

# Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk

Thomas R. Hrabik, Olaf P. Jensen, Steven J.D. Martell, Carl J. Walters, and James F. Kitchell

**Abstract:** The distribution of fishes is influenced by a host of physico-chemical and biological variables, including temperature and oxygen, prey abundance, feeding or assimilation rates, and predation risk. We used hydroacoustics and midwater trawls to measure the vertical distribution of pelagic fishes during a series of research cruises on Lake Superior's western arm in 2001 and 2004. Our objective was to assess vertical structuring in the fish assemblage over varying light levels. We observed variability in vertical structuring of both ciscoes (*Coregonus* spp.) and their primary predator, the siscowet (*Salvelinus namaycush siscowet*). Our results indicate that deepwater predators and prey migrate extensively over a diel cycle. This migration pattern is most consistent with changes in the distribution of prey resources for siscowet and diel variability in predation risk controlled by changing light levels for ciscoes. The magnitude of vertical migration in ciscoes increased with higher abundance of siscowets, supporting predation risk as a driver of cisco distribution. This study describes the extent of vertical migration in each group of fish, provides a statistical description of the pattern, and discusses the implications for trophic interactions in the Lake Superior food web.

**Résumé :** La répartition des poissons est affectée par une quantité de variables physico-chimiques et biologiques, dont la température et l'oxygène, l'abondance des proies, les taux d'alimentation et d'assimilation et le risque de prédation. Nous avons utilisé des méthodes hydroacoustiques et des chaluts de mi-profondeur pour mesurer la répartition verticale des poissons pélagiques durant une série de croisières de recherche dans le bras occidental du lac Supérieur en 2001 et en 2004. Notre objectif était de déterminer la structuration verticale du peuplement de poissons en fonction de la variation des intensités lumineuses. Nous avons observé de la variabilité dans la structuration verticale tant chez les ciscos (*Coregonus* spp.) que chez leur prédateur principal, le touladi siscowet (*Salvelinus namaycush siscowet*). Nos résultats indiquent que les prédateurs et les proies d'eau profonde font d'importantes migrations sur un cycle journalier. Ce patron de migration s'accorde le mieux avec les changements dans la répartition des ressources des proies chez le siscowet et avec la variabilité journalière du risque de prédation contrôlée par les changements de l'intensité lumineuse chez les ciscos. L'étendue de la migration verticale des corégonos augmente en fonction de l'abondance des siscowets, ce qui vient appuyer le risque de prédation comme facteur explicatif de la répartition des ciscos. Notre étude décrit l'étendue de la migration verticale chez chaque groupe de poissons et fournit une description statistique du patron de migration; les conséquences sur les interactions trophiques dans le réseau alimentaire du lac Supérieur font l'objet d'une discussion.

[Traduit par la Rédaction]

## Introduction

The pelagic food web of Lake Superior is unique among the Laurentian Great Lakes in that it is dominated by native species that are well adapted to exist in cold, deep habitats found there. Among the native forage fish, coregonids (*Coregonus* spp.) represent the most abundant prey available

to large piscivores. In addition, native lake trout (*Salvelinus namaycush*) are approaching historical levels of abundance (Bronte et al. 2003). Diel vertical migration (DVM) is evident in coregonids in many pelagic ecosystems (Brandt et al. 1991; Eshenroder and Burnham-Curtis 1999; Knudsen and Gjelland 2003). Furthermore, diel changes in the vertical distribution of coregonids have the potential to influence the

Received 8 November 2005. Accepted 28 June 2006. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 30 September 2006.  
J18986

**T.R. Hrabik.**<sup>1</sup> Department of Biology, 207 Swenson Science Building, University of Minnesota, Duluth Campus, 1035 Kirby Drive, Duluth, MN 55812, USA.

**O.P. Jensen and J.F. Kitchell.** Center for Limnology, 680 N. Park Street, Madison, WI 53706, USA.

**S.J.D. Martell and C.J. Walters.** Fisheries Centre, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

<sup>1</sup>Corresponding author (e-mail: [thrabik@d.umn.edu](mailto:thrabik@d.umn.edu)).

extent to which prey are available to predators. Recent examinations of prey supply – predator demand discrepancies in Lake Superior suggest that predator demand is near the capacity of prey species to support them (Negus 1995; Mason et al. 2005). Increased migratory behavior by prey in response to higher predation risk and the resulting behavioral segregation may further decrease the availability of prey to predators.

The Lake Superior fish community has undergone substantial changes brought about by overfishing, habitat degradation, and the invasion of exotic species. Historically, the pelagic prey fish community in Lake Superior was dominated by a clade of coregonids (Dryer et al. 1965; Christie 1974). However, the community shifted from coregonids to one dominated by exotic rainbow smelt (*Osmerus mordax*) during the 1970s (Selgeby 1982; Bronte et al. 2003). Recently, however, native coregonids have increased in abundance and are the most abundant planktivore in many locations (Hansen 1994). This shift in prey species most likely resulted from increased predatory demand placed on prey species by recovering lake trout populations. Rainbow smelt, a primary prey item for the increasing lake trout, declined as a result of lake trout predation (Hansen 1994). The decline in adult rainbow smelt resulted in a reduction in the predation rate on age-0 coregonid larvae and reduced interaction intensity between rainbow smelt and coregonids (Hansen 1994; Cox and Kitchell 2004).

Although the vertical distribution of the pelagic coregonids in Lake Superior has been characterized using daytime bottom trawl surveys and bottom-set gill net surveys (Selgeby and Hoff 1996), there is no documentation of changes in the vertical distribution of ciscoes in Lake Superior over changes in light levels. Historically, trawl surveys most often were conducted during the day and did not account for day to night variability in the depth distribution of the various species. Currently, the three most abundant pelagic prey fish in the open water areas of Lake Superior are bloater (*Coregonus hoyi*), kiyi (*Coregonus kiyi*), and lake herring (i.e., cisco, *Coregonus artedii*). These ciscoes feed on opossum shrimp (*Mysis relicta*, hereafter referred to as *Mysis*), which exhibit a strong DVM (Beeton 1960; Bowers 1988). Characterization of the abundance and spatial distribution of cisco species based on surveys conducted during the daylight hours may show only a portion of their distribution and ecological niche if they exhibit DVM. Furthermore, there are reports of vertical migrations by bloater in Lake Michigan (Eshenroder and Burnham-Curtis 1999; TeWinkle and Fleischer 1999), although there may be physiological constraints on the magnitude of such migrations (Clemens and Stevens 2003). Eshenroder and Burnham-Curtis (1999) posit that DVM in deepwater ciscoes is an adaptation for feeding on *Mysis* and that ciscoes possess physiological adaptations allowing DVMs (also see TeWinkle and Fleischer 1999).

Native lake trout represent the dominant native predator in Lake Superior, with the deepwater subspecies the siscowet (*Salvelinus namaycush siscowet*) being several times more abundant than the shallow-water form (*Salvelinus namaycush namaycush*) (Bronte et al. 2003). Siscowet, which have flesh lipid content of up to 48% (Eschmeyer and Phillips 1965), are well adapted for extensive vertical movements in

the Great Lakes and feeding on deepwater ciscoes (Eshenroder and Burnham-Curtis 1999). Siscowet are commonly caught in deep, bottom areas in depths >100 m (Thurston 1962; Selgeby and Hoff 1996), but have also been caught in surface waters at night, where they may feed on terrestrial insects and shallow-water organisms (Thurston 1962). Furthermore, Thurston (1962) indicated that siscowets do not experience problems with gas expansion in the swimbladder or bloating that is experienced by lean lake trout when pulled from depths >70 m. Combined, these reports suggest substantial variability in the vertical distribution of siscowets. The derived physiological adaptations that characterize this subspecies of lake trout (e.g., high lipid content and reduced swim bladders) suggest the possibility of extensive vertical migrations (Eshenroder and Burnham-Curtis 1999); however, DVM has not yet been documented for siscowets.

Analyses of stable isotope ratios of Lake Superior fishes indicate a linkage between siscowets and deepwater ciscoes. Siscowets are isotopically distinct from lean lake trout and feed to a large extent on deepwater ciscoes (Harvey and Kitchell 2000). Diet analyses support the contention that large siscowets rely on ciscoes much more so than do lean lake trout (Conner et al. 1993; Ray 2004). Isotopic signatures and diet studies suggest a pelagic food web with strong linkages among *Mysis*, deepwater ciscoes, and siscowets (Harvey and Kitchell 2000). Given that the open-water food web is largely dominated by native species that have adaptations that allow vertical migrations (Eshenroder and Burnham-Curtis 1999), the existence of vertical migration within the pelagic food web has the potential to influence predator-prey interactions. Documentation of the existence and extent of vertical movements and overlap between predator and prey populations are required before a full understanding of energy exchange is possible.

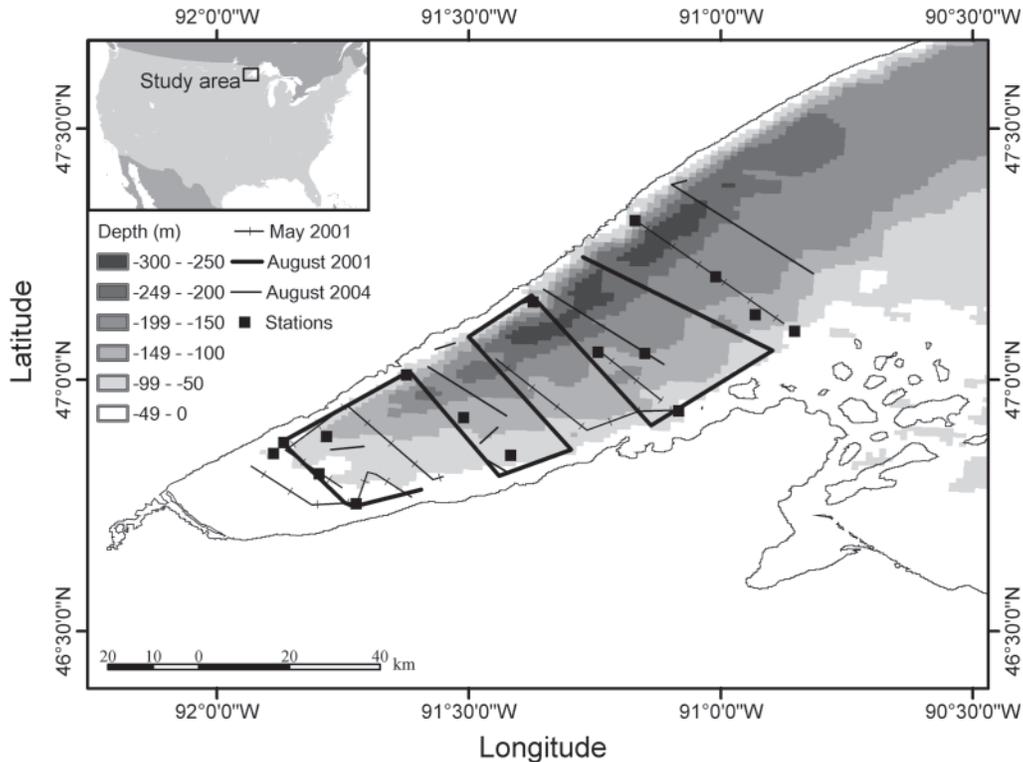
In this paper (part I of II), we examine the vertical distribution of fishes in the open-water area of Lake Superior's western arm during isothermal and thermally stratified periods and among years with varying abundance of predatory siscowets. We hypothesized that the distribution of ciscoes will be influenced by diel changes in light, where darkness represents a potential refuge from predation. In addition, we also hypothesized that the abundance of siscowet within the pelagia would also influence the extent to which cisco vertically migrate. We present and examine evidence of the vertical migration in ciscoes and siscowets based on in situ measurements with midwater trawl gear and scientific echosounders. In addition, vertical changes in the density of *Mysis*, which migrate to shallow-water areas at night, may result in shallow depth distribution of ciscoes at night. The results presented here are used in a companion analysis to explore whether predation avoidance or prey distributions or a combination therein drive the vertical distribution of predators and prey in the open-water area of Lake Superior (Jensen et al. 2006).

## Materials and methods

### Planktivore distribution

We conducted surveys in western Lake Superior on the research vessel *Blue Heron* on 17–21 May 2001, 21–23 Au-

**Fig. 1.** Location of sonar transects and sampling locations in western Lake Superior in 2001 and 2004.



gust 2001, and 14–18 August 2004 (Fig. 1). During the sampling cruises, we estimated the depth distribution, size, and abundance of fish using a split-beam, 120 kHz Biosonics echosounder while performing transects spanning the western arm of Lake Superior during the day and at night on each outing. The software settings for the echosounder included a pulse duration of 0.4 ms and one pulse per second. Standard target calibration was performed shortly before each tow and after the sampling cruise, and target strength never varied significantly ( $<\pm 1$  dB) from the known target strength of the calibration sphere. Analysis procedures included eliminating any bottom anomalies using postprocessing software (Ecoview, SonarData Inc. V. 3.0) and estimation of fish density at each depth strata using echo integration and mean target strength after correcting for system configuration. The transducer was mounted on the Biosonics Inc. Biofin towbody and towed alongside the research vessel at a depth of 1 m from the surface at speeds of 4–5 knots ( $1 \text{ knot} = 1.853 \text{ km}\cdot\text{h}^{-1}$ ) during day and night. In 2004, vertical distribution of fish during dawn, day, and dusk was estimated using stationary pinging, allowing target tracking and rates of movement of fish in the vertical plane to be estimated.

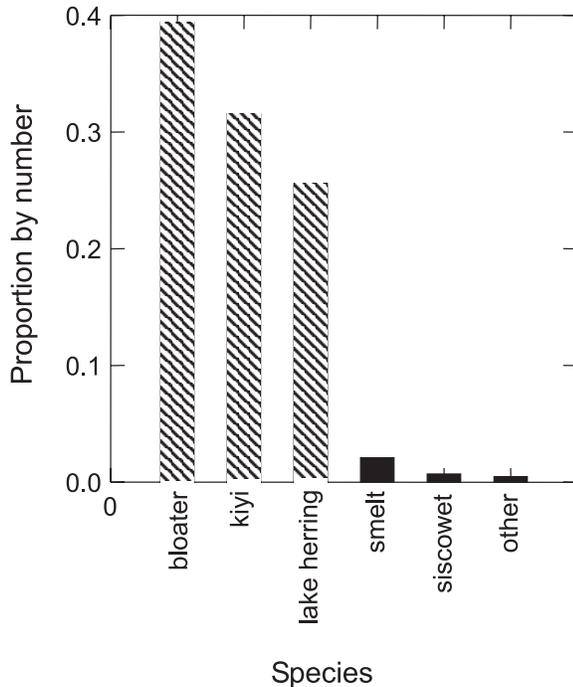
We used a threshold value of  $-65$  dB during echo postprocessing for data used in the echo-squared integration analyses (Thorne 1983). Single target analysis using split-beam data (Ehrenberg 1983) used a threshold of  $-55$  dB. Integrated values were identified for 5 m vertical intervals and horizontal intervals of 20 min. These criteria provided numerous samples for identification of mean backscatter for each depth and time interval.

We used split-beam analysis to determine the target strengths of fish identified within the acoustic beam. Mean backscatter of single fish targets was calculated for each 5 m vertical and 20 min time interval for each transect to convert echo-squared integration into measures of fish density. Target strength values at depth were converted to estimates of fish length using relationships developed using echoes from the dorsal aspect (Love 1977).

We estimated the volumetric density of predators using single target analyses and estimates of the volume of the acoustic beam. We assumed single targets  $> -32$  dB in size represented predatory species; this target strength exceeded the maximum size of ciscoes captured in midwater trawls in the survey areas. We also assumed that a large proportion of predator targets would be single targets, that schooling behavior was uncommon in predatory species, and that prey fish aggregations would avoid a large predator. The number of predator targets was summed over 5 m vertical and 20 min time interval for each transect and divided by the beam volume sum to estimate predator density and depth distributions for a given time interval.

During day, dusk, and dawn periods in 2004, stationary pinging allowed single fish targets to be tracked in the vertical plane. The depth trajectory of prey fish ( $< -32$  dB) tracked for a minimum of three pings in each time period was recorded, and slope was estimated using a linear regression (SAS REG Procedure, SAS Institute Inc., Cary, North Carolina) of target depth vs. time for each target. The mean slopes (i.e., rates of ascent or descent) for each time period (day, dusk, and dawn) were compared using analysis of variance (ANOVA, SAS GLM procedure) to determine if the

**Fig. 2.** Numerical proportion of species caught in nighttime midwater trawls in areas with bottom depths >150 m. The trawls were targeted to the primary scattering layer observed with hydroacoustics and maintained at a constant depth for approximately 1 h. Head rope depth of the trawls ranged between approximately 20 and 40 m and averaged 30 m. Hatched bars indicate coregonid species.



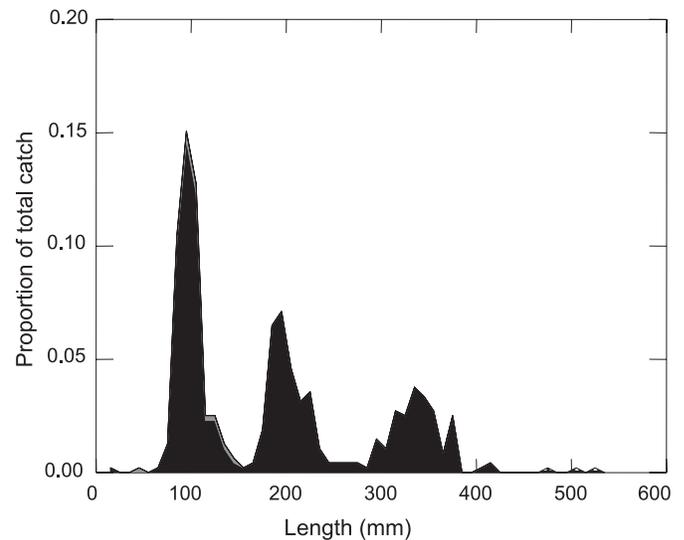
mean slope was substantially different (positive or negative) from zero (or no slope).

#### Biological and physical sampling

In 2004, we used a Gourcock 20 m × 20 m box-type midwater trawl with 5 mm mesh cod end liner to sample fish species composition at various depths. We fished the trawl at discrete depths and aimed to sample scattering layers of fish. We monitored the trawl positions using Imagenex trawl mensuration system that contained a trawl sonar that measured the size of the trawl opening, depth of the trawl, and a temperature at the head rope. All fish captured in each trawl were identified, enumerated, and measured for total length and mass. No trawl information was available for 2001. However, information collected in 1997 and 2003 indicated that approximately 80% of open-water fish captured in midwater trawl surveys were deepwater coregonids (Mason et al. 2005; T.R. Hrabik, unpublished data), a finding that was similar to that observed in 2004. We therefore assume the species identified in 2004 were also representative of fish sampled by hydroacoustics in 2001.

We performed temperature casts near the beginning, mid-point, and end points of each sampling transect using Sea Bird model 19-01 conductivity, temperature, and depth profiler in 2001. In 2004, temperature profiles were recorded using a temperature sensor located within the Imagenex trawl mensuration system. Temperature profiles were recorded during the descent and ascent of each trawl. The average of

**Fig. 3.** Numerical proportion of various sizes of fish (10 mm bins) caught in nighttime midwater trawls. Coregonids, solid area; rainbow smelt (*Osmerus mordax*), shaded area; siscowet (*Salvelinus namaycush siscowet*), hatched area.



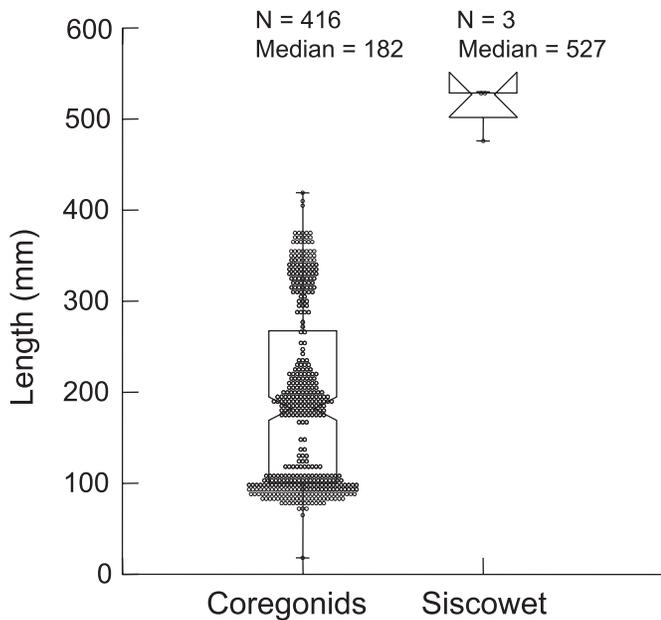
each was used to estimate the temperature profile for transect segment during trawling (Fig. 1).

#### Statistical analysis of DVM trajectories

In addition to estimating regional and lake-wide abundance of different species, the hydroacoustic survey data can be used to describe diel changes in their depth distribution. To estimate DVM trajectories for coregonids and lake trout, targets of the appropriate target strength (< -32 dB for coregonids and > -32 for lake trout) were summarized by 5 m by 20 min depth-time bins for all targets observed in water depths >150 m. Data from all days and stations were combined based on the assumption that DVM trajectories did not vary over the short time scale (3 days) and limited spatial extent of the survey. However, densities of both coregonids and lake trout did vary among stations. Therefore, we standardized densities by dividing the number of targets in each depth-time bin by the total number of targets for that time interval. We also calculated the depth of the 0.01 lx isolume for May and August surface light intensity data for Duluth, Minnesota (NSRDB 2004), and the Beer-Lambert equation (Hutchinson 1957). We use 0.01 lx because it is below the threshold at which the reaction distance of many fish (including lake trout (Vogel and Beauchamp 1999) and coregonids (Link and Edsall 1996)) reaches a minimum.

Weighted, penalized regression splines were fit to the data where depth was the response variable, time the predictor, and the standardized targets were the weights (mgcv v1.0-9 for R v1.9.1). Penalized regression splines allow the flexibility of the curve to be optimized by “rewarding” model fit and “penalizing” model degrees of freedom (Wood and Augustin 2002) rather than setting the model degrees of freedom a priori. To make use of the cyclic nature of DVM without specifying cyclic functions (e.g., sine or cosine transformations), the data were wrapped, such that the last 3 h of the 24 h period were duplicated and added to the be-

**Fig. 4.** Box and whisker diagram showing the size of coregonids and siscowet (*Salvelinus namaycush siscowet*) in the open-water area of Lake Superior's western arm in 2004. Coregonids and siscowet represent approximately 97% of the total catch of fish in the open-water area.



ginning of the 24 h period. Similarly, the first 3 h were duplicated and added to the end such that the curves were fit to data spanning the time interval -180 to 1620 min.

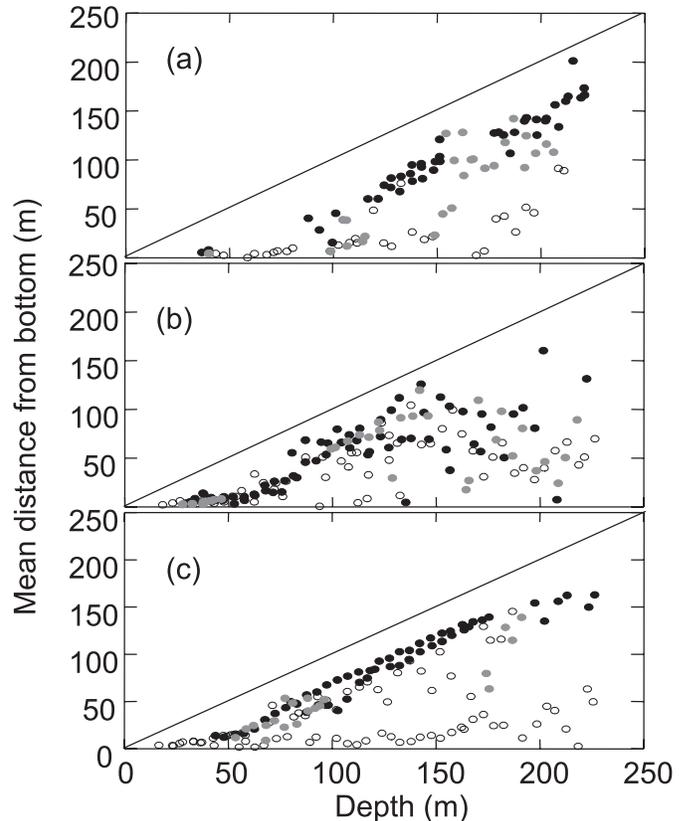
Although the spline curves show diel changes in mean depth for each species, clearly not all individuals are aggregated at the mean depth. Probability density fields for each species were created by overlaying a normal distribution with time-specific mean and standard deviation on each time interval. The assumption of normality was confirmed through histograms of the weighted residuals. In some time intervals where the curve approached the surface or the bottom, the tail of the distribution extended beyond the depth range. When more than 0.1% of the distribution in any time interval extended beyond the depth range, this missing portion was added proportionally to the existing depth bins such that the total probability in any time interval sums to one, and there is equal probability above and below the mean.

## Results

### Fish species composition and size

The numerical composition of fish species in Lake Superior's western arm was dominated by coregonines (97%; 75% represented by bloater and kiyi, 22% by lake herring), followed by rainbow smelt (2%), siscowet (0.7%), and other fish species (0.3%) (Fig. 2). All fish were captured between 12 and 60 m in depth at night. Trawls were performed in the same depth ranges during the day but captured no fish. The size of fish captured in trawls varied according to species. Coregonids ranged in size from 65 to 415 mm total length (Fig. 3). Rainbow smelt sizes ranged from 45 to 145 mm total length (Fig. 3). Siscowets were the largest species captured and ranged from 475 to 535 mm total length (Fig. 3). There was no overlap in size between the predatory siscowet

**Fig. 5.** The mean difference between coregonid depths and bottom depth on three sampling dates. Predator density was substantially higher in May 2001 (a) than in August 2001 (b). Predator density in August 2004 (c) was substantially higher than in May 2001. Night, solid circles; day, open circles; dawn-dusk, shaded circles.



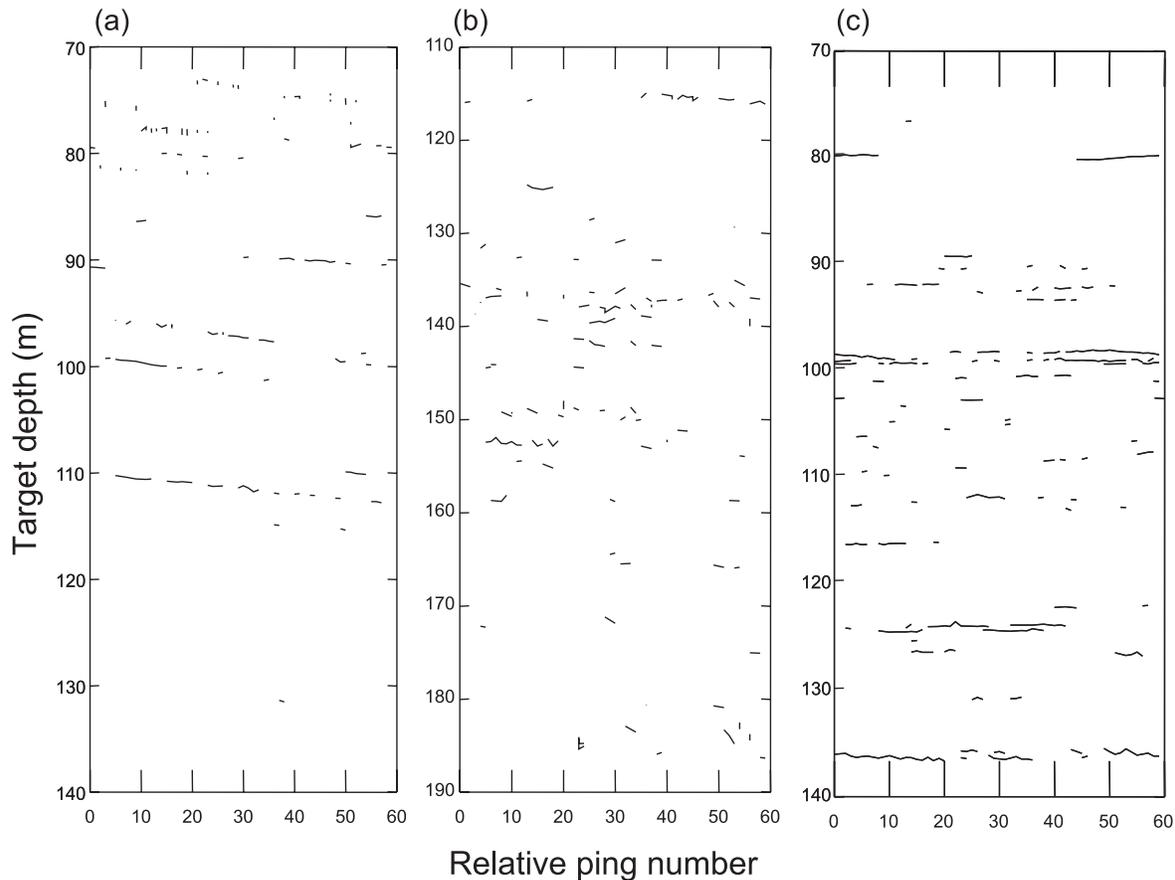
and prey fish species, which differed in median size by ~345 mm (Fig. 4).

### DVMs of fish in western Lake Superior

Data on ciscoes collected over varying light levels indicates that they perform a DVM in western Lake Superior. The difference between the mean depth of ciscoes estimated using hydroacoustics and bottom depth was greatest during night, intermediate at dawn-dusk, and much lower during the day (Fig. 5). The magnitude of difference between the mean depth of ciscoes and the bottom during the low light periods was greatest in areas where total depth exceeded 150 m and relatively small in areas shallower than 50 m (Fig. 5).

In August of 2004, single fish targets were tracked while stationary pinging and allowed directionality and rate of vertical movement during different periods of the daily cycle. The mean  $\pm$  standard deviation (SD) vertical slope of 308 individually tracked fish at dawn was  $-0.129 \pm 0.76 \text{ m}\cdot\text{s}^{-1}$ , which differed significantly from zero ( $F = -5.98, p = 0.003$ ) (Fig. 6). At dusk, the mean  $\pm$  SD vertical slope of 163 single fish targets was  $0.011 \pm 0.068 \text{ m}\cdot\text{s}^{-1}$ , which differed significantly from zero ( $F = 4.0, p = 0.049$ ) and from the dawn slope ( $F = 5.5, p = 0.019$ ). The mean  $\pm$  SD slope estimated for 91 targets identified during the day ( $0.02 \pm 0.26 \text{ m}\cdot\text{s}^{-1}$ )

**Fig. 6.** Tracks of 50 randomly selected single targets tracked over a minimum of three sequential pings. Data for each light period was collected while the vessel was stationary. (a) Dawn, (b) day, (c) dusk.



did not differ significantly from zero ( $F = 0.51$ ,  $p = 0.46$ ) (Fig. 6).

Analyses of vertical density estimates of both lake trout and ciscoes indicated synchronized vertical movements that corresponded to changing light conditions. In portions of the survey area >150 m in depth, the distribution of ciscoes and lake trout in May and August 2001 and in August 2004 was greatest during the day and most shallow at night (Fig. 7). Weighted, penalized regression spline fits of cisco density using time as a predictor explained 38% of variability in depth distributions in May 2001, 20.2% in August 2001, and 54.8% in 2004 (Table 1). A similar analysis of depth distribution of siscowet revealed model fits that explained 78.9% of the variability in depth distribution in May 2001, 25.2% in August 2001, and 22.7% in August 2004 (Table 1). In May and August 2001, however, the magnitude of vertical movement in ciscoes was much lower than that observed in August 2004. Results from the spline fits were consistent with the findings from analyses of tracked single targets. In 2004, the ascent at dusk occurred much more slowly than the descent at dawn (Fig. 7). The vertical movements of siscowet in August 2001 were lower in magnitude and much less predictable. In addition, the pattern of movement did not appear to be influenced by thermal stratification, and the fish appeared to remain below the thermocline when one was present. While the predatory lake trout also showed vertical movements, the magnitude of their movement appeared similar to that exhibited by ciscoes in May 2001 and August

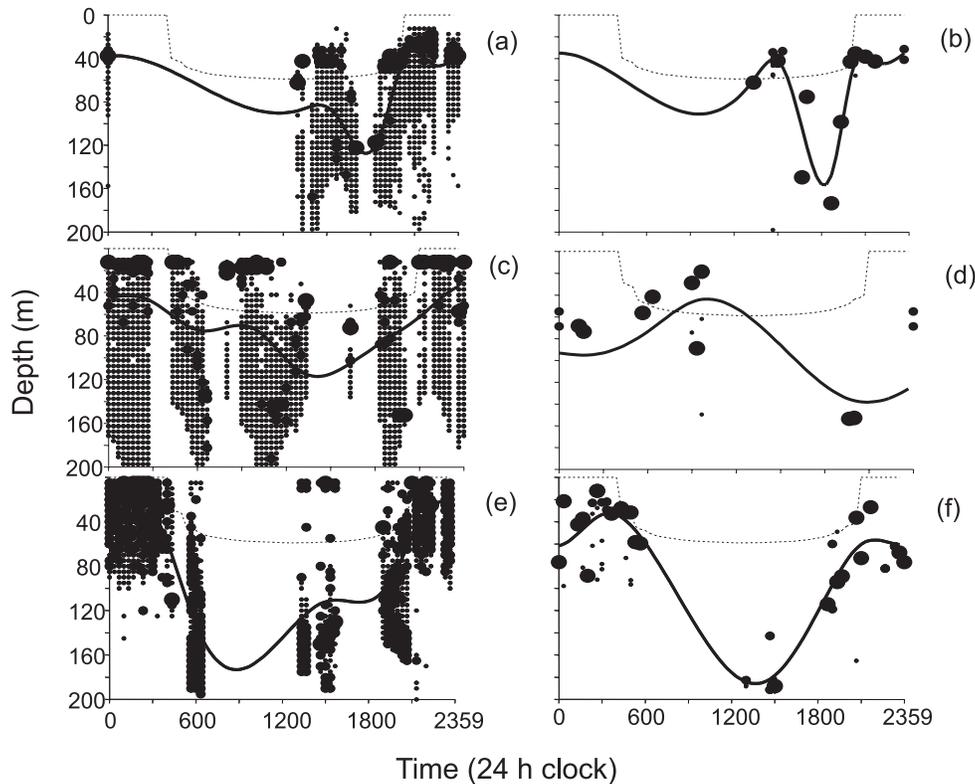
2004 (Fig. 7). In 2004, however, the vertical movement was more pronounced in magnitude for both siscowet and ciscoes than that observed in 2001.

Temperature measurements taken in areas >150 m in depth show isothermal conditions in May 2001 and stratified conditions in August 2001 and 2004 (Fig. 8). Temperature in May 2001 was approximately 2.7 °C throughout the water column. In August 2001, the surface temperature averaged ~17.4 °C, with the average hypolimnion height of ~9 m. The surface temperature in August 2004 was ~12.4 °C, with an average hypolimnion height of ~9 m (Fig. 8). In areas >150 m, secchi depth readings during each sampling period averaged ~10 m and ranged from 7 to 13 m.

#### Variability in fish density

The extent of vertical migration by ciscoes was associated with changes in the density of large predators in deep areas of western Lake Superior. The density of predators and prey varied both among seasons in 2001 and between 2001 and 2004. The density of cisco was highest at 33 411 individuals·km<sup>-2</sup> ( $\pm$ standard error (SE) = 375.43) in May 2001, followed by 26 993·km<sup>-2</sup> ( $\pm$ 1870.31) in August 2001, and lowest at 10 186·km<sup>-2</sup> ( $\pm$ 1063.53) in August 2004 (Fig. 9). The density of predators, however, showed a different pattern among dates. The density of predatory siscowet in open-water areas was highest in August of 2004 at approximately 62.66·km<sup>-2</sup> ( $\pm$ 3.01), followed by 33.14·km<sup>-2</sup> ( $\pm$ 3.10) in May of 2001 and 9.18·km<sup>-2</sup> ( $\pm$ 0.49) in August of 2001. The density of preda-

**Fig. 7.** Coregonid (*Coregonus* spp.; *a*, *c*, and *e*) and lake trout (*Salvelinus namaycush*; *b*, *d*, and *f*) densities at depth from May 2001 (*a* and *b*), August 2001 (*c* and *d*), and August 2004 (*e* and *f*) shown in proportions of total density for each time bin. Coregonid target weights are as follows: large dots, high (>0.33); medium dots, medium (0.1–0.33); small dots, low (<0.1). Lake trout target weights are as follows: large dots, high (>0.66); medium dots, medium (0.33–0.66); small dots, low (<0.33). Weighted, penalized regression splines (solid line) and the 0.01 lx isolume (broken line) are also shown.



**Table 1.** Weighted, penalized regression spline fits predicting coregonids (*Coregonus* spp.) and siscowet (*Salvelinus namaycush siscowet*) depth based on time of day.

Sampling period	Coregonids				Siscowet			
	<i>N</i>	df	Dev. exp. (%)	<i>p</i>	<i>N</i>	df	Dev. exp. (%)	<i>p</i>
May 2001	995	8.7	38.9	<0.001	28	7.9	78.9	<0.001
August 2001	1788	8.7	20.2	<0.001	21	4.0	25.2	<0.001
August 2004	1180	8.8	54.8	<0.001	71	7.8	77.5	<0.001

**Note:** Model degrees of freedom (df) were chosen by generalized cross-validation (Wood and Augustin 2002) using mgcv v1.0–9 for R v1.9.1. *N*, the number of 5 m by 20 min intervals for which observations were available; Dev. exp., the percent of deviance explained.

tors corresponded to the magnitude of migration by ciscoes, such that the deepest migration and the fewest coregonids present above the depth of light penetration during the day occurred when predator density was highest (Fig. 7).

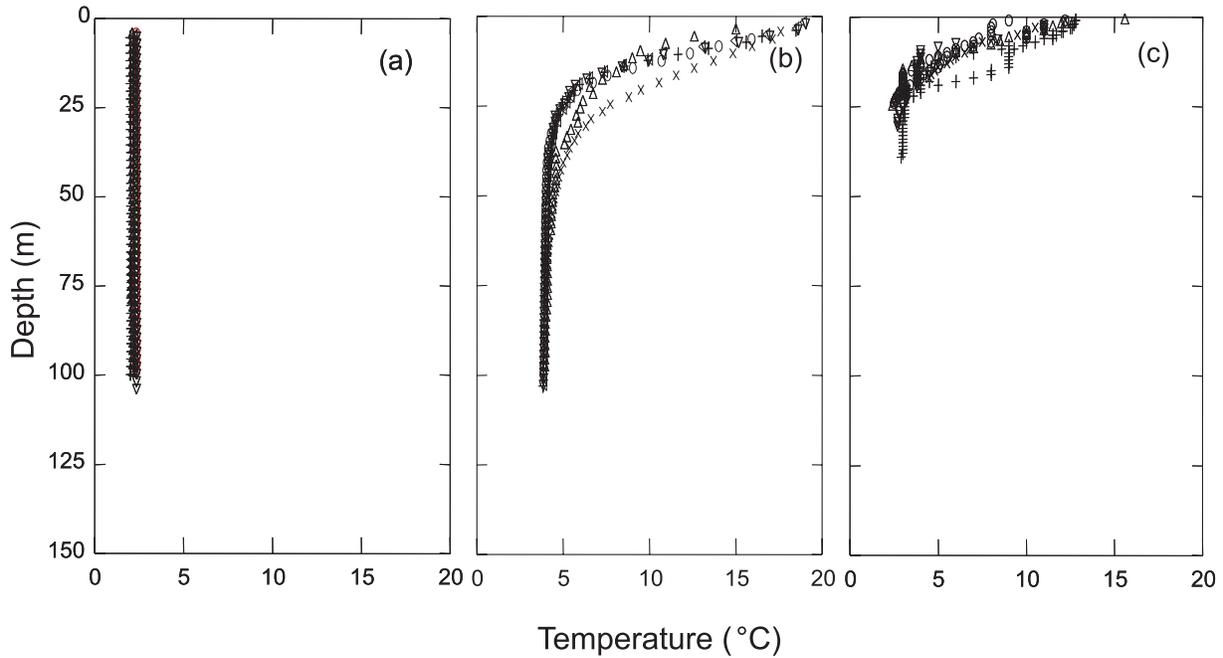
## Discussion

The DVM pattern exhibited by ciscoes and siscowet in Lake Superior suggests a strong behavioral response to changing light levels that is consistent with predation avoidance and the distribution of their preferred prey, respectively. Our findings are consistent with other reports of DVM shown for bloaters in Lake Michigan (e.g., Brandt et al. 1991; Eshenroder and Burnham-Curtis 1999; TeWinkle and Fleischer 1999). Such movement patterns are often associ-

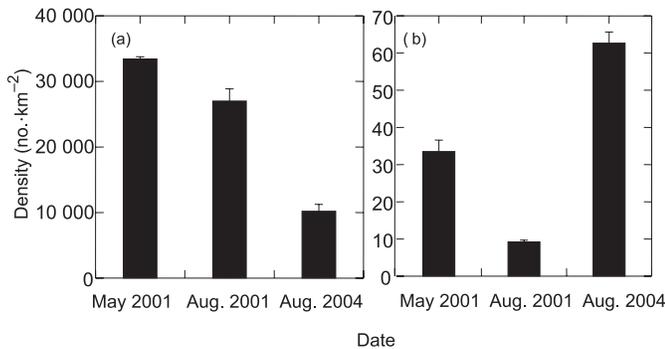
ated with thermoregulation and bioenergetic optimization, foraging maximization, or predation avoidance (Eggers 1978; Bevelhimer and Adams 1993; Scheuerell and Schindler 2003). The rates of vertical movement in ciscoes differ between dawn and dusk, suggesting that ciscoes may control their rate of ascent to compensate for decreasing hydrostatic pressure and positive buoyancy as they rise. Furthermore, the presence of a strong migration pattern has ramifications for interaction intensity between predators and prey and ongoing analyses of demand and supply in the Lake Superior food web.

Lake Superior is unique in that its food web is dominated by native fish species that are well adapted to the unique set of environmental conditions that include exceedingly cold temperatures and great depth. Lake Superior differs from

**Fig. 8.** Temperature profiles taken at deep (>130 m) locations in western Lake Superior during (a) spring 2001, (b) summer 2001, and (c) summer 2004. Different symbols indicate different sites deeper than 130 m.



**Fig. 9.** The density of (a) coregonids and (b) predatory species estimated from hydroacoustic sampling in waters >150 m in total depth in Lake Superior’s western arm on each sampling interval. Error bars indicate the standard error about the mean estimated using 1 km segments of transects as samples.



other Great Lakes in that the thermocline in open-water areas is often relatively shallow even in late summer. In addition, many of the open-water fish species remain below 30 m in depth even at night when at the shallowest point in their migration. This observation coupled with the consistent vertical migration in the isothermal period in May 2001 suggests that thermoregulation is not a major variable in the process.

The migration patterns of ciscoes observed in this study are consistent with those observed in other Great Lakes. Stationary acoustic tracking of single target data documented many individual fish rising during dusk and diving during the dawn periods. We detected no fish in shallow waters during daytime sampling. However, we often observed a large number of acoustic targets in water >150 m during the day. During dusk, repeated pings on single fish targets while stationary revealed rates of ascent that were lower than rates of

descent, suggesting possible compensation for positive buoyancy while in the process of migration. These findings are consistent with reports of DVM in Great Lakes ciscoes by others (Brandt et al. 1991; Eshenroder and Burnham-Curtis 1999; TeWinkle and Fleischer 1999) and indicate that ciscoes are able to perform large vertical movements that may exceed 150 m in magnitude over the span of a few hours. The slower rate of ascent than descent at dusk may offer insight into how coregonids compensate for large decreases in hydrostatic pressure as they move vertically and contribute to the buoyancy compensation debate (Eshenroder and Burnham-Curtis 1999; Clemens and Stevens 2003).

The observed vertical movement by siscowets supports the contention that high fat content is associated with their ability to move readily over large depth ranges (Eshenroder and Burnham-Curtis 1999). In 2004, a year with the highest observed predator densities, the vertical movement by siscowets exceeded 150 m and was similar to that exhibited by ciscoes. The increase in the magnitude of migration in this year corresponds to the highest predator densities and lowest prey density and suggests that foraging opportunity may underlie the process. This finding supports previous reports of siscowet moving to upper portions of the water column at night (e.g., Thurston 1962) and that this species is well adapted to extensive and rapid vertical movements while foraging.

The depth distribution records for bloater and kiyi suggest that these species live in deep areas (>100 m) and rarely foray into shallow areas (Becker 1983; Selgeby and Hoff 1996). Our findings suggest that historical depth characterization based on information collected using daytime bottom trawls or gill nets set on the bottom may not reflect the true distributions of either bloater or kiyi in Lake Superior over a 24 h cycle. We routinely caught kiyi and bloater in midwater trawls deployed at depths near 30 m at night and very few

fish below 50 m. These findings indicate these species may follow *Mysis* from deep areas and feed on abundant prey near 30 m during low light periods.

The existence of DVM patterns in the dominant prey fish species has implications for assumptions of prey availability for increasing siscowet and lean lake trout populations in Lake Superior. Predatory lake trout are now approaching historical abundance in Lake Superior (Hansen et al. 1995; Anonymous 1996). The rate of increase in abundance of siscowet is much higher relative to the lean lake trout (Kitchell et al. 2000; Bronte et al. 2003). Given an assumption of maximum prey size of ~50% of siscowet body length, ~78% of the coregonids collected would be vulnerable to predation by siscowets in our trawl samples. In 2004, the year in which the strongest migration pattern by both cisco and siscowet occurred, it was apparent that each moved extensively over a 24 h cycle. Our findings suggest that the magnitude of the migration pattern may be influenced by predator abundance and that the extreme depth range of the migration may be linked to higher densities of siscowet in the deep areas of western Lake Superior. However, given that a primary food item of ciscoes, the *Mysis*, undergoes a similar vertical migration pattern, testing of these hypotheses using a mathematical modeling approach is required to eliminate food supply as a likely mechanism (Jensen et al. 2006).

In summary, our findings document the existence of strong migratory behavior that has the potential to influence energy transfer between the planktivore and piscivore trophic levels and further complicate supply–demand analyses. Siscowets are capable of extensive vertical migrations. Given that the shallow-water lean lake trout is not, siscowet may indirectly influence prey resource availability for lean lake trout by inducing large migration patterns in the prey and possibly reducing prey density. As prey become more difficult to capture in the open water, siscowet may switch to alternative prey and place further competitive pressure on the shallow-water form (Harvey et al. 2003). Recent findings indicate that siscowets may foray into shallow water to feed on prey used by lean lake trout and that the dietary overlap between the two forms now exceeds 90% during the spring and early summer period (Ray 2004). These findings highlight the need to understand the mechanisms underlying the vertical migration patterns within the Lake Superior community and the consequences of this behavior for energy transfer through the food web to top predators exploited by fisheries.

## Acknowledgements

We thank the crew of the R/V *Blue Heron* and the Large Lakes Observatory for their service during sampling cruises. We thank Don Schreiner and Steve Schram for providing support for portions of the field surveys. Funding for this research was provided by the Minnesota Department of Natural Resources, the Wisconsin Department of Natural Resources, the Minnesota Sea Grant College program, the Wisconsin Sea Grant, and the University of Minnesota, Duluth Campus.

## References

- Anonymous. 1996. Lake Superior lake trout restoration proclaimed a victory. Fisheries (Bethesda), **21**: 47–48.
- Becker, G.C. 1983. Fishes of Wisconsin. The University of Wisconsin Press, Madison, Wis.
- Beeton, A.M. 1960. The vertical migration of *Mysis relicta* in Lakes Huron and Michigan. J. Fish. Res. Board Can. **17**: 517–539.
- Bevelhimer, M.S., and Adams, S.M. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. **50**: 2336–2349.
- Bowers, J.A. 1988. Diel vertical migration of the opossum shrimp *Mysis relicta* in Lake Superior — observations and sampling from the Johnson-Sea-Link II Submersible. Bull. Mar. Sci. **43**: 730–738.
- Brandt, S.B., Mason, D.M., Patrick, E.V., Argyle, R.L., Wells, L., Unger, P.A., and Stewart, D.J. 1991. Acoustic measures of abundance and size of pelagic planktivores in Lake Michigan. Can. J. Fish. Aquat. Sci. **48**: 894–908.
- Bronte, C.R., Ebener, M.P., Schreiner, D.R., Devault, D.S., Petzold, M.M., Jensen, D.A., Richards, C., and Lozano, S.J. 2003. Fish community change in Lake Superior, 1970–2000. Can. J. Fish. Aquat. Sci. **60**: 1552–1574.
- Christie, W.J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. **31**: 827–854.
- Clemens, B.J., and Stevens, E.D. 2003. Buoyancy range, gas bladder volume, and lipid content of adult bloater, *Coregonus hoyi* Gill, in the Laurentian Great Lakes. Environ. Biol. Fishes, **68**: 175–182.
- Conner, D.J., Bronte, C.R., Selgeby, J.H., and Collins, H.L. 1993. Food of salmonine predators in Lake Superior, 1984–1987. Great Lakes Fish. Comm. Tech. Rep. 59.
- Cox, S.P., and Kitchell, J.F. 2004. Lake Superior ecosystem, 1929–1998: simulating alternative hypotheses for recruitment failure of lake herring (*Coregonus artedii*). Bull. Mar. Sci. **74**: 671–683.
- Dryer, W.R., Erkkila, L.F., and Tetzloff, C.L. 1965. Food of the lake trout in Lake Superior. Trans. Am. Fish. Soc. **94**: 169–176.
- Eggers, D.M. 1978. Limnetic feeding-behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnol. Oceanogr. **23**: 1114–1125.
- Eschmeyer, P.H., and Phillips, A.M. 1965. Fat content of the flesh of siscowets and lake trout from Lake Superior. Trans. Am. Fish. Soc. **94**: 62–74.
- Eshenroder, R.L., and Burnham-Curtis, M.K. 1999. Species succession and sustainability of the Great Lakes fish community. In Great Lakes fisheries policy and management. Edited by W.W. Taylor and C.P. Ferreri. Michigan State University Press, East Lansing, Mich. pp. 145–184.
- Ehrenberg, J.E. 1983. A review of in situ target strength estimation techniques. FAO Fish. Rep. 300: 85–90.
- Hansen, M.J. (Editor). 1994. The state of Lake Superior in 1992. Great Lakes Fish. Comm. Spec. Publ. 94-1.
- Hansen, M.J., Peck, J.W., Schorffhaar, R.G., Selgeby, J.H., Schreiner, D.R., Schram, S.T., Swanson, B.L., MacCallum, W.R., Burnham-Curtis, M.K., Curtis, G.L., Heinrich, J.W., and Young, R.J. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. J. Great Lakes Res. **21**(Suppl. 1): 152–175.
- Harvey, C.J., and Kitchell, J.F. 2000. A stable isotope study of the structure and spatial heterogeneity of the Lake Superior food web. Can. J. Fish. Aquat. Sci. **57**: 1395–1407.

- Harvey, C.J., Schram, S.T., and Kitchell, J.F. 2003. Trophic relationships among lean and siscowet lake trout in Lake Superior. *Trans. Am. Fish. Soc.* **132**: 219–228.
- Hutchinson, G.E. 1957. A treatise on limnology. Vol. I. Geology, physics, and chemistry. Wiley, New York.
- Jensen, O.P., Hrabik, T.R., Martell, S.J.D., Walters, C.J., and Kitchell, J.F. 2006. Diel vertical migration in the Lake Superior pelagic community. II. Modeling trade-offs at an intermediate trophic level. *Can. J. Fish. Aquat. Sci.* **63**: 2296–2307.
- Kitchell, J.F., Cox, S.P., Harvey, C.J., Johnson, T.B., Mason, D.M., Schoen, K.K., Aydin, K., Bronte, C., Ebener, M., Hansen, M., Hoff, M., Schram, S., Schreiner, D., and Walters, C.J. 2000. Sustainability of the Lake Superior fish community: interactions in a food web context. *Ecosystems*, **3**: 545–560.
- Knudsen, F.R., and Gjelland, K.O. 2003. Hydroacoustic observations indicating swimbladder volume compensation during the diel vertical migration in coregonids. *Fish. Res.* **66**: 337–341.
- Link, J., and Edsall, T.A. 1996. The effect of light on lake herring (*Coregonus artedii*) reactive volume. *Hydrobiologia*, **332**: 131–140.
- Love, R.H. 1977. Target strength of an individual fish at any aspect. *J. Acoust. Soc. Am.* **62**: 1397–1403.
- Mason, D.M., Johnson, T.B., Harvey, C.J., Kitchell, J.F., Schram, S.T., Bronte, C.R., Hoff, M.H., Lozano, S.J., Trebitz, A.S., Schreiner, D.R., Lamon, E.C., and Hrabik, T.R. 2005. Hydroacoustic estimates of abundance and spatial distribution of pelagic fishes in western Lake Superior. *J. Gt. Lakes Res.* **31**: 426–438.
- Negus, M.T. 1995. Bioenergetics modeling as a salmonine management tool applied to Minnesota waters of Lake Superior. *N. Am. J. Fish. Manag.* **15**: 60–78.
- NSRDB (National Solar Radiation Database). 2004. NSRDB hourly data files for Duluth (Weather Bureau Army Navy (WBAN) Identification Number 14913) [online]. Available from [http://tredc.nrel.gov/solar/old\\_data/nsrdb/hourly/1990/14913\\_90.txt](http://tredc.nrel.gov/solar/old_data/nsrdb/hourly/1990/14913_90.txt) [accessed on 8 December 2004].
- Ray, B.A. 2004. Spatial and temporal analysis of the Lake Superior fish community and predator diets. M.Sc. thesis, University of Minnesota, Duluth Campus, Minn.
- Scheuerell, M.D., and Schindler, D.E. 2003. Diel vertical migration by juvenile sockeye salmon: empirical evidence for the anti-predation window. *Ecology*, **84**: 1713–1720.
- Selgeby, J.H. 1982. Decline of lake herring (*Coregonus artedii*) in Lake Superior: an analysis of the Wisconsin herring fishery 1936–78. *Can. J. Fish. Aquat. Sci.* **39**: 554–563.
- Selgeby, J.H., and Hoff, M.H. 1996. Seasonal bathymetric distributions of 16 fishes in Lake Superior, 1958–1975. *Nat. Biol. Serv. Biol. Sci. Rep.* **7**.
- TeWinkle, L.M., and Fleischer, G.W. 1999. Vertical migration and nighttime distribution of adult bloaters in Lake Michigan. *Trans. Am. Fish. Soc.* **128**: 459–474.
- Thorne, R.E. 1983. Assessment of population abundance by hydroacoustics. *Biol. Oceanogr.* **2**: 253–262.
- Thurston, C.E. 1962. Physical characteristics and chemical composition of two subspecies of lake trout. *J. Fish. Res. Board Can.* **19**: 39–43.
- Vogel, J.L., and Beauchamp, D.A. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Can. J. Fish. Aquat. Sci.* **56**: 1293–1297.
- Wood, S.N., and Augustin, N.H. 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. *Ecol. Model.* **157**: 157–177.