

Diel vertical migration in the Lake Superior pelagic community. II. Modeling trade-offs at an intermediate trophic level

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Abstract: Several hypotheses have been proposed to explain diel vertical migration (DVM); however, they have generally been applied to DVM behavior of a single trophic level. We evaluate the costs (predation risk) and benefits (foraging rate and growth rate potential) of different hypothetical and observed DVM trajectories for a three-level pelagic food chain in Lake Superior containing opossum shrimp (*Mysis relicta*), deepwater ciscoes (*Coregonus* spp.), and lake trout (*Salvelinus namaycush*). Lake trout appear to be maximizing foraging and growth rates by tracking vertically migrating ciscoes, while the DVM trajectories of ciscoes suggests a trade-off between predation risk and growth. For ciscoes, two alternative DVM trajectories both minimize the ratio of risk to growth: a shallow trajectory that follows low light levels down to 80 m during the day and a deep trajectory (below 150 m) that tracks highest *Mysis* densities. Observed cisco DVM trajectories appear to follow the shallow high risk – high growth trajectory in 2001, but switch to the deep, low risk – low growth trajectory in 2004 when lake trout density was higher and the density of ciscoes was lower.

Résumé : Plusieurs hypothèses cherchent à expliquer les migrations verticales journalières (DVM); elles ont, cependant, généralement été appliquées au comportement DVM d'un seul niveau trophique. Nous évaluons les coûts (risque de prédation) et les bénéfices (taux potentiels d'alimentation et de croissance) de différentes trajectoires DVM hypothétiques et réelles dans une chaîne alimentaire pélagique à trois échelons au lac Supérieur comprenant la crevette opossum (*Mysis relicta*), des ciscos d'eau profonde (*Coregonus* spp.) et le touladi (*Salvelinus namaycush*). Le touladi semble maximiser ses taux d'alimentation et de croissance en poursuivant les ciscos en migration verticale, alors que les trajectoires DVM des ciscos semblent refléter un compromis entre le risque de prédation et la croissance. Chez les ciscos, deux trajectoires DVM de rechange permettent toutes deux de minimiser le rapport du risque de prédation sur la croissance, une trajectoire peu profonde qui suit les faibles intensités lumineuses pendant le jour jusqu'à une profondeur de 80 m et une trajectoire profonde (sous 150 m) qui suit les densités maximales de *Mysis*. Les trajectoires DVM observées chez les ciscos en 2001 semblent avoir suivi le type de trajectoire plus superficielle de risque élevé et de croissance rapide. En 2004 quand les densités de touladis étaient plus fortes et celles des ciscos réduites, les ciscos ont adopté plutôt la trajectoire de risque faible et de croissance lente.

[Traduit par la Rédaction]

Introduction

Understanding the mechanisms underlying diel vertical migration (DVM) continues to be one of the unresolved questions in limnology and behavioral ecology despite the many hypotheses that attempt to provide general explanations for this frequently observed phenomenon. Because this question sits at the intersection of several important ecological concepts (e.g., trophic interactions, bioenergetics, foraging theory), DVM has attracted a correspondingly diverse array of approaches. Implicit in many of these approaches are trade-offs between the costs and benefits of being at a given depth at a given time. We combine several of the most

commonly advanced hypotheses regarding DVM in a modeling framework that elucidates these trade-offs and allows for comparisons between theoretically ideal DVM trajectories and those observed in the field. The model is applied to data on the diel vertical distribution of three trophic levels, opossum shrimp (*Mysis relicta*), deepwater ciscoes (*Coregonus* spp.), and lake trout (*Salvelinus namaycush*), in a Lake Superior pelagic food chain. The framework, however, is general and can be applied to any system for which depth–time distribution data exist.

Observations of similar DVM trajectories for fishes and their prey led to the development of foraging hypotheses (Narver 1970; Schoener 1971), which predict that DVM al-

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lows fish to maximize consumption rates (or conversely to minimize foraging time required to obtain a given quantity of food). In the Laurentian Great Lakes, DVM in alewives (*Alosa pseudoharengus*; Janssen and Brandt 1980) and ciscoes (Eshenroder and Burnham-Curtis 1999, 2001) has been explained as a means of maximizing feeding rates on vertically migrating *Mysis*. Foraging hypotheses were extended by bioenergetic theories to include temperature-dependent metabolic costs as well as foraging benefits (Brett 1971). Bioenergetic hypotheses predict that DVM will allow fish to maximize growth rate, and they provide a rationale for migration trajectories that do not place fish in depths of highest prey density (Bevelhimer and Adams 1993). Foraging and bioenergetic hypotheses have been most successful at explaining DVM patterns for species at top trophic positions where predation risk is not a consideration.

Foraging and energetic approaches have failed to explain DVM at intermediate trophic levels for which predation is an important source of mortality (Levy 1990a, 1990b, 1991). Experimental evidence has shown that the addition of predators can induce changes in behavior and habitat use by fishes (Werner et al. 1983; He et al. 1993) and that the effects of such predator-induced changes depend on food availability (Biro et al. 2003a, 2003b). Eggers (1978) postulated predation risk as a driving factor in juvenile sockeye salmon (*Oncorhynchus nerka*) distributions in Lake Washington where zooplankton prey are comparatively abundant and observed that a variety of foraging strategies, including brief feeding near the surface and prolonged feeding at low light intensity, might all result in similar food intake and similar predation risk.

For a visual planktivore preyed upon by a visual piscivore, the ratio of predation risk (μ) to growth rate (G) (Werner and Gilliam 1984) is minimized at intermediate light intensity, assuming that the reaction distances of predator and prey are similar and respond in a similar manner to changes in light intensity (Clark and Levy 1988). In addition to predicting that sockeye salmon should use DVM to allow them to feed during crepuscular periods when foraging rates are high relative to predation risk (the "antipredation window"), the model used by Clark and Levy (1988) predicts that to achieve maximum fitness, sockeye should follow a DVM trajectory that would allow them to obtain a critical minimum size at the lowest possible risk.

For understanding DVM of fish at intermediate trophic levels, which are subject to the constraints of both growth and risk avoidance, the model of Clark and Levy (1988) was a substantial improvement over previous hypotheses, which focused on only one side of the equation. More recent laboratory feeding experiments, however, have shown that at least for some fish species, the relationship between reaction distance and light intensity differs substantially between planktivores and piscivores (De Robertis et al. 2003). Scheuerell and Schindler (2003) modified the Clark and Levy (1988) model for calculating μ/G by adding empirically derived reaction distance functions for both predators and prey and found that juvenile sockeye experience daily antipredation windows of seasonally varying duration and timing.

DVM has been documented at three trophic levels of the Lake Superior pelagic community. Vertical migration of

Mysis has been observed in Lakes Superior (Bowers 1988), Michigan (Beeton 1960; Grossnickle and Morgan 1979; Janssen and Brandt 1980), and Huron (Beeton 1960). Recent work in Cayuga Lake, New York, and Lake Ontario has shown that *Mysis* vertical migration patterns are driven by diel changes in light intensity at depth (Gal et al. 1999), with the thermocline setting the upper limit of the nighttime migration (Gal et al. 2004). Hydroacoustic and trawl surveys show clear evidence of DVM among ciscoes in Lake Michigan (Eshenroder et al. 1998; TeWinkel and Fleischer 1999) and Lake Superior (Hrabik et al. 2006). Predation risk from piscivorous lake trout has been previously considered as a driver of DVM in sockeye (Stockwell and Johnson 1999; Hardiman et al. 2004), and DVM by lake trout has been observed in Lake Superior (Hrabik et al. 2006).

We consider DVM of ciscoes in light of three previously hypothesized goals of the behavior: (i) maximizing foraging or growth rate potential, (ii) minimizing predation risk, and (iii) minimizing the ratio of predation risk to growth rate potential. Predation risk is considered at both the individual and the population level. DVM patterns of lake trout are evaluated in terms of the first hypothesis, since adult lake trout are not subject to predation.

Materials and methods

Biomass fields

Depth- and time-specific costs and benefits of DVM for each trophic level were calculated for a hypothetical 0.0075 g *Mysis*, 125 g coregonid, and 675 g lake trout over a 200 m by 24 h depth-time field divided into 5 m by 20 min intervals. We consider only the pelagic fraction of each trophic level, since individuals near the bottom are difficult to distinguish using hydroacoustic methods. Biomass fields and DVM trajectories were derived from field observations of *Mysis*, ciscoes, and lake trout in Lake Superior.

Concurrent hydroacoustic and midwater trawl sampling of ciscoes and lake trout was conducted in May and August 2001 and August 2004 (Hrabik et al. 2006). Because the DVM pattern was clearest in 2004, the model is developed from data collected at that time; however, DVM trajectories of coregonids observed in 2001 are also considered. Probability density functions, which describe the depth distribution of ciscoes and lake trout by 20 min intervals, were developed by fitting cubic regression splines to the hydroacoustic data (Hrabik et al. 2006). To limit the effect of depth on DVM patterns, we used only those portions of the hydroacoustic survey track that occurred in depths of 150–250 m. Thermal profiles and secchi depths were measured during the course of the surveys and showed little inter-annual variation (Hrabik et al. 2006).

Mysis vertical migration patterns could not be evaluated using the hydroacoustic survey data because of low-level ship noise. We therefore used published data from vertical stage net tows and submersible collections in eastern Lake Superior on 26–27 July 1986 (Bowers 1988). This study collected data over three depth intervals: 0–50, 50–200, and 200–280 m. To evaluate vertical migration patterns over a 200 m depth range (the approximate average of our hydroacoustic survey), we proportionally compressed the two deeper strata to 50–150 and 150–200 m. In addition, field

Table 1. Biological and physical parameters used in the foraging and predation risk models.

Parameter	Value	Unit	Source
Biological			
Lake trout			
Weight (W_{T3})	675	g	Assumption
Swimming speed (v_{T3})	$11.7 W_{T3}^{0.05} e^{(0.0405T)} = 20-24$	m·min ⁻¹	Stewart et al. 1983
Areal density	0.000 063	individuals·m ⁻²	Hrabik et al. 2006
Coregonids			
Weight (W_{T2})	125	g	Assumption
Swimming speed (v_{T2})	$7.23 W_{T2}^{0.25} = 24 \text{ cm} \cdot \text{s}^{-1} = 14.5$	m·min ⁻¹	Rudstam et al. 1994
Areal density	0.01	individuals·m ⁻²	Hrabik et al. 2006
<i>Mysis</i>			
Length (L_{T1})	0.015	m	Johannsson 1995
Dry weight (W_{T1})	0.0075	g	Johannsson 1995
Swimming speed (v_{T1})	0.6	m·min ⁻¹	Mason and Patrick 1993
Areal density	750	individuals·m ⁻²	Bowers 1988
Physical			
Extinction coefficient (k)	0.15	m ⁻¹	Koenings and Edmundson 1991 ^a
Turbidity (τ)	0.5	NTU	Koenings and Edmundson 1991 ^a
Temperature (T)	6–10	°C	Measured
Light level at surface (I_0)	$0-5.7 \times 10^4$	lx	NSRDB 2004

^aBased on relationships between average Secchi depth (10 m) and k and turbidity for clear lakes.

observations showed a high concentration of *Mysis* in the deep scattering layer just below the thermocline during thermally stratified periods (Beeton 1960; Bowers and Grossnickle 1978; Levy 1991). This high concentration of *Mysis* could not be adequately represented using the 0–50 m net data. We therefore assumed that 70% of the *Mysis* biomass recorded by Bowers (1988) in the 0–50 m interval at night was found in the 5 m interval at the top of the hypolimnion (15–20 m), with the remaining biomass for the 0–50 m interval spread equally among the other depth bins. The sensitivity of the model results to this assumption and to potential changes in *Mysis* density is evaluated.

Foraging model

Foraging rate potential (FRP) was calculated using the general encounter rate model of Gerritsen and Strickler (1977), as applied by Mason and Patrick (1993):

$$(1) \quad \text{FRP} = \left(\frac{\pi R_{ij}^2}{3} \right) \left(\frac{3v_j^2 + v_i^2}{v_j} \right) d_i$$

where R_{ij} is the reaction distance of predator j (lake trout or ciscoes) preying on prey i (ciscoes or *Mysis*, respectively), v_j and v_i are predator and prey swimming speeds, respectively, and d_i is the depth- and time-specific prey density (depth and time subscripts are suppressed for clarity). Swimming speeds of *Mysis* and ciscoes were assumed to be constant, while swimming speed of lake trout is temperature-, and consequently depth-dependent, as defined in Table 1. FRP is a theoretical quantity based on encounter rates. It is useful for comparing foraging opportunities among different depths and times, but is not meant as an estimate of consumption.

Reaction distance

Reaction distance, or the distance at which fish show an attack response to prey, has been measured for coregonids and lake trout in laboratory feeding studies. It is important to distinguish between reaction distance and visual acuity. For piscivores, the latter may remain high at distances much greater than those that trigger a strike (Breck 1993). For ciscoes feeding on *Mysis*, we modified the parameters of the slope (β) equation of the reaction distance model developed by Wright and O'Brien (1984) for planktivorous white crappie (*Pomoxis annularis*) to fit reaction distances observed for lake herring (*Coregonus artedii*) feeding on *Limnocalanus macrurus* (2.46 mm) at light levels of 2–1500 lx (Link and Edsall 1996):

$$(2) \quad R = 1.44\beta(l - 0.2)$$

where l is the length of *Mysis* (15 mm), and β is a function of turbidity (τ) and depth- and time-specific light intensity (I):

$$(3) \quad \beta = 1.65 [1.49 + 7.86 \arctan(\log I)](1 - \tau/30 + 4.6)$$

Ciscoes are known to feed in the dark (TeWinkel and Fleischer 1999), indicating that there is a positive reaction distance even at 0 lx. Lacking laboratory studies of coregonids or similar planktivores feeding below 2 lx, this minimum reaction distance was adjusted until the daily growth rate predicted by the model was equal to the average daily growth increment predicted for a 125 g kiyi (*Coregonus kiyi*) from a von Bertalanffy growth model fit to data from Lake Michigan (Carlander 1969). The minimum reaction distance estimated using this method was 2 cm.

For lake trout feeding on ciscoes, we used the reaction distance function developed by Vögel and Beauchamp (1999):

$$(4a) \quad R = 26.84 + 2.81 I - 6.09 \ln(\tau) - 0.025 \ln(\tau)I$$

for light intensities less than the saturation intensity threshold (SIT, 17.83 lx) and

$$(4b) \quad R = 77.79 + 0.046 I - 6.09 \ln(\tau) - 0.025 \ln(\tau)I$$

for light intensities greater than SIT.

Light intensity at the surface, I_0 , was based on the average irradiance ($\text{W}\cdot\text{m}^{-2}$) recorded at Duluth, Minnesota, for August 1990 (NSRDB 2004), the most recent year for which data were available, and a conversion factor for visible light of $1 \text{ W}\cdot\text{m}^{-2}$ equals 120 lx (Lampert and Sommer 1997). All three hydroacoustic surveys were conducted under clear skies to light clouds and within 5 days of the new moon (i.e., low nighttime light). Light intensity at depth x was calculated using the Beer–Lambert equation (Hutchinson 1957):

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

where k is the extinction coefficient (m^{-1}).

Bioenergetic model

A bioenergetic model based on the framework of Kitchell et al. (1977) was used to translate depth- and time-specific estimates of FRP into growth rate potential (GRP, sensu Brandt et al. 1992). Similar approaches to mapping GRP have been used by Tyler (1998) and Roy et al. (2004). All prey encounters predicted from the FRP model were assumed to have resulted in consumption up to a species- and temperature-specific maximum consumption rate (C_{max}). The bioenergetic model used the same equations as those in Hanson et al. (1997), with parameters for ciscoes taken from the generalized coregonid model (Rudstam et al. 1994) and those for lake trout taken from Stewart et al. (1983). We refer interested readers to these two papers for details of the temperature dependency of C_{max} , respiration, specific dynamic action, egestion, and excretion. The bioenergetic model used to calculate GRP was validated by comparison with Fish Bioenergetics v. 3.0 (Hanson et al. 1997).

Predation risk model

Predation risk is difficult to quantify precisely, since, as game-theory models have shown, different assumptions about the behavioral flexibility of predators and prey can lead to substantial differences in risk (Hugie and Dill 1994). To bracket this uncertainty, we consider two separate formulations of risk that represent extremes of behavioral flexibility: one based on observed predator and prey distributions and one based on the assumption that predator DVM trajectories will track (imperfectly) changes in the DVM trajectory of the prey population. The first formulation is relevant for assessing the implications of alternative DVM trajectories for an individual prey, since it holds predator and prey distributions constant. The assumption here is that predators are unlikely to change their distribution in response to an individual prey. The second formulation assumes that the observed overlap between lake trout and coregonid DVM trajectories represents the equilibrium outcome of a game between predators and prey (Iwasa 1982) (i.e., if prey change their DVM trajectory, predators will be able to ad-

just, so that the degree of overlap remains the same). Predator and prey densities in this case are defined as the average over a 24 h day of the predator and prey densities found along the mean prey DVM trajectory. In both cases, we can define the probability of dying due to predation in a given time and depth interval as the ratio of prey consumed (d_{cons}) to total prey (d_{total}) in that interval:

$$(6) \quad \mu = d_{\text{cons}}/d_{\text{total}}$$

The number of consumed prey is defined by the depth- and time-specific FRP (up to C_{max}) for an individual predator multiplied by the observed (the individual formulation) or average (the population formulation) predator density. Similarly, the total prey in the interval is either the observed or the average prey density. For the individual formulation, eq. 6 is not defined for intervals in which no prey were observed. Therefore, for these intervals, we follow Mason and Patrick (1993) and define μ based on the encounter rate with predators using eq. 1, with the substitution of predator density for prey density, d_i . Equation 1 gives an encounter rate (i.e., the expected number of predators encountered per unit of time). Predation risk, however, is defined as the probability of encountering any predator (again, we assume that all encounters result in consumption). If we assume that the encounter rate estimated using eq. 1 represents the mean of a Poisson distribution (appropriate for unbounded count data), this distribution can be used to calculate the probability of encountering one or more predators.

Balancing predation risk and growth rate potential

The trade-off hypothesis was evaluated by calculating the risk ratio (μ/G) based on DVM trajectories through the depth–time fields for μ and GRP according to the following formula:

$$(7) \quad \frac{\mu}{G} = \frac{1 - \left[\prod_{t=1}^{72} (1 - \mu_t) \right]^{T_{\text{max}}}}{\left(\sum_{t=1}^{72} \text{GRP}_t \right) T_{\text{max}}}$$

where μ_t and GRP_t are, respectively, the probability of dying due to predation and the GRP for the 20 min time interval t (there are 72 of these time intervals in a 24 h day), and T_{max} is the number of days over which μ/G is calculated. The risk ratio was calculated for 1-day and 100-day intervals to demonstrate how diel patterns in μ/G may vary depending on the time horizon.

We performed an individual parameter perturbation analysis (Bartell et al. 1986) on the parameters in Table 1, the minimum reaction distances of ciscoes and lake trout, and the vertical distribution of *Mysis*. Each parameter was increased and decreased by 20%, and the model was rerun with the new parameter value. Critical threshold densities of *Mysis* (i.e., the point at which qualitative changes occurred in the pattern of FRP, GRP, risk, and the risk ratio) were estimated.

Fig. 1. Volumetric densities (individuals·m⁻³) of *Mysis relicta* (a), ciscoes (*Coregonus* spp.) (b), and lake trout (*Salvelinus namaycush*) (c) by depth and time of day. Broken lines in panels (a) and (b) show the diel vertical migration of ciscoes and lake trout, respectively, in 2004. Data for *Mysis* are from Bowers (1988). Data for ciscoes and lake trout are from Hrabik et al. (2006).

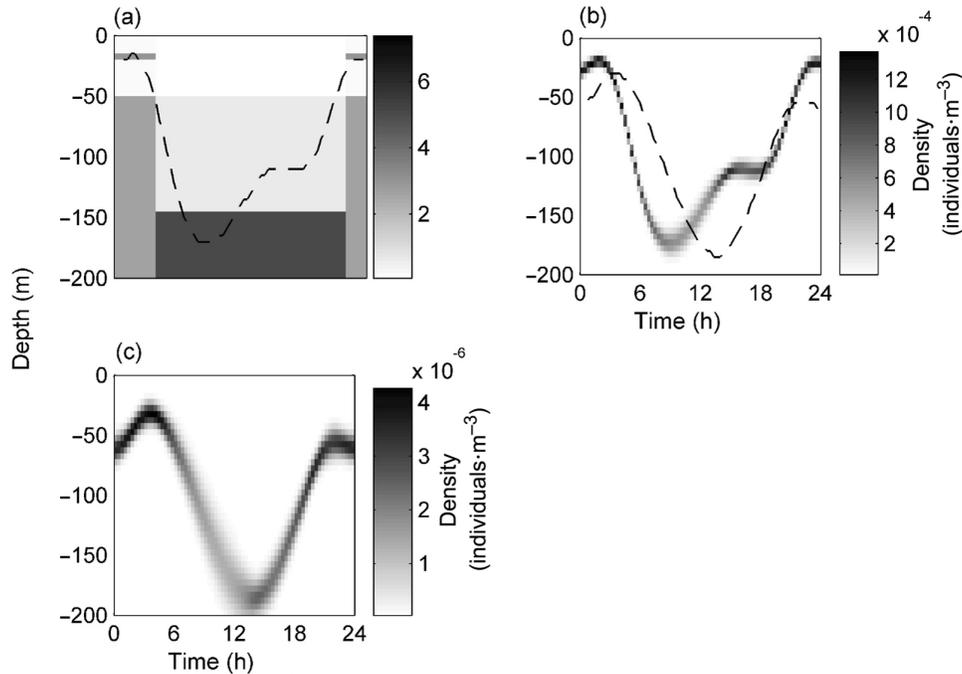
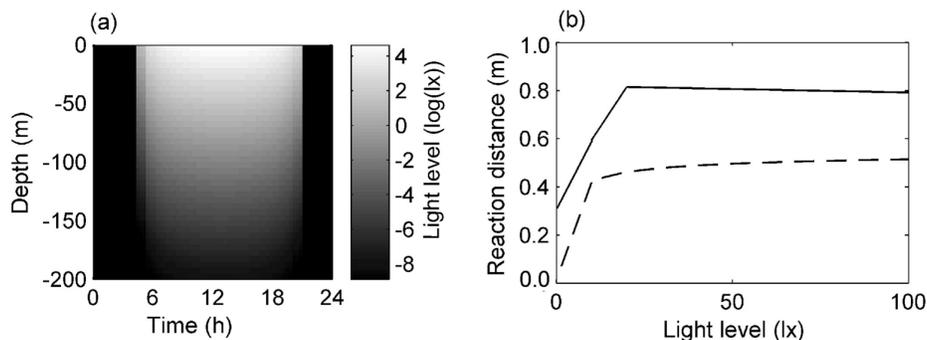


Fig. 2. Light level (log (lx)) by depth and time of day (a) based on surface light data recorded at Duluth, Minnesota, in August 1990 (NSRDB 2004) and reaction distance of ciscoes (*Coregonus* spp., broken line) and lake trout (*Salvelinus namaycush*, solid line) as a function of light level (b). The reaction distance function for ciscoes is based on experiments by Link and Edsall (1996). The function for lake trout is based on a study by Vogel and Beauchamp (1999).



Results

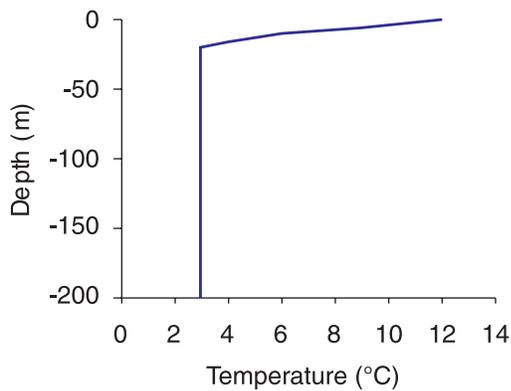
Biomass fields

The biomass fields of all three trophic levels (Figs. 1a–1c) show distinct DVM behavior. The vertical net tow data from Bowers (1988) show that *Mysis* occur throughout the water column, with highest densities found at the thermocline–hypolimnion interface at night and in the deepest stratum during the day. Volumetric densities of *Mysis* from Bowers (1988) varied from 0.16 individuals·m⁻³ in the 0–50 m stratum during the day to 7.4 individuals·m⁻³ in the 150–200 m stratum during the day. Biomass fields of ciscoes and lake trout show fish density concentrated within only a few depth bins at any given time interval. Volumetric densities of ciscoes and lake trout ranged from 0 to 1.4 × 10⁻³ individuals·m⁻³ and 0 to 4.3 × 10⁻⁶ individuals·m⁻³, respectively.

Foraging and growth rate potential

FRP for ciscoes and lake trout varied over time and depth because of the distribution of prey and because of differences in light intensity (Fig. 2a), which affects reaction distance (Fig. 2b), and temperature (Fig. 3), which affects lake trout swimming speed. The FRP field for ciscoes was dominated by light intensity and *Mysis* density (Fig. 4a). At night, FRP for ciscoes was greatest in the dense *Mysis* layer below the thermocline. During the day, highest FRP for ciscoes occurred at 50–80 m. Lowest FRP for ciscoes occurred in the unlit portions of the 0–50 m stratum, including the intervals just before sunrise and just after sunset. FRP in these areas was 0.06 *Mysis* consumed per 20 min time interval compared with a maximum FRP of 198 *Mysis* consumed at midday at 50 m. At this higher FRP, the maximum daily ration for a 125 g coregonid at 3 °C (1.25 g dry weight or 167

Fig. 3. Temperature (°C) profile from August 2004 taken in the western arm of Lake Superior.



Mysis) could be consumed in less than 20 min. The daily FRP of a coregonid following the mean observed DVM trajectory for 2004 (white line in Fig. 4a) is ~60 *Mysis*.

FRP for lake trout (Fig. 4b) closely mirrors the distribution of ciscoes, since ciscoes generally remained in the dark. The maximum FRP for lake trout was approximately 0.15 ciscoes consumed in a 20 min time interval, compared with a maximum daily ration of 18.5 g (or equivalently one 125 g coregonid·week⁻¹) for a 675 g lake trout at 3 °C. The daily FRP of a lake trout following the mean observed DVM trajectory for 2004 (white line in Fig. 4b) is 0.64 ciscoes.

GRP for ciscoes (Fig. 4c) is strikingly different than FRP, with GRP patterns dominated by temperature. The region of highest GRP for ciscoes occurs in the warm, well-lit waters above the thermocline during the day. Regions of positive GRP for ciscoes occurred in daytime from the surface to depths of approximately 70–90 m, below which light intensity is extremely low. Positive daytime GRP resumed below 150 m because of increased *Mysis* density. At night, positive GRP for ciscoes occurred at depths >50 m and in the depth interval just below the thermocline (15–20 m). The region of highest FRP, from 50–80 m during the day, does not exhibit particularly high GRP because the high FRP in this region exceeds the maximum daily ration for a 125 g coregonid at 3 °C. Daily GRP of a coregonid following the mean observed DVM trajectory is 0.13 g.

GRP of lake trout (Fig. 4d) is dominated by the distribution of ciscoes, but a temperature effect is apparent as well above the thermocline. The peaks seen in the FRP field are flattened in the GRP field because many of the FRP peaks correspond to foraging rates greater than the maximum daily ration. Daily GRP of a lake trout following the mean observed DVM trajectory is 0.75 g.

Predation risk and the risk vs. growth trade-off

The individual risk field (Fig. 5a) for ciscoes closely matches the distribution of lake trout. Highest individual risk occurs in depth–time bins in which lake trout are most concentrated. By definition, there is zero individual risk in bins containing no lake trout. The lower individual risk in places where ciscoes and lake trout overlap reflects the reduction in individual risk associated with being one of many individuals in a large group. The population risk field (Fig. 5b), which assumes that lake trout would be able to track

changes in the coregonid DVM trajectory, reflects differences in light intensity and temperature. Dark regions (i.e., at night or at depths below the depth of light penetration during the day) below the thermocline all show equal and low population risk. Highest population risk occurs in the surface layer during the day. Population risk in this region is ~28 times greater than that in dark regions below the thermocline.

The ratio of individual risk to GRP for ciscoes calculated over 1 day (Fig. 6a) reflects the distribution of lake trout as well as the location of depth–time bins in which GRP is negative. Population risk to GRP calculated over 1 day (Fig. 6b) is minimized at night in the high *Mysis* density layer below the thermocline. During the day, two alternative zones show approximately equal population risk to GRP: (i) a crescent of low light (approximately 0.2–1 lx) that extends from the surface at dusk and (ii) the region from 150 to 200 m. Two regions of high population risk to GRP are evident: one in the shallowest depth bin during full daylight and one occurring in a semicircle above the low-light crescent. Risk becomes relatively more important when individual risk to GRP is calculated over a period of 100 days (Fig. 6c). When population risk/GRP is calculated over 100 days (Fig. 6d), there is a reversal in the high risk, high growth area near the surface during the day, which now becomes a minimum for the risk/GRP ratio.

Sensitivity analysis

Changes in swimming speed and prey density generally had a proportional effect on FRP (i.e., a 20% increase in either variable yielded a 20% increase in FRP), since encounter rate is a product of these variables and search area. The exception was the swimming speed of prey, which had very little effect. For example, a 20% change in swimming speed of ciscoes resulted in only a 10% change in FRP of lake trout. The swimming speed of *Mysis* had virtually no effect on FRP of ciscoes. The effect of swimming speed and prey density on GRP, risk, and the risk ratio was less pronounced than the effect on FRP, and in depths–times where FRP exceeded the maximum consumption rate, there was no effect. The assumed weight of prey had a proportional effect on consumption (by weight) of predators and a smaller effect on GRP, risk, and the risk ratio. An independent 20% perturbation in the length of *Mysis* (used in the reaction distance model for ciscoes) resulted in ~40% change in the maximum FRP of ciscoes, but no change in the FRP experienced by ciscoes along the mean DVM trajectory in 2004, since this trajectory was largely in the dark where reaction distance was set by the minimum reaction distance. The perturbation in *Mysis* length had a much smaller effect on GRP and the risk ratio, since the maximum FRP greatly exceeded the maximum consumption rate.

Perturbations to the light parameters (k , τ , I_0) resulted in vertical shifts in the daytime portions of the depth–time field for FRP. For example, a 20% decrease in k (the most sensitive of the light parameters) extended the region of maximum daytime FRP for ciscoes from 50–80 to 50–100 m because of increased light penetration. Maximum values of FRP for ciscoes (i.e., at 50 m at noon) increased by 28%. Smaller changes in FRP were observed at other depths and

Fig. 4. Foraging rate potential (FRP, individuals encountered·day⁻¹) of ciscoes (*Coregonus* spp.) (a) and lake trout (*Salvelinus namaycush*) (b) and growth rate potential (GRP, g·day⁻¹) of ciscoes (c) and lake trout (d) by depth and time of day. White lines represent the mean diel vertical migration trajectories of ciscoes (a, c) and lake trout (b, d) in 2004.

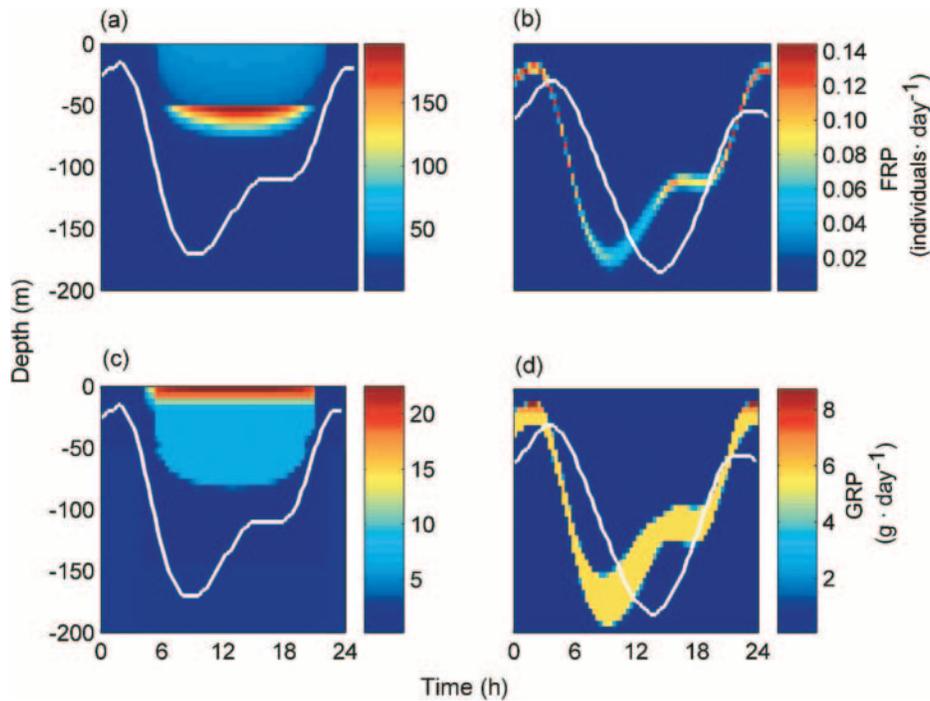
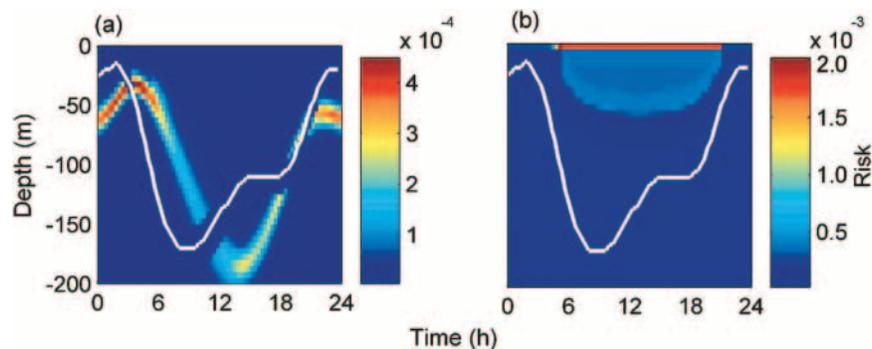


Fig. 5. Individual (a) and population (b) predation risk for ciscoes (*Coregonus* spp.) by depth and time. White lines represent the mean diel vertical migration trajectory of ciscoes in 2004.



times. Changes in GRP, risk, and the risk ratio were less extreme. For example, the 20% decrease in k resulted in an 8% increase in μ for ciscoes at 50 m at noon.

Values of FRP for ciscoes and lake trout were sensitive to the minimum reaction distance. A 20% change in reaction distance resulted in a 40% change in FRP in the dark and lesser changes in the light.

The relatively high FRP and GRP for ciscoes just below the thermocline at night depended on the existence of a high-density *Mysis* layer. Such a layer has been frequently observed (Beeton 1960; Bowers and Grossnickle 1978; Levy 1991), but could not be quantitatively estimated from the available data on *Mysis* vertical distribution. If less than 62% of the *Mysis* observed by Bowers (1988) in the 0–50 m layer at night occurred in the depth bin just below the thermocline, higher FRP would be found below 50 m at night. During the day, the presence of highest FRP in the 50–80 m layer was based on modest densities of *Mysis* (0.94 individuals·m⁻³) at

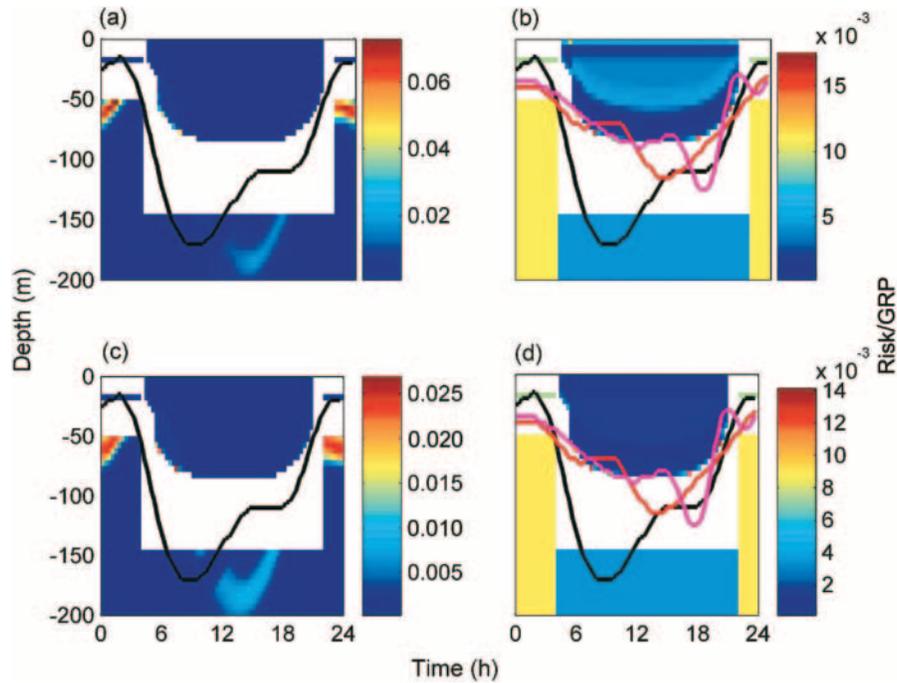
these depths. These densities would need to be lower than 0.013 individuals·m⁻³ for higher FRP during the day to be found in deeper water.

Discussion

Do coregonids undergo vertical migration to increase foraging and growth or to reduce predation risk?

Previous consideration of coregonid vertical migration has focused on the potential foraging and growth benefits of migrating along with *Mysis*. Eshenroder and Burnham-Curtis (1999) suggested that vertical migration in deepwater ciscoes might have evolved in response to the vertical migration of *Mysis*. TeWinkel and Fleischer (1999) debated whether *Mysis* were driving the vertical migration, but noted that vertically migrating bloater (*Coregonus hoyi*) in Lake Michigan had a higher percentage of stomachs containing

Fig. 6. The ratio of predation risk to growth rate potential (GRP) for ciscoes (*Coregonus* spp.) by depth and time of day calculated over a time period of 1 day using individual (a) and population (b) risk formulas and calculated over 100 days using individual (c) and population (d) risk formulas. Depth–time bins in which GRP was less than $0.25 \text{ g}\cdot\text{day}^{-1}$ are unshaded. Lines represent the mean diel vertical migration trajectories of ciscoes in May and August 2001 (magenta and red, respectively) and August 2004 (black).



recently ingested prey than did bloater that remained on the bottom.

Our results offer little support for the hypothesis that a deep vertical migration confers a foraging or growth rate benefit for ciscoes. Higher foraging rates and GRP could be achieved through any number of alternative trajectories. At night, the maximum foraging rate and growth rate are found in the depth bin just below the thermocline, and DVM trajectories of ciscoes from all three time periods pass through or near this interval. During the day, however, substantially higher foraging rates and GRP can be found at depths with higher light levels, even though *Mysis* densities are dramatically lower at such depths. This is because even relatively low light levels increase the reaction distance of ciscoes, allowing them to search much larger volumes of water. Since all three observed DVM trajectories for ciscoes remain in low light and below the thermocline, they do not seem to be taking advantage of foraging opportunities available in higher light environments or more favorable temperatures for growth available near the surface. There are, of course, aspects of foraging behavior that are not captured by the model. For example, *Mysis* suspended in the water column may also be more visible to ciscoes from below if they are silhouetted against the surface. Other less understood aspects of visual predation such as polarization contrast (Sabbah and Shashar 2006) or near-ultraviolet light (Loew et al. 1993) may also be important.

Reducing predation risk is a more compelling explanation for the observed vertical migration of ciscoes, but is still incomplete. From the point of view of the individual, following the DVM trajectory chosen by the bulk of conspecifics results in lower individual risk; however, this observation begs the question: why does the group follow a particular

DVM trajectory? The observed DVM trajectories of ciscoes kept them at low light levels, but not in complete darkness, throughout the day. A risk-minimizing population would stay entirely below the thermocline and below the depth of light penetration. This situation is approached by the deep DVM trajectory observed in 2004; however, all hypothetical DVM trajectories that avoid light and avoid the warmer epilimnion result in equally low risk.

The risk ratio based on population risk offers the best evidence for the benefit of a vertical migration. Two alternative minimum μ/G DVM trajectories are apparent. These trajectories overlap in the layer below the thermocline at night. During the day, the shallow trajectory follows a crescent that begins at the surface at dawn, moves progressively deeper during the day down to 80 m at noon, and ascends to near the surface at dusk. The deep trajectory descends from the layer below the thermocline into the 150–200 m stratum during the day. Both of these minimum μ/G trajectories are apparent in the risk ratio calculated over 1 and 100 days. The DVM trajectories observed in 2001 appear to follow the shallow (high risk, high growth) minimum μ/G trajectory. For 2004, when local lake trout densities were higher and coregonid densities were lower (Hrabik et al. 2006), the DVM trajectory is substantially deeper and appears to follow the deep (low risk, low growth) trajectory. This comparison assumes similar vertical distribution of light intensity and *Mysis* in 2001 and 2004.

Time-dependency of the risk ratio

Substantial differences in the μ/G patterns were apparent when these values were calculated over 100 days rather than 1 day. Werner and Gilliam (1984) proposed the ratio of risk to growth as a fitness-optimizing criterion for the timing of

ontogenetic habitat shifts. Clark and Levy (1988) and Scheuerell and Schindler (2003) used the same criterion to understand trade-offs in juvenile sockeye vertical migration. Both growth and predation risk in Werner and Gilliam's (1984) example were instantaneous rates. In Scheuerell and Schindler's (2003) analysis and in the analysis presented here, growth and predation risk are modeled as discrete time functions, with the result that the value of μ/G depends on the time interval chosen, since survival probability is an exponential function of time, while over limited time periods, growth is approximately linear (Fig. 7; and see eq. 7 above). At very low or very high risk levels, the rate of increase in risk is low, and increases in growth dominate the equation. The opposite condition prevails at intermediate risk levels, where risk rises rapidly with time. Additionally, neither growth nor risk should be extrapolated indefinitely based on daily rates, as seasonal and ontogenetic changes in vital rates are likely. Figures 6b and 6d highlight a limitation of the risk ratio when extrapolated into the future. The shallow depth intervals in the daytime show relatively high μ/G when calculated for a single day, but low μ/G for the 100-day period. This result occurs because risk (the probability of predation mortality over the time period) reaches a maximum of one, while growth continues to accrue. Such time-dependency of μ/G must be considered when using discrete time calculations. The presence of size-dependent mortality bottlenecks (not considered here), such as winter periods when smaller individuals are likely to starve, will also influence the risk ratio (Schindler 1999).

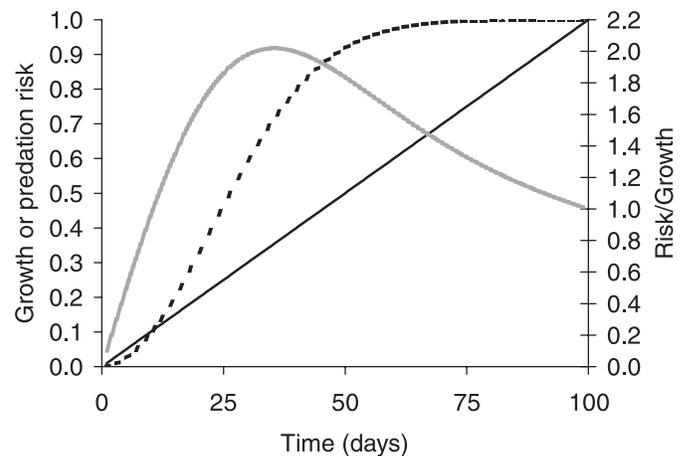
Foraging and growth maximization by lake trout

In sharp contrast with ciscoes, lake trout appear to be following a DVM trajectory that offers substantial foraging and growth benefits. In Lake Superior, lake trout achieve high GRP not by seeking optimal temperatures, but by tracking the DVM trajectory of their coregonid prey. The fact that lake trout apparently do not follow a DVM trajectory that perfectly maximizes their GRP is not surprising considering that (i) ciscoes have likely evolved predator avoidance strategies and (ii) lake trout have limited sensory information regarding the location of their prey. Avoidance behavior by coregonids has been evaluated by Savitz and Bardygala (1989), who estimated that 60% of coregonid encounters with piscivores result in escape. This rate is undoubtedly sensitive to environmental conditions at the time of encounter, including the respective reaction distances of predator and prey (discussed below). Assuming a 40% capture efficiency, however, would lower the daily FRP of lake trout following the mean DVM trajectory from 0.64 to 0.26 ciscoes-day⁻¹, a value that is closer to the maximum consumption rate at 3 °C of one 125 g coregonid-week⁻¹. Previous applications of foraging models (e.g., Beauchamp et al. 1999) have also predicted that piscivores should encounter more than enough prey to satisfy observed growth and consumption. These results highlight the importance of understanding predator-prey interactions at fine temporal and spatial scales (Walters and Juanes 1993; Scheuerell 2004).

Changing trade-offs under changing conditions

The DVM patterns presented here represent a snapshot in space and time. Although all three components of this pe-

Fig. 7. Predation risk (probability of dying due to predation during the given time period, broken black line), growth (solid black line), and risk/growth (solid gray line) as a function of time (days), assuming a daily predation risk of 0.001 and a daily growth rate of 0.01.

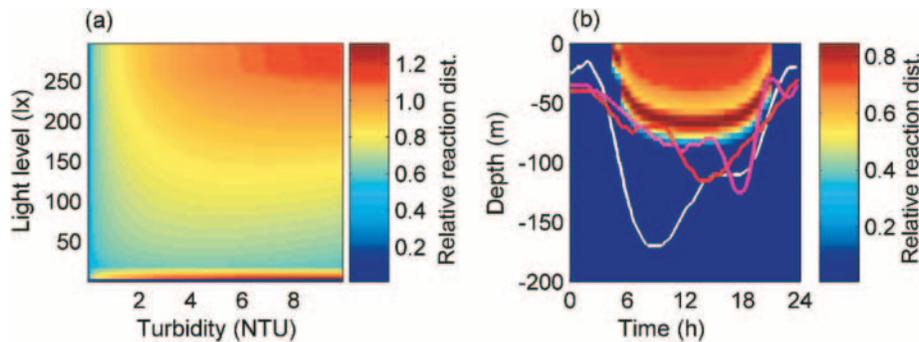


logic food chain have been shown to exhibit DVM in other times and places, the specific trajectories can differ substantially. For example, in 2001, ciscoes in the western arm of Lake Superior exhibited a much shallower and more variable DVM trajectory, with many individuals present in the 15–40 m depth range (Hrabik et al. 2006), well above the depth at which reaction distance of lake trout reaches a minimum. The model results suggest that ciscoes at this depth during the daytime experience high foraging rates, but also high risk. GRP is high above the thermocline and modest below it, because foraging rates that exceed the maximum daily ration are available at many depths. The risk ratio shows a crescent-shaped region of optimal conditions, discussed above, that occurs in deeper water.

Why are ciscoes in 2001 using this high-risk, high-growth region rather than remaining in the relative safety of deeper water? The explanation may lie in the lower lake trout and higher coregonid densities in 2001 compared with 2004. The ratio of ciscoes to lake trout in the survey area in May and August 2001 was 1008 and 2940, respectively, while in August 2004 it was down to 163 (Hrabik et al. 2006). It appears that lower lake trout densities and higher densities of ciscoes in 2001 resulted in reduced predation risk per individual cisco, allowing ciscoes to take advantage of foraging and growth opportunities at shallower depths during the day. Density-dependent changes in risk-taking behavior (Walters and Juanes 1993) may also play a role if the lower coregonid densities in 2004 (70% and 62% lower compared with May and August 2001, respectively) resulted in less competition for food. The lack of data on *Mysis* densities for these two time periods unfortunately precludes a definitive test of this hypothesis.

The observed change in DVM behavior associated with a 7- to 18-fold decline in the coregonid to lake trout ratio suggests the possibility of a behavioral cascade (Romare and Hansson 2003). Predator-induced changes in DVM behavior have already been observed in the field for marine copepods (Frost and Bollens 1992) and *Daphnia* (Stirling et al. 1990). Cascading changes in DVM behavior could have potentially

Fig. 8. Relative reaction distance (i.e., the ratio of the reaction distance of ciscoes (*Coregonus* spp.) to that of lake trout (*Salvelinus namaycush*)) as a function of light level (I_x) and turbidity (nephelometric turbidity units, NTU) (a) and over depth and time of day (b). Lines in panel (b) represent the diel vertical migration trajectory of ciscoes in May and August 2001 (magenta and red, respectively) and August 2004 (white).



important practical and ecological consequences. For example, the two most common fishery-independent survey techniques, trawling and gill nets, target specific depths. If the vertical distribution of lake trout or coregonids changes with abundance, the catchability coefficient for these survey techniques will also change. Such changes have potentially dangerous implications for stock assessment, since they result in a violation of the assumption that catch per unit of effort is proportional to stock size. If ciscoes increasingly engage in risk avoidance behavior as the coregonid to lake trout ratio declines, then the predation rate will decline faster than simple “reaction vat” or Lotka–Volterra models suggest. This is one of the fundamental predictions of arena foraging theory (Walters and Juanes 1993). The potential for behavioral cascades in DVM behavior suggests that future studies of DVM should be broadened to include as many trophic levels as possible.

Large changes in turbidity are also likely to have an effect on the costs and benefits of different DVM trajectories. Increased turbidity results in greater light attenuation and therefore lower light intensity at depth, a result that would compress the region of highest FRP and highest risk into shallower depths. Experimental evidence, however, suggests that turbidity is likely to effect planktivores and piscivores differently. De Robertis et al. (2003) showed that feeding rates of piscivorous sablefish (*Anoplopoma fimbria*) were substantially reduced at turbidity levels that did not hamper feeding by planktivorous juvenile chum salmon (*Oncorhynchus keta*) and walleye pollock (*Theragra chalcogramma*). This result is consistent with the reaction distance models used here for lake trout and ciscoes. The relative reaction distance (i.e., the ratio of the reaction distance of ciscoes to that of lake trout) increases with turbidity, particularly at high light levels (Fig. 8a). The maximum relative reaction distance occurs at very low light intensity, but not in complete darkness when turbidity is low; however, at high turbidity, a second maximum appears at high light levels. Mapped across depth and time (Fig. 8b) at the low turbidities observed in the study area, the region of maximum relative reaction distance occurs in a crescent that is roughly coincident with the crescents seen in the illustration of risk/growth (Figs. 6b, 6d). At higher turbidities, such as those found on the south shore of the western arm of Lake Superior, the maximum relative reaction distance would

occur at shallower depths during the day. This model prediction is consistent with observations that planktivorous rainbow smelt (*Osmerus mordax*) and larval lake herring are found nearer to the surface in high turbidity areas of the south shore of the western arm (Swenson 1978). Secchi disk casts conducted during the survey indicate low turbidity in the survey area and little difference in water clarity between 2001 and 2004 (Hrabik et al. 2006).

Model assumptions and sensitivity

The model assumptions of no predator avoidance ability and no silhouetting effect for prey viewed from below are discussed above. The limitations that the lack of *Mysis* data imposes on the interannual comparison are also stated. Two remaining assumptions deserve mention. First, fine-scale patchiness is not included in the model but is potentially important for calculations of μ . *Mysis* distributions were based on vertical net tows that integrate densities over wide depth intervals. The echo integration analysis (Hrabik et al. 2006) also precludes estimation of fine-scale patchiness of ciscoes. Patchiness of prey could increase foraging rates if patches were easier to locate than individual prey, but would otherwise make foraging rates more variable. Patchiness of predators would reduce μ , since risk is defined not by the number of encounters with predators, but by the probability of encountering any predators. If the patchiness of predators was known, its effect could be included in the model by adding an overdispersion parameter to the Poisson distribution used to calculate risk.

Reaction distances of lake trout and ciscoes are the most influential parameters in this model. Fortunately, feeding experiments have described the effect of a wide range of light intensities on reaction distance for both species. The experiments used to develop the reaction distance function for lake trout were conducted using a nested tank design in which prey were held in a small tank inside the larger experimental tank (Vogel and Beauchamp 1999). This design was used to eliminate all but visual stimuli. At short distances and in low light conditions, however, other sensory modes may increase the minimum reaction distance beyond what would be expected based on strictly visual experiments. Lake trout are known to be capable of feeding in near total darkness (Mazur and Beauchamp 2003), indicating that the minimum reaction distance is greater than zero and that nonvisual

stimuli may be important at night or at depths below the limits of light penetration.

In conclusion, understanding the drivers of DVM requires a quantitative framework that allows foraging, growth, predation risk, and risk/growth trade-offs to be evaluated simultaneously for multiple trophic levels. Previous hypotheses concerning DVM in coregonids have focused on the putative foraging benefits of tracking vertically migrating *Mysis*. The model presented here indicates that predation risk is also an important factor and that a migration by ciscoes into deeper water during the day results in a more favorable trade-off between risk and growth and a greater relative reaction distance compared with lake trout. Lake trout feeding on ciscoes can generally achieve higher foraging and growth rates by tracking their vertically migrating prey. Such growth benefits suggest that the siscowet (*Salvelinus namaycush siscowet*) morphotype, with its high fat content and reduced swim bladder, may indeed be an evolutionary response to the vertical migration behavior exhibited by their coregonid prey, as suggested by Eshenroder and Burnham-Curtis (1999).

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