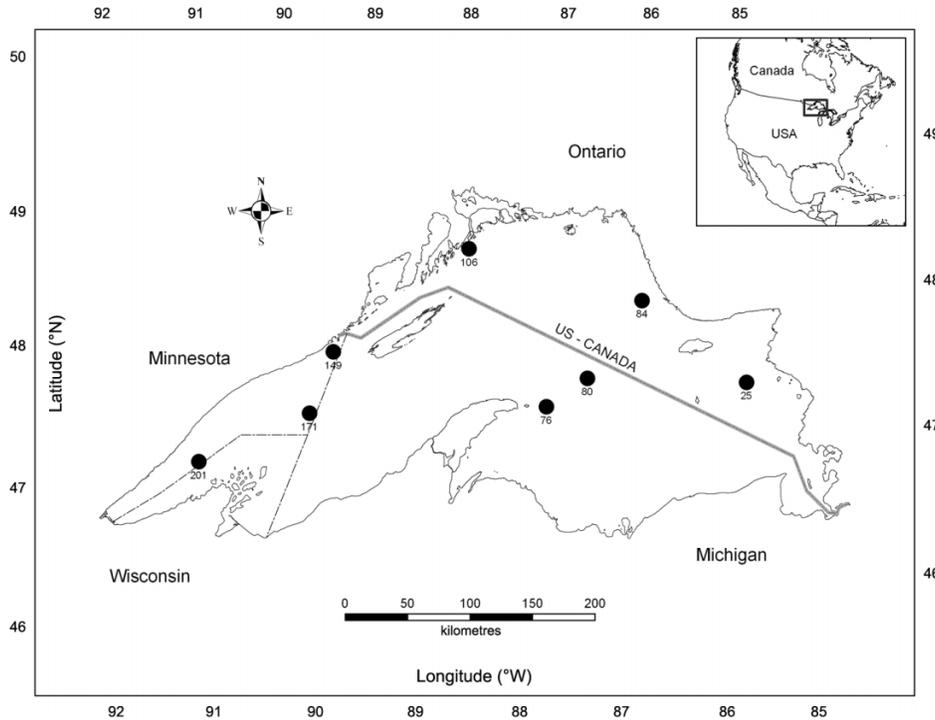

Table 2. Stations, bathymetric depths, and frequencies (kHz) used to sample fish density, size, and depth distributions with acoustics.

			Spring		Summer		Fall	
Year	Station	Bathymetric depth (m)	Day (kHz)	Night (kHz)	Day (kHz)	Night (kHz)	Day (kHz)	Night (kHz)
2005	25	297	120[a]	120 (2)	N/A	70 (1)	N/A	120 (1)
2005	76	168	120	120 (2)	70	70 (2)	120	120 (2)
2005	80	327	120[a]	120 (2)	N/A	70 (2)	N/A	N/A
2005	84	180	120	120 (2)	N/A	70 (2)	N/A	120 (2)
2005	106	147	120	120 (2)	70	70 (2)	N/A	120 (1)
2005	149	245	120	120 (2)	N/A	N/A	N/A	120 (2)
2005	171	160	120	120 (2)	N/A	70 (2)	120	120 (2)
2005	201	191	120	120 (2)	N/A	N/A	N/A	120 (2)
2006	171	160	120	120 (2)	120	120 (2)	120	120 (2)
2006	201	191	120	120 (2)	120	120 (2)	120	120 (2)

Note: The two acoustic units were both DT-X digital echosounders (Biosonics, Inc., Seattle, Washington) with either a 120 kHz split-beam transducer (beam width = 6.7°) or a 70 kHz split-beam transducer (beam width = 5.3°). Numbers in parentheses in the Night columns indicate the number of replicates used to estimate fish density, size, and depth distributions at night with acoustics. For sampling events with two replicates, the average of the two replicates was used. Only one replicate was collected during day sampling. N/A, not available.

[a]Not included in daytime analyses because station depth exceeded the range of acoustic gear (see Materials and methods).

system (Northstar Technical, Inc., St. John's, Newfoundland).

We sampled pelagic fish at night using a midwater trawl with 15.2 m headrope and footrope lines and 13.7 m breast lines. The mesh tapered from a stretch measure of 152 mm at the mouth to 13 mm at the cod end. Midwater trawl tows were conducted in a stepped-oblique fashion (Kirn and LaBar 1991) at 4–5 km·h^{-1} over the same transect path of bottom trawl tows. The trawl was fished starting at 5 m headrope depth and stepped down in 10–15 m increments to a maximum headrope depth of 80–90 m, with approximately equal fishing time at each depth. Few acoustic targets were detected below 100 m at night at all sites. Midwater trawl tow durations (range, 35–80 min; median, 54 min) were greater than those for bottom trawl tows to increase fish sample sizes in midwater trawls. Midwater trawls were not fished during the day. Previous attempts were not successful, suggesting that fish evade the trawl during this time (Yule et al. 2007).

All trawl catches were sorted by species, enumerated, and weighed in aggregate to the nearest gram. We measured total length to nearest millimetre for individuals of each species. When catches were large (>200 individuals for a species), we randomly selected 50–100 individuals to measure total length. We estimated density for each species captured in bottom trawl tows by dividing numbers caught by area swept (distance on bottom multiplied by average wingspread).

Acoustic sampling

Acoustic data to measure fish densities, acoustic sizes, and depth distributions were collected concurrently with all bottom and midwater trawl samples. For most sampling, we used a DT-X digital echosounder (Biosonics, Inc., Seattle, Washington) equipped with a 120 kHz split-beam circular transducer with a half-power beam width of 6.7° (Table 2). The transducer was mounted on a 1.2 m tow body and deployed approximately 1 m below the surface on the port side of the R/V *Kiyi*. During the summer of 2005 when our 120 kHz sounder failed (Table 1), we used a Biosonics DT-X digital echosounder equipped with a 70 kHz split-beam circular transducer with a half-power beam width of 5.3°. Previous studies (Rudstam et al. 1999; Mason and Schaner 2001; Godlewska et al. 2009) have shown that these two frequencies provide comparable data.

Acoustic signals were collected with BioSonics Visual Acquisition Software (version 4.1), and output files were stored to a laptop computer hard drive. Vessel position was measured with an Ashtech BRG2 (Ashtech Corp., Santa Clara, California) differentially corrected global positioning system (GPS) unit (accurate to 1 m), and this information was embedded in the acoustic data files. A transmit pulse duration of 0.4 ms was used at all times. Sampling rate was set at 3 pings·s^{-1} when transect maximum depths were less than 150 m. Stations with bathymetric depths greater than 150 m were sampled at 1–2 pings·s^{-1}. This approach maximized the amount of acoustic information collected while eliminating the problem of acoustic "cross talk" that occurs when one ping is not allowed to return to the transducer before a subsequent ping is transmitted. At the two deepest stations, we set the maximum range at 248 m — the maximum range at which the DT-X system could collect data in split-beam mode. Thresholds were set to allow detection of all echoes exceeding –75 dB on the acoustic axis.

The acoustic systems were calibrated periodically in the field using a 33 mm calibration sphere with an expected –40.5 dB (dB) target strength (TS) using techniques recommended by BioSonics. Results of these field tests indicated agreement with laboratory calibrations and consistent sensitivity throughout the study.

Acoustic data were processed using Echoview software (version 3.45.54.2627, SonarData Pty Ltd., Tasmania, Australia). Regions of echograms containing non-fish echoes (e.g., noise from electrical interference) were excluded from analyses. A line was drawn in each echogram at approximately 0.5 m above the lake bottom to exclude bottom echoes from analysis. The water column was analyzed in 5 m depth layers for the full length of each transect. We applied a minimum threshold of –65 dB before measuring the average volume backscattering of fish echoes in each 5 m layer.

Single targets were grouped into two TS size classes: small prey (–55 < TS < –35.6 dB) and large prey (–35.6 ≤ TS < –32 dB). Yule et al. (2006, 2009) demonstrated that large cisco (>250 mm total length) could be separated effectively from other pelagic prey species in Lake Superior using a –35.6 dB breakpoint. For each layer, the proportion of all single targets occurring in each TS size class was used to allocate total volume backscattering to the two TS size classes. The mean TS for each prey size class was then used to calculate density (fish·ha^{-1}) in each 5 m layer by scaling the proportional echo backscattering. Backscatter from predatory fish (TS > –32 dB; Hrabik et al. 2006) was subtracted from the total backscatter prior to density estimation of prey fish. Total areal densities of each size class were calculated by summing fish densities of all of the 5 m vertical layers. To understand how fish depth distributions were related to temperature, we collected a thermal profile using a SEACAT Model 19 Profiler (Sea-Bird Electronics, Inc., Bellevue, Washington) at each station during each sampling event.

To estimate pelagic prey fish species densities at night for a given station, we assigned captured fish from the corresponding midwater trawl to two size classes (small, < 250 mm; large, ≥250 mm). We summed the number of small and large fish captured in each midwater trawl and calculated the proportion of each species in each size class. We then multiplied the acoustic density estimate of small and large prey fish by the species proportions of each size class to estimate densities of each species. In some instances, large fish (i.e., >250 mm) were not captured in a midwater trawl despite an acoustic density estimate greater than 0 for large fish. In these cases, we assumed that these large fish were cisco. Densities of pelagic siscowet were not calculated because of their near absence in night midwater trawl samples. Siscowet densities at each station were estimated from bottom trawl samples only.

Statistical analyses

To test for DVM behavior, we compared day and night density estimates from bottom trawl tows for each species using a paired *t* test. Based on observations from Hrabik et al. (2006), we expected day bottom trawl densities to be

higher than night densities for each species. We therefore used a one-tailed test ($\alpha = 0.05$).

Because of the preponderance of siscowet and kiyi in day bottom trawl tows, we compared density estimates of the two species from day bottom trawl tows using Pearson's correlation coefficient r. We performed two tests: the first used density estimates of all sizes of siscowet and the second used density estimates of siscowet exceeding 478 mm. We used densities of siscowet exceeding 478 mm to correspond to the sizes of predatory siscowet defined in the Hrabik et al. (2006) study. Our significance level was set at $\alpha = 0.05$, but we adjusted α using a Bonferroni correction for the two tests (i.e., $\alpha = 0.05/2 = 0.025$).

To test hypotheses regarding the magnitude of DVM of prey species, we estimated the median depths occupied by kiyi and cisco on each sampling event. We used density estimates from both pelagic (acoustic) and demersal (bottom trawl) habitats for these calculations. For most night sampling events, we had two replicates of acoustic data (one for bottom trawl and one for midwater trawl sampling; see Table 2), so depth-specific densities were estimated by averaging these replicates. Estimating median depths from night samples was straightforward because we could assign pelagic density estimates to species based on midwater trawl catches. For day pelagic estimates, we did not have any midwater trawl samples, so we assumed that all small prey ($<$–35.6 dB) were kiyi and all large prey (–32 dB > targets > –35.6 dB) were cisco. We calculated the magnitude of DVM as the difference between day and night median depths.

We used a paired t test to examine the difference in the magnitude of DVM between kiyi and cisco. We expected kiyi to exhibit a greater migration so we used a one-tailed test ($\alpha = 0.05$). We used linear regression to test for an effect of siscowet density on magnitude of DVM for kiyi and cisco. Siscowet density was calculated from day bottom trawl samples. We performed two tests using density estimates for all sizes of siscowet and for large siscowet ($\geq$478 mm) separately. Our significance level was set at $\alpha = 0.05$, which we adjusted using a Bonferroni correction for the two tests (i.e., $\alpha = 0.05/2 = 0.025$).

Results

Species composition and size distributions

We caught an estimated 30 753 fish in all trawls at the eight offshore stations. Four species (deepwater sculpin, kiyi, siscowet, and cisco) represented 99.5% of the total catch. Deepwater sculpin was the most numerous (12 190 individuals) species in day bottom trawls, followed by kiyi (3141) and siscowet (141). Deepwater sculpin was also the most numerous (14 368) in night bottom trawls, followed by siscowet (32), kiyi (13), and slimy sculpin (*Cottus cognatus*; 13). Kiyi was the most numerous (640) species captured in night midwater trawls, followed by cisco (79) and rainbow smelt (*Osmerus mordax*; 33).

Collectively, the two predominant coregonid species had three distinct size modes. The length–frequency distribution for kiyi was bimodal, with modes at 130 mm and 190–210 mm (Fig. 2a), whereas most cisco were large (mode = 325 mm; Fig. 2b). Only one cisco was captured with day bottom trawl tows.

Fig. 2. Length–frequency distributions of (*a*) kiyi (*Coregonus kiyi*), (*b*) cisco (*Coregonu artedi*), and (*c*) siscowet (*Salvelinus namaycush*) captured in day bottom trawl (BTR) samples (open bars), night BTR samples (solid bars), and night midwater (MTR) trawl samples (shaded bars) in 2005 and 2006. Sample sizes (*n*) are listed in each panel. The equation for maximum (Max) prey length in (*c*) is prey length (cm) = 0.535 × predator length (cm) – 0.487 (Damsgård 1995).
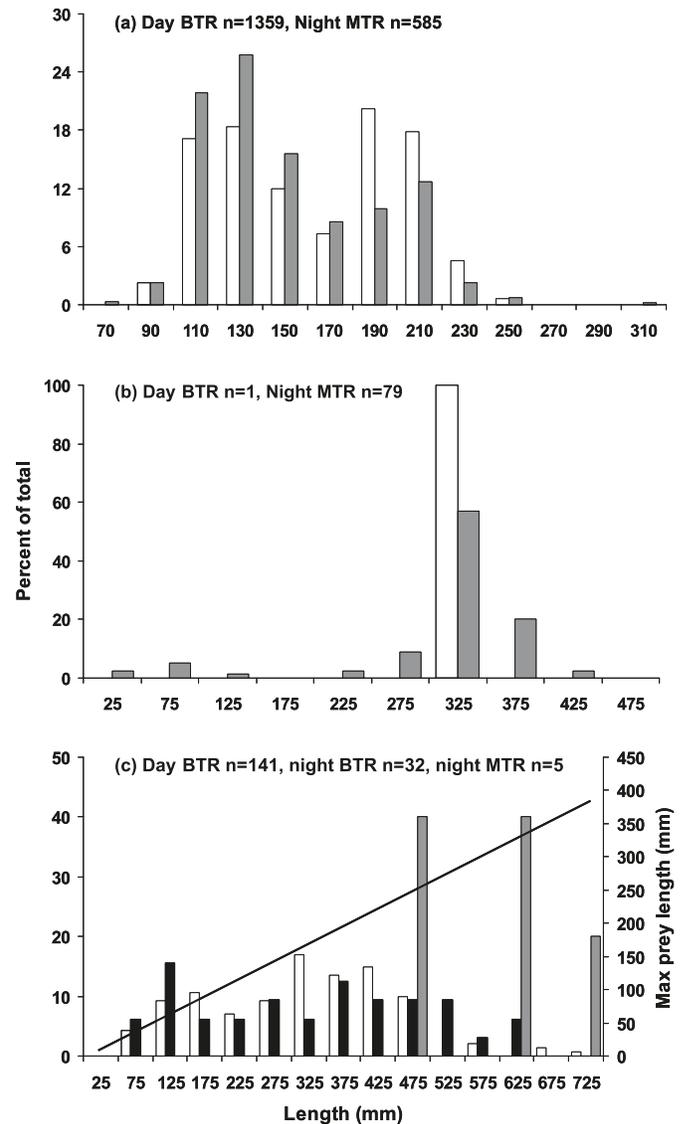
Siscowet captured in both day and night bottom trawl tows had a broad length–frequency distribution, with lengths ranging from 50 mm to >750 mm (Fig. 2c) with no prominent modes. Only five siscowet were captured in midwater trawl tows at night, but these fish were generally larger (range 450–750 mm) than siscowet captured in bottom trawl tows (Fig. 2c).

Based on the maximum predicted prey size equation for brown trout (*Salmo salar*) developed by Damsgård (1995), we calculated that only 7% of all siscowet captured were of sufficient size (>550 mm) to consume a prey fish larger than 300 mm (Fig. 2c). In contrast, 46% of all siscowet captured were of sufficient size (>380 mm) to consume a prey

fish smaller than 200 mm. For coregonids, 80% of all cisco captured exceeded 300 mm (Fig. 2b), whereas 80% of all kiyi captured were less than 200 mm (Fig. 2a).

Spatial coherence between siscowet and kiyi

There was a significant positive correlation between density of kiyi and siscowet (all sizes) in day bottom trawl tows ($r = 0.80$, $p < 0.0001$, $n = 19$; Fig. 3a), suggesting that siscowet maintain a spatial association with kiyi. The correlation was positive ($r = 0.44$) but not quite significant ($p = 0.06$) between large siscowet (≥ 478 mm) and kiyi (Fig. 3b).

Diel vertical migration

Data for the two dominant coregonid species indicate differing DVM patterns. Kiyi appear to undergo very strong DVM, with much of their population on or near the bottom during daylight hours. Mean density (± standard deviation, SD) from day bottom trawl tows across 18 station/season samples was 76.0 ± 95.2 fish·ha^{-1} compared with 0.4 ± 0.8 fish·ha^{-1} from night bottom trawl tows (mean difference = 75.6 fish·ha^{-1}, SD = 94.7, t ratio = 3.39, $p = 0.0017$, df = 17; Fig. 4a). Pelagic density estimates of small prey fish (<-35.6 dB; presumably kiyi) during the day averaged 13.9 ± 9.8 fish·ha^{-1}, or 18% of the mean density of kiyi from day bottom trawl tows. Night pelagic density estimates for kiyi ranged from 12 to 295 fish·ha^{-1}, with a mean density of 111.0 ± 77.8 fish·ha^{-1}.

The magnitude of cisco DVM appears smaller than kiyi. Only one cisco was captured with day bottom trawl tows, and none was captured with night bottom trawl tows, suggesting that this species was pelagic during both photoperiods. Pelagic density estimates for cisco at night using acoustics and midwater trawls ranged from <1 to 29 fish·ha^{-1} and averaged 5.4 ± 5.8 fish·ha^{-1}. Pelagic density estimates of large prey fish during the day (≥ -35.6 dB; presumably cisco) ranged from 0.1 to 1.6 fish·ha^{-1} and averaged 0.7 ± 0.6 fish·ha^{-1}.

Changes in density estimates of siscowet between day and night bottom trawl tows suggest that most siscowet perform DVM (Fig. 4b). Mean density (±SD) from day bottom trawl tows across the 18 sampling events was 4.2 ± 3.4 fish·ha^{-1} compared with 1.0 ± 0.9 fish·ha^{-1} from night bottom trawl tows (mean difference = 3.1 fish·ha^{-1}, SD = 3.3, t ratio = 4.08, $p = 0.0004$, df = 17). Density estimates of siscowet ≥ 478 mm in our day and night bottom trawl tows averaged 0.4 ± 0.5 fish·ha^{-1} and 0.2 ± 0.5 fish·ha^{-1}, respectively, but these were not significantly different (mean difference = 0.2 fish·ha^{-1}, SD = 0.7, t ratio = 0.92, $p = 0.18$, df = 17).

Kiyi were concentrated primarily on the bottom during the day, regardless of season, but were found in distinct depth layers at night, which varied by season (Fig. 5). Night distributions peaked at 65 m in the spring (Fig. 5a), 12.5 m in summer (Fig. 5b), and 17.5 m in the fall (Fig. 5c). Season explained 96% of the variation in median depth of kiyi at night (F ratio = 289.1, $p < 0.0001$, df = 26). Thermal profiles indicated isothermal conditions in the spring, strong stratification in the summer, and weakening of the thermocline in fall (Fig. 5).

Day distributions of cisco were much more variable than kiyi and appeared to be split between shallower and deeper pelagic depths during all three seasons (Fig. 5). Season explained a significant amount of variation ($R^2 = 0.39$) in the

Fig. 3. Bivariate plot of siscowet (*Salvelinus namaycush*) ((a) all sizes and (b) ≥478 mm) and kiyi (*Coregonus kiyi*) densities from day bottom trawl (BTR) tows.
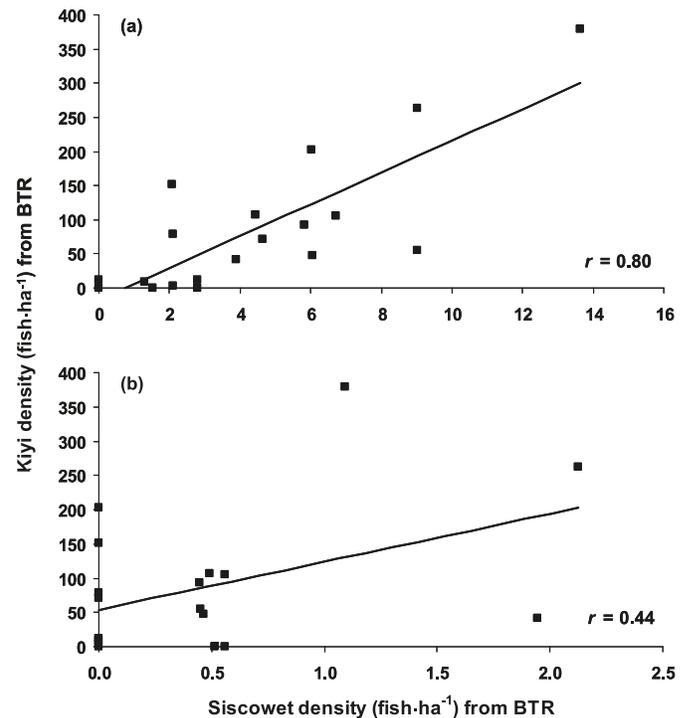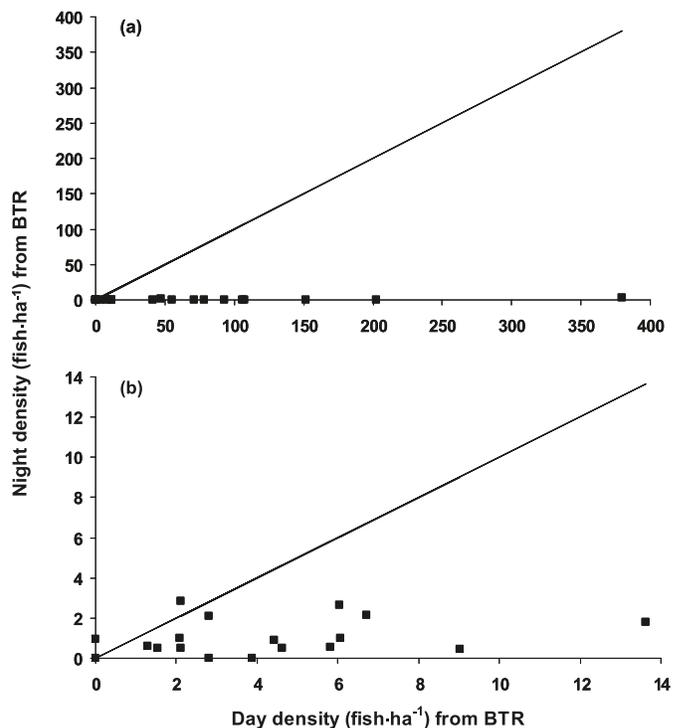

Fig. 4. Paired day and night bottom trawl (BTR) density estimates of (a) Lake Superior kiyi (*Coregonus kiyi*) and (b) siscowet (*Salvelinus namaycush*). Line represents unity in each panel.

median night depth distribution of cisco (F ratio = 7.75, $p < 0.003$, df = 26), but much less than the variation explained for kiyi ($R^2 = 0.96$).

Fig. 5. Mean relative density of kiyi (*Coregonus kiyi*) (continuous line) and cisco (*Coregonus artedi*) (broken line) as a function of depth in Lake Superior during day and night sampling in (*a*) spring, (*b*) summer, and (*c*) fall of 2005 and 2006. Mean thermal profiles for each season are also shown.
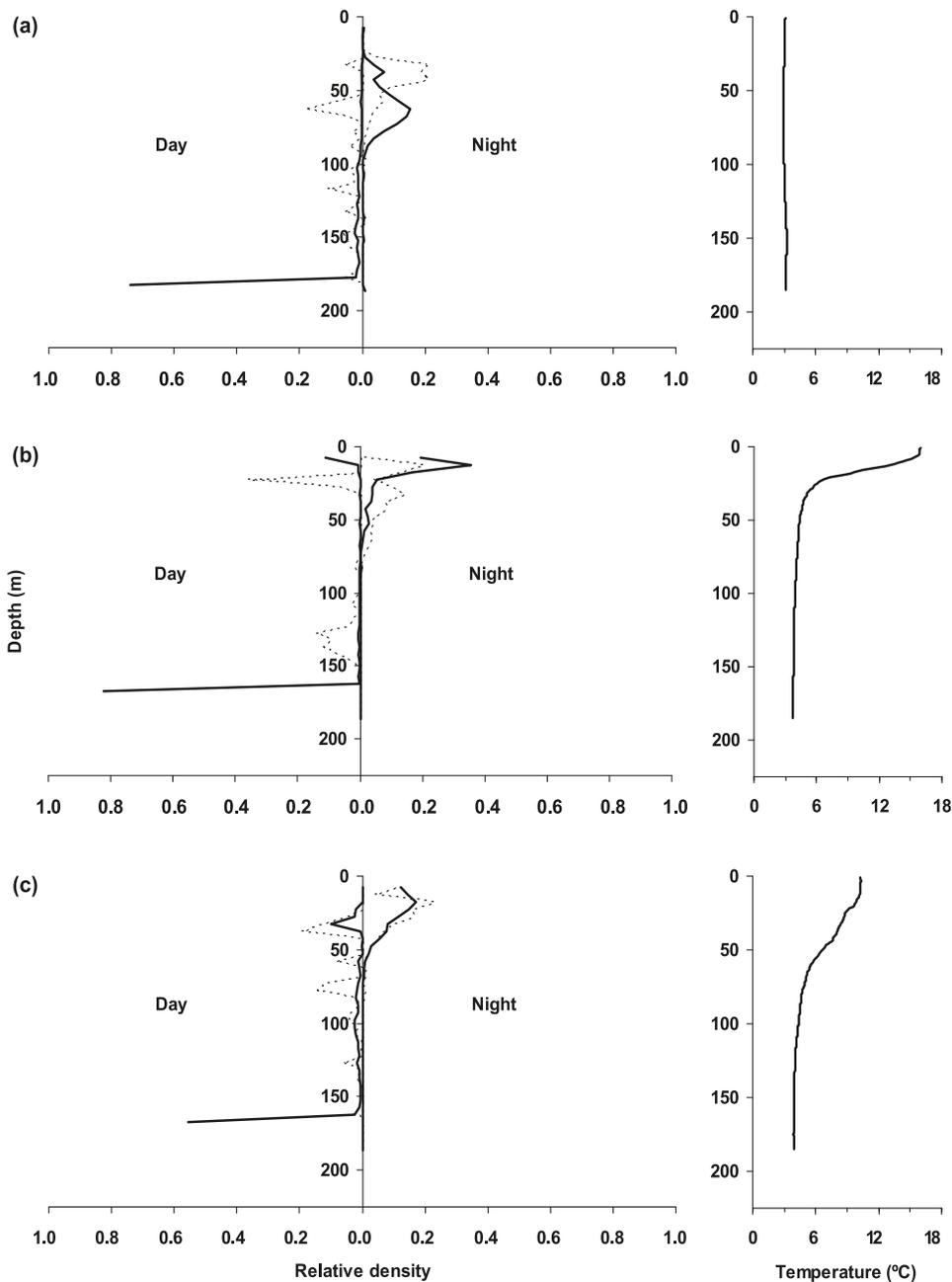

When kiyi and cisco DVM trajectories were compared, several patterns emerged. First, kiyi were much deeper than cisco during the day (Fig. 5). Second, kiyi were mostly demersal during the day. Third, the general pattern in night distributions changed across seasons. Kiyi were deeper than cisco in spring, shallower in summer, and similar in fall (Fig. 5). Finally, night depth distributions of kiyi were remarkably consistent across stations within each season (Fig. 6), whereas cisco exhibited more variability (Fig. 5). Kiyi performed significantly greater DVM than cisco (mean difference in DVM = 63 m, SD = 52.4, t ratio = 4.82, $p <$ 0.0001, df = 15; Fig. 7). The magnitudes of DVM for kiyi

and cisco were not related to density of all siscowet (for kiyi, p = 0.67, R^2 = 0.01; for cisco, p = 0.30, R^2 = 0.08; Fig. 8*a*) or siscowet ≥ 478 mm (for kiyi, p = 0.60, R^2 = 0.02; for cisco, p = 0.72, R^2 = 0.01; Fig. 8*b*) as measured by day bottom trawl samples.

Discussion

One prediction of the antipredation window hypothesis is that DVM behavior is a size-dependent process. That is, as an individual grows and begins to attain a size refuge from predators, the relative importance of potential predation risk in the risk versus growth trade-off should decrease. Within

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Fig. 6. Night depth distribution of kiyi (*Coregonus kiyi*) and thermal profiles of Lake Superior in (*a*) spring, (*b*) summer, and (*c*) fall of 2005 (continuous lines) and 2006 (broken lines). Each profile represents an individual site. The depth axis is truncated at 100 m because very few fish were observed below this depth at night.
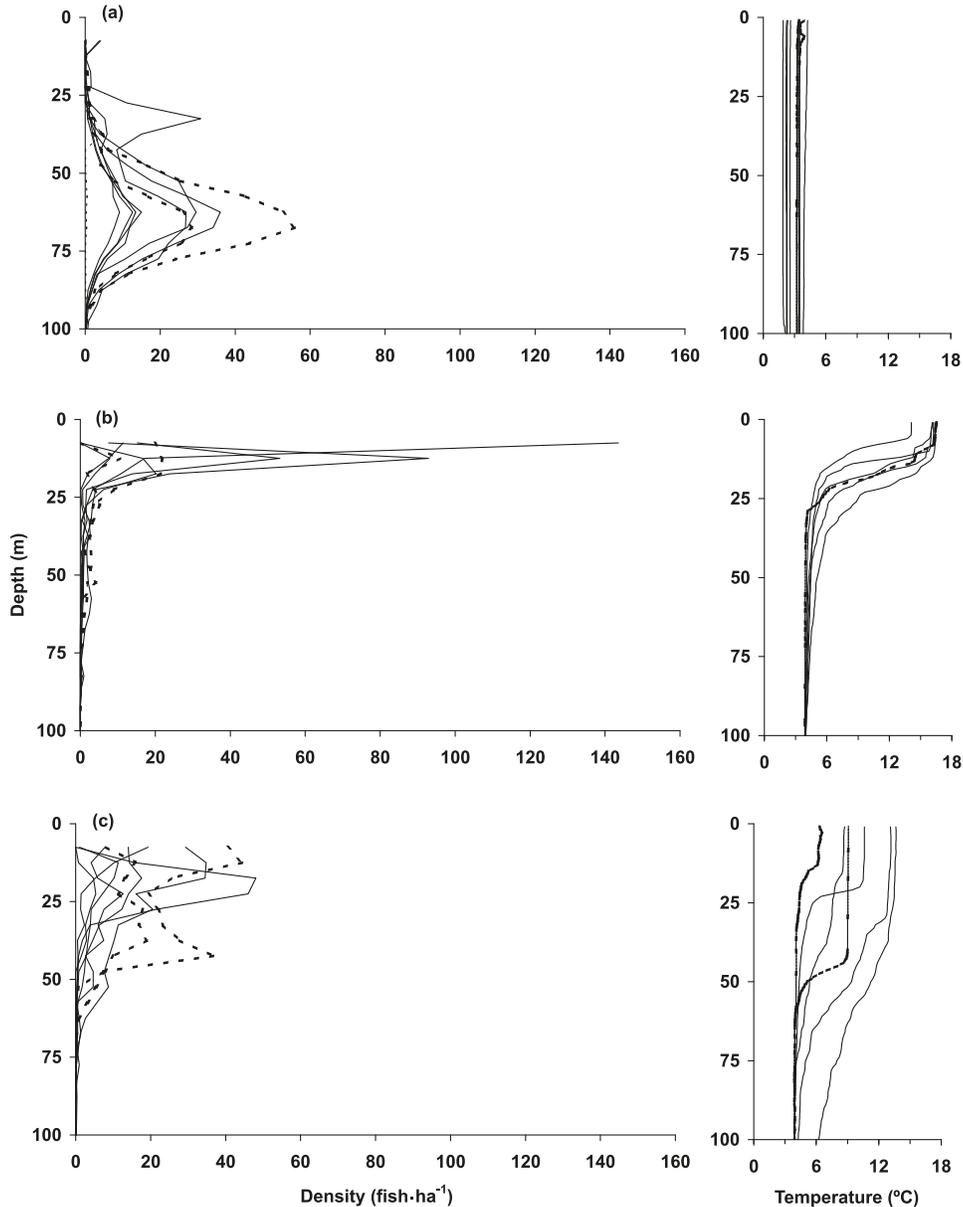
the framework of Jensen et al. (2006), we would expect larger-bodied cisco to follow a shallower DVM trajectory compared with kiyi. Although differences that we observed in this study are consistent with this prediction, known differences in the ecology of kiyi and adult cisco, the demersal co-occurrence of kiyi and siscowet during the day, and the apparent size refuge of adult cisco from siscowet predation suggest that predator avoidance is not a proximate factor responsible for their divergent DVM behaviors. We compare and contrast the DVM behavior of kiyi and adult cisco in the context of potential predation risk, foraging opportunities and bioenergetic efficiencies, and food web dynamics.

Potential predation risk

Our results show that the extent of adult cisco DVM is of

lesser magnitude than that of kiyi. Cisco are located higher in the water column during the day, an area where the reaction distance of visually foraging siscowet is high (Jensen et al. 2006). However, Harvey and Kitchell (2000) and Harvey et al. (2003) provided isotopic evidence that cisco are not key components of siscowet diet in Lake Superior where depths exceed 80 m. We found that 80% of the cisco in offshore waters exceeded 300 mm. Using the Damsgård (1995) model to predict maximum prey size, we estimated that a 300 mm cisco would be vulnerable to only 7% of the siscowet that we captured. Keeley and Grant (2001) provide evidence that Damsgård's (1995) model provides reasonable predictions for piscivorous lake trout. Recent work on Lake Superior has shown that adult cisco have high annual survival rates (>0.75; Yule et al. 2008) and that cisco are a mi-

Fig. 7. A comparison of the magnitude of diel vertical migration (DVM) for kiyi (*Coregonus kiyi*) and cisco (*Coregonus artedi*) in spring (solid circles), summer (open squares), and fall (solid triangles). Line represents unity.
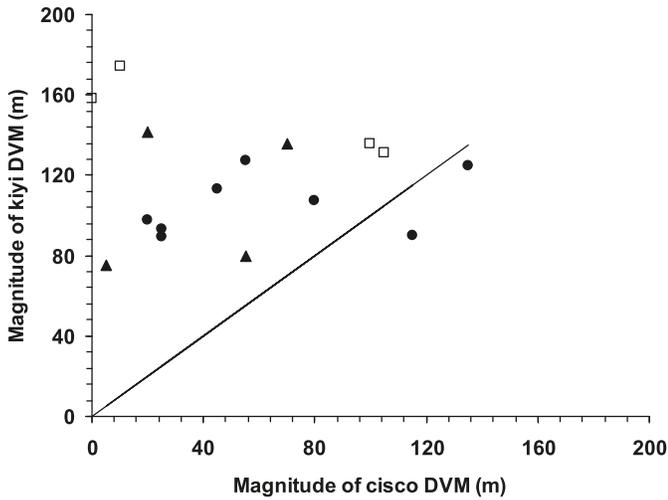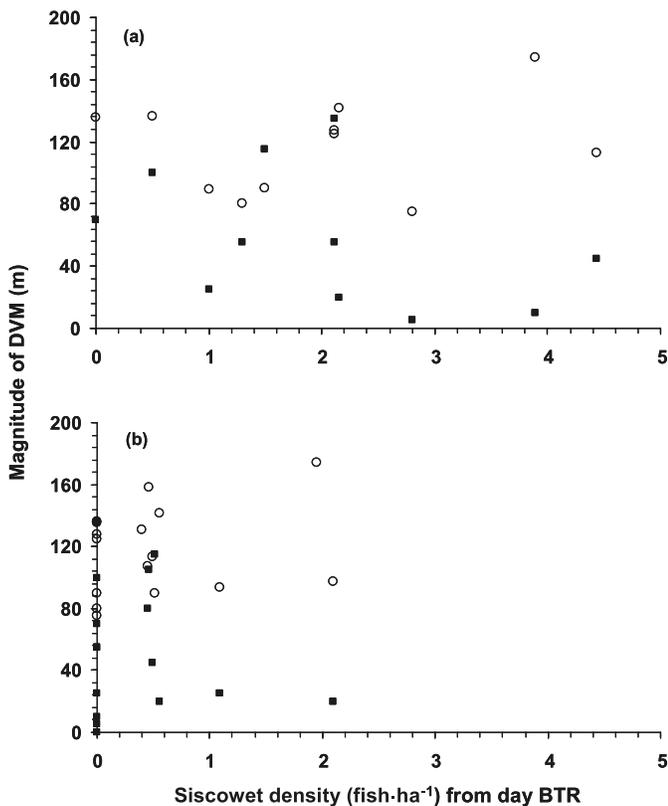

Fig. 8. Relationship between magnitude of diel vertical migration (DVM) of kiyi (*Coregonus kiyi*) (open circles) and cisco (*Coregonus artedi*) (solid squares) and density estimates of (*a*) all siscowet (*Salvelinus namaycush*) and (*b*) large (>478 mm) siscowet from day bottom trawl (BTR) samples.

nor component of the siscowet diet (Negus et al. 2008). Both studies suggest that cisco have a functional size refuge from most siscowet in offshore waters of Lake Superior. Without strong constraints imposed by predators, they should exhibit shallower and more variable daytime depth

distributions (Jensen et al. 2006). Our findings support this prediction.

If adult cisco are largely invulnerable to siscowet predation, why do they conduct DVM? Negus et al. (2008) reported that "lean" lake trout (the shallow-water morphotype of lake trout) were the dominant predator in nearshore (<80 m bathymetric depths) waters of Wisconsin and Minnesota, with coregonids (mostly cisco) representing approximately 60% of their diet by weight. Cisco are widely distributed in Lake Superior, with younger cisco smaller than 250 mm generally occupying nearshore waters and adults occupying the entire lake (Stockwell et al. 2006). Although cisco have an apparent size refuge in offshore waters, predation pressure on cisco in nearshore waters appears to be greater (Negus et al. 2008). We hypothesize that cisco DVM behavior in offshore waters may be a residual effect of managing potential predation risk from lean lake trout in nearshore waters.

Unlike cisco, a large proportion of the kiyi that we sampled were likely vulnerable to predation by siscowet, which is consistent with recent siscowet diet data from Negus et al. (2008). Kiyi exhibited greater DVM than adult cisco and were consistently deeper during the day. This observation indicates more risk-averse behavior for kiyi and follows expectations of the antipredation window hypothesis. However, at the spatial and temporal scale of this study, we found no evidence that kiyi (or cisco) alter the extent of their DVM in response to differences in predator densities. Moreover, the co-occurrence of kiyi and siscowet at great demersal depths during the day, where the lack of light most likely precludes the use of vision for predation by either siscowet (on kiyi) or kiyi (on *M. relicta*), indicates that light is not likely a proximate factor for daytime distributions of siscowet or kiyi and that predator avoidance is not an ultimate factor for daytime distributions of kiyi.

Foraging opportunities and bioenergetic efficiency

Although cisco feed to a small extent on the macroinvertebrate *M. relicta*, copepods and cladocerans are the primary prey of cisco in Lake Superior (Dryer and Beil 1964; Anderson and Smith 1971; Johnson et al. 2004). These smaller plankters generally occupy upper parts of the water column and perform limited DVM (Conway 1977; Zhou et al. 2001; Yurista et al. 2009). An alternative to the hypothesis that adult cisco perform DVM in the offshore waters as a residual effect from potential predation risk in nearshore waters by lean lake trout is that cisco perform DVM to optimize their energetic efficiency. This alternative hypothesis could be tested using the framework of Jensen et al. (2006), modified for the species-specific characteristics of adult cisco.

In contrast to the diet of adult cisco, *M. relicta* is the primary prey of kiyi (Anderson and Smith 1971; A. Gamble, University of Minnesota, Department of Biology, Duluth, Minnesota, unpublished data) and undergoes extensive DVM in Lake Superior (Bowers 1988; Jensen et al. 2009). We observed that the vertical distributions of kiyi at night varied across seasons but showed remarkable consistency across stations separated by 100s of kilometres within each season. During the day, kiyi were primarily bottom-oriented in all seasons. In spring when the water column was isothermic, nighttime distributions of kiyi were deeper than in

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summer or fall. In summer and fall, kiyi ascended nearer to the surface at night and appeared to relate to thermal structure in these depth zones. Temperature and light are primary drivers of *M. relicta* DVM and explain the deeper depth distributions of this macroinvertebrate in Lake Ontario in the spring during isothermic conditions and their proximity to the thermocline in summer and fall (Gal et al. 2004; Boscarino et al. 2007). If *M. relicta* in Lake Superior follow similar patterns, it might explain the deeper night distributions of kiyi during the spring and their association with the thermocline in summer and fall. Such relationships between nighttime distributions, invertebrate prey, and temperature across seasons have also been observed for vendace (*Coregonus albula*) and Fontane cisco (*Coregonus fontanae*), suggesting that thermal stratification may play an important role in the magnitude of DVM and nighttime depths of coregonids (Helland et al. 2007; Mehner et al. 2007; Busch and Mehner 2009).

Eshenroder and Burnham-Curtis (1999) hypothesized that deepwater ciscoes in the Great Lakes, including kiyi, evolved to feed on vertically migrating *M. relicta*. Kiyi likely underwent adaptive radiation from colonizing cisco (i.e., *C. artedi*) after the last glacial retreat 11 000 years ago (Smith and Todd 1984; Todd and Smith 1992). The species had to overcome a number of physical and biological challenges, including the effects of pressure changes when performing DVM, colder temperatures associated with a largely hypolimnetic existence, and possible foraging on *M. relicta* at great depths with presumably no light. Little, if any, research has been conducted on these facets of kiyi ecology. For example, comparison of gas bladder anatomy and lipid levels of cisco and bloater with kiyi would address ongoing questions of buoyancy regulation in coregonids (TeWinkel and Fleischer 1998; Eshenroder and Burnham-Curtis 1999; Clemens and Don Stevens 2007). Species-specific differences in thermal performance functions (e.g., swimming, standard and active metabolism) in sympatric coregonids suggest species adaptation to different temperature regimes (Helland et al. 2007; Ohlberger et al. 2008a, 2008b). By extension, energetic costs to kiyi and cisco performing DVM under similar environmental conditions (e.g., in a modeling context) are likely different. Similarly, foraging abilities and environmental constraints of each species likely differ. For example, large differences in eye size between kiyi and cisco suggest that kiyi may have greater visual acuity under low light conditions and presence of *M. relicta* in kiyi captured on bottom during the day suggests that kiyi are capable of nonvisual predation (A. Gamble, University of Minnesota, Department of Biology, Duluth, Minnesota, unpublished data).

Collectively, these thermal and physiological considerations strongly suggest that kiyi and adult cisco experience different growth (forage) rate potentials as a function of vertical depth, photoperiod (i.e., light), and prey fields. Development of bioenergetics-based foraging models reflective of each species' ecology and estimates of fine-scale spatiotemporal densities of *M. relicta*, especially in demersal habitats, would greatly improve modeling efforts to evaluate kiyi and cisco foraging and growth rate potential.

Food web dynamics

Strong horizontal correlation between predator and prey may occur at a variety of spatial and temporal scales (e.g., Rose and Leggett 1990; Benoit-Bird and Au 2003). The strong positive correlation between siscowet and kiyi across stations suggests that siscowet exhibit spatial coherence with kiyi over large spatial scales. Alternatively, but less likely, is the possibility that the correlation was caused by both siscowet and kiyi responding to a common indirect factor such as *M. relicta*. Stable isotope and diet studies indicate that *M. relicta* is not a key diet component of siscowet (Conner et al. 1993; Harvey and Kitchell 2000; Negus et al. 2008). Thus, it seems most probable that siscowet are tracking kiyi, which are likely aggregating near patches of their preferred prey, *M. relicta*. Future research in this area may shed light on the mechanisms underlying this association.

Deepwater sculpin are common in diets of siscowet (e.g., Conner et al. 1993; Ray et al. 2007; Negus et al. 2008) and have relatively high densities in offshore waters of Lake Superior (mean density ± SD; 388 ± 373.4 fish·ha^{-1} during the day and 467 ± 465.4 fish·ha^{-1} at night in our bottom trawl samples). Given that visual foraging by siscowet at the bathymetric depths we sampled is unlikely (Jensen et al. 2006), we hypothesize that siscowet are able to use senses other than vision to forage in deepwater benthic habitats (i.e., their reaction distance > 0 at 0 lx; Mazur and Beauchamp 2003). Further, we hypothesize that the more sedentary deepwater sculpin is likely an easier target for siscowet in this habitat compared with the more mobile kiyi.

Uncertainties

Although we documented a significant decrease in siscowet density using bottom trawl samples between day and night, our midwater trawl catches at night caught very few siscowet (five) that were disproportionately larger than bottom trawl catches. These patterns suggest that smaller-sized siscowet may (*i*) evade the midwater trawl, (*ii*) vertically migrate to unsampled habitats at night (e.g., suspended below 100 m or in surface waters), or (*iii*) move into nearshore areas. We suspect the first explanation is unlikely because larger siscowet would presumably be able to avoid the trawl better than smaller siscowet. The second explanation appears feasible, although it is not clear what benefit these habitats would provide compared with occupying similar nighttime depths as kiyi. It is unlikely that siscowet are concentrated at depths greater than 100 m because we observed very few acoustic targets in these depth zones, consistent with Mason et al. (2005). The third explanation is possible as Harvey et al. (2003) suggested that smaller siscowet might rely on nearshore production to some degree, a finding substantiated by the diet work of Ray et al. (2007). This may be feasible for deepwater habitats relatively close to shore (e.g., stations 149 and 106) but unlikely for those further from shore (e.g., stations 171 and 80). Future work should consider shallowset suspended gill nets in offshore waters or biotelemetry studies to better understand habitat usage of siscowet.

We assumed that all targets smaller than –35.6 dB in the water column during the day were kiyi. However, we captured some (albeit very few) smaller cisco and rainbow smelt in the same size range as kiyi (25–250 mm) in night midwater trawl tows, suggesting that smaller prey targets

during the day may not have been (entirely) kiyi. Kiyi in the size range of 80–100 mm were captured in day bottom trawl tows, suggesting even these small fish undergo strong DVM. If smaller targets during the day were cisco, the distinct vertical distributions of large and small prey in summer in fall would be consistent with known ontogenetic thermal preferences within species (e.g., Viljanen 1983). Additionally, the bi- and multi-modal depth distributions of large prey targets during the day may also suggest size-dependent thermal preferences of adult cisco. However, given the narrow TS range that we defined for cisco (between –35.6 and –32 dB), such comparisons within this range would be meaningless. Milne et al. (2005) successfully captured cisco during daylight with suspended gillnets, so it is possible that this gear type could also lend itself to better understanding of daytime distributions of coregonids in Lake Superior.

In summary, we found that the two most effective DVM strategies modeled for a generalized coregonid in offshore waters of Lake Superior (Jensen et al. 2006) are utilized by two congenerics with different ecological niches. DVM patterns of kiyi and adult cisco were consistent with size-dependent predation risk as predicted by the antipredation window hypothesis. However, the apparent size refuge of adult cisco suggests that their potential predation risk is low regardless of their DVM trajectories, and the continual overlap of kiyi with siscowet day and night suggests that their potential predation risk is high despite an extensive DVM trajectory. The former nullifies the importance of the antipredation window for adult cisco, and the latter is contrary to expectations of the antipredation window hypothesis for kiyi. Both suggest that alternative factors play primary roles in DVM behavior. We suspect that because of their size refuge, adult cisco DVM in offshore waters likely optimize their bioenergetic efficiency. The consistency in the DVM pattern of kiyi with known DVM patterns of their primary prey *M. relicta* suggests that kiyi are vertically tracking their prey. The lack of a pelagic layer of kiyi during the day in the antipredation window may be a result of lack of suitable prey in that vertical layer; kiyi follow their prey to the bottom to realize some growth potential. Similarly, siscowet likely follow kiyi to the bottom where they also encounter an alternative prey source (deepwater sculpin) that they are known to consume rather than remain pelagic where appropriately sized prey appear to be scarce. In addition to prey tracking, ascent to the thermocline in summer and fall by kiyi, and presumably siscowet, may also increase gut evacuation rates and thus increase bioenergetic efficiency (Bevelhimer and Adams 1993).

Our study suggests that the factor(s) driving coregonid DVM may be more complex than first identified. It is apparent that the costs (potential predation risk) and benefits (foraging and growth) of DVM behavior differ drastically between kiyi and adult cisco. Light-based foraging theory is likely not applicable in the offshore demersal habitats of Lake Superior. Other factors need to be explored to better understand the extensive DVM of kiyi and siscowet. The challenge will be linking food web interactions between the two- (bottom) and three-dimensional (pelagic) habitats to account for alternative prey, shifts in foraging strategies and abilities, physiological performance in different thermal environments, and changes in potential predation risk that are

likely present and driving the underlying differences in DVM exhibited by each coregonid species and siscowet.

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