

Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores

David A. Beauchamp, Casey M. Baldwin, Jason L. Vogel, and Chad P. Gubala

Abstract: We developed a visual foraging model for piscivores that predicts search volume as a function of light and turbidity. We combined this model with diel hydroacoustic measurements of depth-specific prey fish densities during summer stratification in Lake Tahoe, Lake Washington, and Strawberry Reservoir to examine differences in diel, depth-specific visual encounter rates of prey. These study sites were selected to represent gradients of increasing limnetic prey fish density and declining transparency. The model predicted over a 30-fold difference in maximum depth-specific diel encounter rates among the three lakes. Lake Washington, which was characterized by intermediate transparency and moderate limnetic prey density, had the highest predicted prey encounter rates. The pattern of prey encounter rates among the three lakes was similar to the proportional contribution of limnetic prey fishes observed in the diet of piscivores from these waters. This approach may be used to construct temporally and spatially explicit trophic interaction models for examining mechanisms underlying predator and prey distributions or to predict the response of existing or introduced predators to changing environmental conditions, prey abundance, or distribution.

Résumé : Nous avons élaboré un modèle de recherche visuelle de nourriture pour les piscivores qui prévoit que le volume de recherche est fonction de la lumière et de la turbidité. Nous avons combiné ce modèle avec des mesures hydroacoustiques nyctémérales des densités de poissons proies à des profondeurs spécifiques durant la période de stratification estivale dans le lac Tahoe, le lac Washington et le réservoir Strawberry pour étudier les différences dans les taux nyctéméraux de rencontre visuelle de proies à des profondeurs spécifiques. Nous avons choisi ces sites d'étude parce qu'ils présentaient un gradient croissant de densité des poissons proies limnétiques et un gradient décroissant de transparence. Le modèle a prévu une différence d'un facteur de plus de 30 dans les taux maximaux de rencontre nyctémérale aux profondeurs spécifiques entre les trois lacs. C'est dans le lac Washington, caractérisé par une transparence intermédiaire et une densité modérée de proies limnétiques, que le modèle a prévu le plus haut taux de rencontre de proies. Le profil des taux de rencontre de proies parmi les trois lacs reflétait la contribution proportionnelle des poissons proies limnétiques observée dans le régime alimentaire des piscivores de ces eaux. Cette approche peut être utilisée pour construire des modèles d'interaction trophique temporellement et spatialement explicites permettant d'examiner les mécanismes qui régissent les distributions de prédateurs et de proies ou de prévoir la réponse des prédateurs en place ou introduits au changement dans les conditions environnementales et dans l'abondance ou la distribution des proies.

[Traduit par la Rédaction]

Introduction

In lakes and reservoirs, large pelagic piscivores are typically the target of recreational fisheries and are often manipulated through introductions to new waters, supplementary stocking, and regulated harvest. The influence of these top

predators on the structure and function of aquatic communities has been recognized for over a decade (e.g., Carpenter et al. 1985; Northcote 1988). However, the mechanisms that determine the magnitude of top-down control in systems of varying environmental characteristics, basin morphometries, and trophic status are less well understood. Given the uncer-

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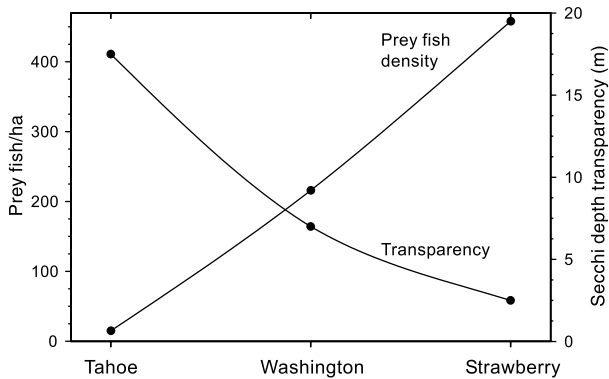
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Fig. 1. Ultraoligotrophic Lake Tahoe, mesooligotrophic Lake Washington, and mesoeutrophic Strawberry Reservoir represent a gradient of increasing productivity illustrated by increasing prey fish density and declining transparency. Fish densities were estimated from hydroacoustic surveys in Lake Tahoe (August 1993), Lake Washington (July 1992), and Strawberry Reservoir (June 1996). Secchi disk transparencies represent average values during summer stratification.



tainty about community-level responses to these frequent manipulations of piscivores, we need to develop tools for predicting responses to these changes to enable careful evaluation of potential impacts from proposed manipulations before irreversible actions are taken.

The distribution and behavior of predators and prey in limnetic communities are largely determined by vertical or horizontal gradients of biotic and abiotic factors (e.g., light, transparency, temperature, water chemistry). Brandt et al. (1992) described a spatially explicit model that integrated the effects of environmental conditions and food supply to estimate the volume of different habitat zones offering specific growth potentials for predators during different seasons. A visual foraging model converted prey biomass and density into a daily ration size using a simple, static prey encounter rate model. Daily ration was then converted to growth rate potential of the predator using a bioenergetics model (Hewett and Johnson 1992). For simplicity, the initial foraging model in Brandt et al. (1992) estimated prey encounters assuming a constant search volume, independent of the change in optical qualities of the waters by depth or diel period. Mason and Patrick (1993) elaborated on this approach by explicitly modeling temporal and depth-specific changes in search volume for planktivorous alewife (*Alosa pseudoharengus*). Piscivory in pelagic waters often occurs during crepuscular periods (Beauchamp 1990; Beauchamp et al. 1992) when prey distributions and light intensity are dynamic functions of depth and time (Clark and Levy 1988; Luecke and Wurtsbaugh 1993; Appenzeller and Leggett 1995). As light intensity decreases at dusk, piscivores react to prey at rapidly declining distances (reaction distance); this pattern is reversed at dawn. Thus, prey densities and search volumes can change simultaneously in complex patterns that result in dynamic probabilities of encounter. By modeling prey encounters at appropriate temporal and spatial scales, we should gain new insights regarding the ability of pelagic piscivores to influence the behavior and population dynamics of lower trophic levels in different limnetic communities.

However, for a model to be a useful management tool, inputs should be minimal and their acquisition timely and affordable. The model proposed here requires information on water transparency and diel distributions of limnetic predators and prey.

Hydroacoustic measurement of temporal, spatial, and size-specific prey fish densities enables an assessment of diel prey availability patterns (Brandt 1996) experienced by piscivores, based on the predator's depth and foraging path in the water column. By linking a visual foraging model with diel prey distribution patterns, we can estimate diel changes in encounter rates by predators for various prey. By comparing encounter rates at different prey densities, or between prey species, or under different conditions of light and transparency, we can predict which species, or which life stage of a species, is most vulnerable to predation and under what conditions we might expect piscivores to switch to alternative prey. This approach can therefore make predictions about the effect of predation among or within systems representing a wide range of environmental conditions and prey densities.

The purpose of this paper was to briefly summarize the visual encounter rate model and then describe its application for estimating depth-specific diel prey encounters in Lake Tahoe (California–Nevada, U.S.A.), Lake Washington (Washington State, U.S.A.), and Strawberry Reservoir (Utah, U.S.A.). These waters represent opposing gradients of increasing limnetic prey fish densities and declining transparencies (Fig. 1); therefore, application of the model to these waters serves to demonstrate how foraging opportunities of piscivores, and conversely, predation risk to prey fishes, vary among waters across a representative range of prey densities and transparencies. The piscivore–prey assemblages examined in this study were lake trout (*Salvelinus namaycush*) foraging on kokanee (*Oncorhynchus nerka*) in Lake Tahoe, rainbow (*Oncorhynchus mykiss*) and cutthroat trout (*Oncorhynchus clarki*) foraging on juvenile sockeye salmon (*O. nerka*) and longfin smelt (*Spirinchus thaleichthys*) in Lake Washington, and cutthroat trout foraging on juvenile cutthroat trout and kokanee in Strawberry Reservoir.

Methods

Visual foraging rate model

We modeled prey encounter rates $ER_{z,t}$ (prey per hour at depth z and diel time period t) as the product of spatially and temporally explicit search volumes $SV_{z,t}$ and the vertical density distribution of prey fishes $PD_{z,t}$:

$$(1) \quad ER_{z,t} = SV_{z,t} PD_{z,t}.$$

Search volume varied with diel changes in piscivore swimming speeds SS_t (centimetres per second) (Henderson and Northcote 1985; Warner and Quinn 1995) (Table 1) and reaction distances $RD_{z,t}$ (centimetres) to prey in response to diel shifts in the photic environment:

$$(2) \quad SV_{z,t} = \pi RD_{z,t}^2 SS_t.$$

Swimming speeds (body lengths per second) were computed from the laboratory data of Henderson and Northcote (1985) for cutthroat trout and Dolly Varden (*Salvelinus malma*) and from in situ telemetry data from rainbow trout in Lake Washington (Warner and Quinn 1995) and cutthroat trout in Strawberry Reservoir

Table 1. Diel swimming speeds, as a percentage of fork length (FL), applied to piscivores in Lake Tahoe (50-cm lake trout), Lake Washington (42-cm rainbow trout and cutthroat trout), and Strawberry Reservoir (42-cm cutthroat trout).

Piscivore	Day		Crepuscular		Night	
	Mean	SD	Mean	SD	Mean	SD
Lake trout (50 cm) ^a						
% FL/s	59	0	47	14	8	—
cm/s	29.5	0.0	23.5	7.0	4.0	—
Rainbow trout (42 cm) ^b						
% FL/s	41	24	39	29	20	19
cm/s	17.2	10.1	16.4	12.2	8.4	8.0
Cutthroat trout (42 cm) ^c						
% FL/s	79	51	29	16	38	21
cm/s	33.2	21.4	12.2	6.7	16.0	8.8
Cutthroat trout (42 cm) ^d						
% FL/s	78	1	26	32	0	—
cm/s	32.8	0.4	10.9	13.4	0.0	—

Note: Dolly Varden data from Henderson and Northcote (1985) were applied to lake trout in Lake Tahoe. Cutthroat trout data from Henderson and Northcote (1985) are presented for comparison with the estimates derived from in situ telemetry data from cutthroat trout in Strawberry Reservoir.

^aHenderson and Northcote (1985) data on Dolly Varden.

^bWarner and Quinn (1995).

^cC.M. Baldwin (unpublished data).

^dHenderson and Northcote (1985).

(C. Baldwin, unpublished data) (Table 1). Although telemetry-based estimates of swimming speed are generally assumed to underestimate actual swimming speeds, the laboratory and telemetry-based estimates for diel swimming speeds by cutthroat trout were similar (Table 1). Diel swimming speeds were applied to piscivorous (mean fork length = 42 cm in June–July) cutthroat trout and rainbow trout in Lake Washington and Strawberry Reservoir. Diel swimming speeds for Dolly Varden (Henderson and Northcote 1985) were applied to lake trout (mean fork length = 50 cm) in Lake Tahoe (Table 1).

The $RD_{z,t}$ s (centimetres) were determined as a function of light level and prey size from the experimental data of Howick and O'Brien (1983) on largemouth bass (*Micropterus salmoides*) foraging on bluegill (*Lepomis macrochirus*):

$$(3) \quad RD_{z,t} = 24.5I_{z,t}^{0.4747}TL^{0.9463} \quad (r^2 = 0.986)$$

where TL is total length (centimetres) of prey, $I_{z,t}$ is ambient light intensity (microeinsteins per square metre per second, lux, foot-candles, etc.), and the subscripts z and t represent depth (metres) and time (diel period), respectively. The intercept of 24.5, used for light in microeinsteins per square metre per second, would be converted to 3.787 when using lux or to 11.7 when using foot-candles.

We compared eq. 3 with experimentally measured RD for lake trout foraging on salmonid prey (Vogel and Beauchamp 1999). Equation 3 compared well with experimental data for $I < 17.8$ lx but overestimated RD for $I > 17.8$ lx and was overly sensitive to changes in prey size (Fig. 2). Howick and O'Brien (1983) reported that RD for largemouth bass to bluegill (2.9–9.9 cm TL) and redbfin shiner (*Lythrurus umbratilis*, 3.1–7.5 cm TL) showed a strong prey-size effect and greater maximum RD (about 200 cm) than was observed for salmonids. Prey size had no effect on RD by lake trout to salmonid prey (5.5–13.8 cm TL; Vogel and Beauchamp 1999). For $I_{z,t} < 17$ lx and prey size of 7.5 cm TL, eq. 3 compared well with experimentally measured RD for lake trout responding to 5.5- or 13.8-cm cutthroat trout (Fig. 2). Therefore, since the model was applied to salmonid predators and salmoniform prey, the effect of prey size was removed by setting TL = 7.5 cm. Thus, eq. 3 becomes

$$(4) \quad RD = 164.9I_{z,t}^{0.4747}$$

when used for light in microeinsteins per square metre per second. The intercept would be converted to 25.490 when using lux or to 78.8 when using foot-candles. The effect of prey size on RD may be specific for different taxonomic groups and represents a hypothesis requiring further experimentation over a broader range of taxa, prey sizes, and light levels.

At higher light levels ($I_{z,t} \geq 17.8$ lx), RD generated from eq. 3 continued to increase, whereas experimentally measured RD for lake trout remained relatively constant at 94.5 cm (2 SE = 6.7 cm) over 17.8–1103 lx (Vogel and Beauchamp 1999). This threshold effect was termed the saturation intensity threshold (SIT) by Henderson and Northcote (1985), which they demonstrated for salmonids (cutthroat trout and Dolly Varden), and has also been reported for centrarchids (largemouth bass and bluegill, Howick and O'Brien 1983). Thus, when $I_{z,t} > 17.8$ lx (SIT), eq. 3 was modified to set $RD = RD_{\max} = (\text{mean} + 2 \text{ SE}) = 94.5 + 6.7 = 101.2$ cm:

$$(5) \quad RD = 164.9I_{z,t}^{0.4747} \quad \text{for } I_{z,t} \leq 17.8 \text{ lx}$$

$$RD = RD_{\max} = 101.2 \text{ cm for } I_{z,t} > 17.8 \text{ lx.}$$

RD also declines with increasing turbidity at a given light level (Miner and Stein 1996). We modeled turbidity as a proportional reduction of RD referenced to RD under clear water conditions at the same light level (i.e., no interaction with light or prey size). From Miner and Stein (1996), RD declined with increasing turbidity as a proportion of the observed maximum RD = 208 cm in clear water (0.3 NTU for a 24-cm largemouth bass at 135 lx) compared to RD at higher turbidity levels:

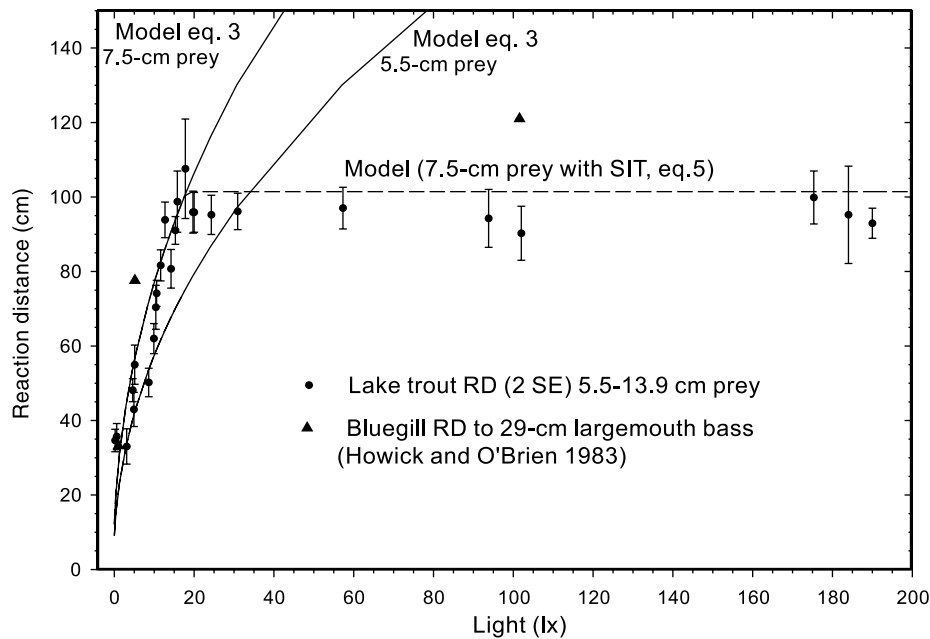
$$(6) \quad RD_{\text{NTU}}/RD_{\text{clear}} = 98.2\text{NTU}^{-0.624}/208 \\ = 0.472\text{NTU}^{-0.624}.$$

Combining eqs. 5 and 6 for light measured in microeinsteins per square metre per second yields

$$(7) \quad RD = 77.9I_{z,t}^{0.4747}\text{NTU}^{-0.624} \quad \text{for } I_{z,t} \leq 17.8 \text{ lx}$$

$$RD = RD_{\max} = 47.8\text{NTU}^{-0.624} \quad \text{for } I_{z,t} > 17.8 \text{ lx}$$

Fig. 2. Visual foraging model predictions of piscivore RD as a function of light for two prey sizes (5.5 and 7.5 cm). RD reached a constant maximum value above the SIT at light levels ≥ 17.8 lx (broken line). Model estimates were compared with laboratory measurements of lake trout responding to 5.5- to 13.9-cm cutthroat trout (Vogel and Beauchamp 1999) and bluegill responding to 29-cm largemouth bass (Howick and O'Brien 1983).



where “clear water” has a minimum turbidity of 0.3 NTU. When $I_{z,t} \leq 17.8$ lx, the intercept 77.9 would be converted to 12.034 for lux and to 37.2 for foot-candles.

Depth- and temporally specific search volumes were computed from estimates of ambient light and turbidity for each lake and reservoir corresponding to the dates and times of the diel hydroacoustic surveys of prey density and distribution during summer stratification. Surface light intensity $I_{0,t}$ varied as a function of time (date and diel period), cloud cover, and location (latitude, longitude, surrounding topography) and was estimated by supplying these data to a computer program by Janiczek and Young (1987). The diel change in ambient light $I_{z,t}$ experienced by a predator at a given depth, date, and time was computed as

$$(8) \quad I_{z,t} = I_{0,t} e^{zk}$$

We set $k = -0.0677$ (Tahoe Research Group, unpublished data) and $NTU = 0.30$ (the minimum turbidity allowed in this formulation of the model) for Lake Tahoe, $k = -0.3500$ (Eggers 1978; and computed from Lehman 1988) and $NTU = 0.35$ for Lake Washington, and $k = -0.3778$ and $NTU = 5.00$ for Strawberry Reservoir (C.M. Baldwin, unpublished data).

Hydroacoustic measurements

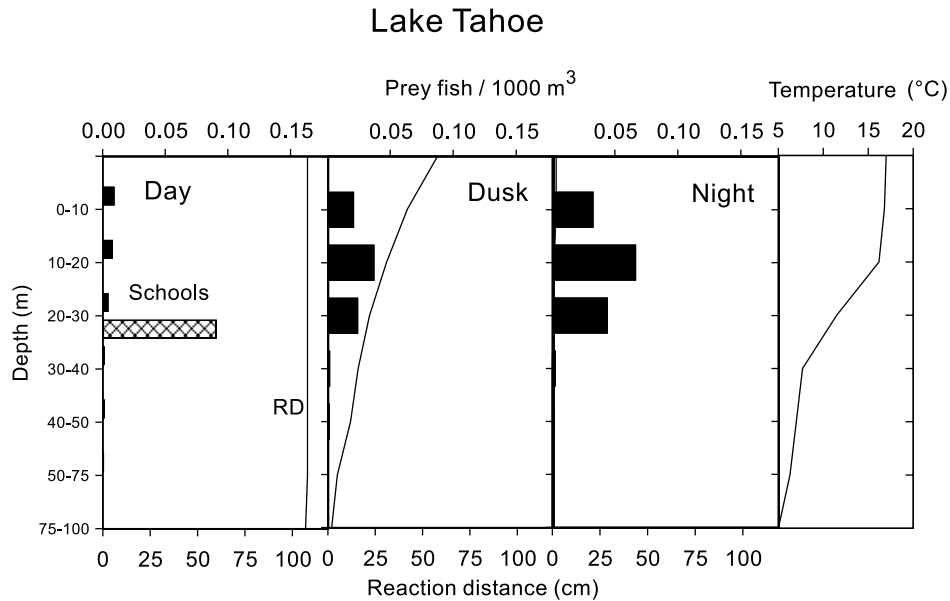
Prey fish densities ($PD_{z,t}$) were estimated from diel hydroacoustic and net surveys (Brandt 1996) during summer stratification to obtain species- and size-specific densities of prey fishes in each depth interval and diel period. We measured size-specific diel vertical distributions of fish density along limnetic transects perpendicular to shore using a dual-beam echo sounder. Data from Lake Washington (July 17–18, 1992), Lake Tahoe (August 19–20, 1993), and Strawberry Reservoir (June 26–28, 1996) were collected using a BioSonics model 105 echo sounder with a 420-kHz dual-beam ($6 \times 15^\circ$) transducer and ESP 2.0 signal-processing software. The transducer was towed 0.5 m deep off the port bow of a planing-hull boat at an average speed of 2.5 m/s. We acquired data at 2 pings/s with a 0.4-ms pulse width. Only echoes within 3° (-6 dB off-axis) of the acoustic axis were included in the analyses.

Echo counting was employed to measure density of single targets (fish per 1000 m^3). Ordinarily, echo integration would have been used to detect fish schools; however, problems with operating the echo integrator forced us to use paper chart recordings. These paper charts provided information on the vertical and temporal distribution of fish schools but could not be used to quantify biomass or numbers of fish in schools. Since target densities increased toward the surface in Strawberry Reservoir, transducers were alternately oriented vertically and horizontally on transects. The side-facing transects measured relative densities of the near-surface targets that would not have been detected by the conventional down-looking transducer due to near-field effects, small diameter of the acoustic beam, and potential boat avoidance. Transects were repeated during day, dusk, and night periods within the same region of each lake to characterize size-specific depth distribution and density in offshore regions. The sizes of prey fishes available to piscivores varied among lakes. Kokanee were 7–30 cm (fork length) with mean weight = 46.3 g during August in Lake Tahoe, juvenile sockeye salmon and longfin smelt were 5–10 cm with mean weight = 3.3 g during July in Lake Washington, and juvenile kokanee and cutthroat trout were 7–12 cm with mean weight = 13 g during June in Strawberry Reservoir. In each lake, identification of acoustic targets was determined by depth-specific midwater trawling and vertical gill nets. Based on these samples, we assumed that all limnetic targets greater than -35 dB in Lake Tahoe were lake trout.

The horizontal patchiness of nonschooling prey fishes was examined by computing the density (fish per cubic metre) of prey-sized targets in 20-ping (25-m-long) “patches” within each depth interval (3-m intervals in Strawberry Reservoir, 5-m intervals in Lake Washington, and 10-m intervals in Lake Tahoe) for each transect during daylight and crepuscular periods. The proportion of empty patches and frequency of different patch densities were compared graphically between diel periods and among waters.

Diel depth distributions of the piscivores were estimated from their depth-specific relative abundance using a combination of net sampling (vertical and sinking horizontal gill nets, midwater trawls, purse seines, Beauchamp et al. 1992), ultrasonic telemetry

Fig. 3. Diel depth distribution of prey fish (18–30 cm) in Lake Tahoe in August 1993 during the day, dusk, and night. Densities of individual targets are indicated by solid bars, and schooling kokanee are represented on a relative scale by cross-hatched bars. The line represents the decline in RD of piscivores to prey with depth for each diel period. The vertical temperature during this period is also shown.



(Warner and Quinn 1995; C.M. Baldwin and C.P. Gubala, unpublished data), and hydroacoustics.

Model evaluation

Prey encounter rates predicted from the visual foraging model were compared with predation rates that were estimated independently from field samples and bioenergetics modeling in Lake Tahoe (Thiede 1997), Lake Washington (Beauchamp 1994), and Strawberry Reservoir (Baldwin 1998). Daily numerical encounter rates were converted to the biomass of prey fish encountered, based on the size distribution of prey fishes available. To standardize for differences in predator and prey sizes among these waters, the prey biomasses that were encountered or consumed were presented as percentages of predator body weight.

We performed several sensitivity analyses on the model. An individual parameter perturbation analysis (e.g., Bartell et al. 1986) was performed on the variables and parameters in eq. 7 for light levels below SIT. Variables (light, turbidity) and parameters (intercept, light dependence coefficient, and turbidity-dependence coefficient) were varied by $\pm 10\%$ and the resulting RD was compared with the nominal RD. A Monte Carlo simulation of eq. 8 was also performed across a range of seven turbidities (0.3, 0.5, 1.0, 3.0, 5.0, 7.0, and 9.0 NTU) and five light levels below SIT (0.2, 5.0, 10.0, 15.0, and 17.8 lx) to estimate the collective propagation of error in estimates of RD. Each parameter was assumed to be normally distributed with means equal to the values in eq. 8 and SD = 10% of each mean. For each combination of light and turbidity, RD was estimated 30 times to generate a mean, SD, and coefficient of variation (CV). Since SD for the three parameters was set at 10% of the mean, CV < 10% for RD from the Monte Carlo simulation would suggest that parameter errors were dampened in the model, whereas CV > 10% would indicate that the model was relatively volatile to parameter error.

Results

Diel distribution of prey fish and depth-specific RDs

Diel vertical distributions of piscivores, prey fishes, and RD varied among the three lakes. In Lake Tahoe, kokanee

primarily remained in 0–30 m depths throughout the diel cycle (Fig. 3). Kokanee formed aggregations (seen on chart recordings) in and below the thermocline (20–30 m) during daylight, whereas extremely low densities of individual targets (<0.01 target/1000 m³) were found from the surface down to 50 m. Due to the high light intensity and extremely low turbidity, depth-specific RDs remained at maximum saturation levels ($RD_z = 101.2$ cm) over 0–75 m and just started declining at 100 m ($RD_z = 100$ cm). Any kokanee occupying depths below 120 m would not have been detected with our hydroacoustic surveys due to degradation of the signal-to-noise ratio. However, no measurable density of targets ascending from below 100 m was evident at dusk or dawn, so we concluded that kokanee remained in the upper 50 m throughout the diel cycle. Schools dispersed at dusk, and the density of single (nonaggregated) targets increased to 0.021–0.037 target/1000 m³ in 0–30 m depths. RDs declined rapidly at all depths during dusk, but RD_z (midway between sunset and astronomical twilight) declined from 58 cm at the surface to 2 cm at 100 m. At night, individual targets were more abundant (0.033–0.066 target/1000 m³) but were still concentrated in depths of 0–30 m. Piscivores' nocturnal RD_z declined from 2 cm at the surface to 0 cm below 50 m. The vertical distribution of piscivores in Lake Tahoe was similar among diel periods. Piscivore-sized acoustic targets (target strength greater than or equal to -35 dB) remained in 10–50 m depths throughout the diel period, and the modal depth of piscivorous lake trout from both overnight gillnet catches and large acoustic targets was 30 m (Fig. 4).

In Lake Washington during July 1992, juvenile sockeye salmon and longfin smelt formed schools in and below the thermocline during daylight, whereas individual targets were bimodally distributed with peak densities at 15–18 m (0.45 target/1000 m³) and 39–45 m (0.62 target/1000 m³) (Fig. 5). During daylight, RD_z remained high at 97 cm from the

Fig. 4. Vertical distribution of predatory lake trout in Lake Tahoe during August 1993 as determined from mean catch per unit effort in sinking horizontal gill nets set overnight down the shore slope and from the vertical density of acoustic targets greater than -35 dB. The acoustic depth distribution patterns were similar between day and night transects, so they were averaged together. Error bars represent ± 1 SE.

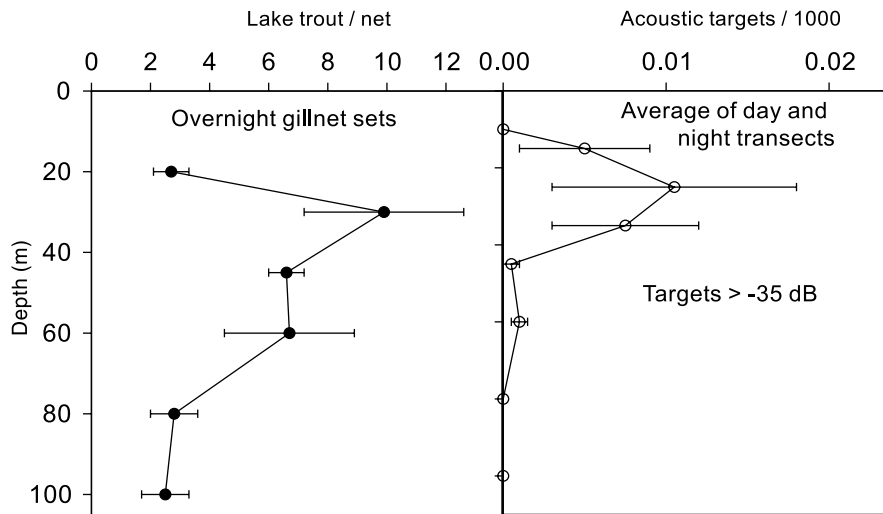
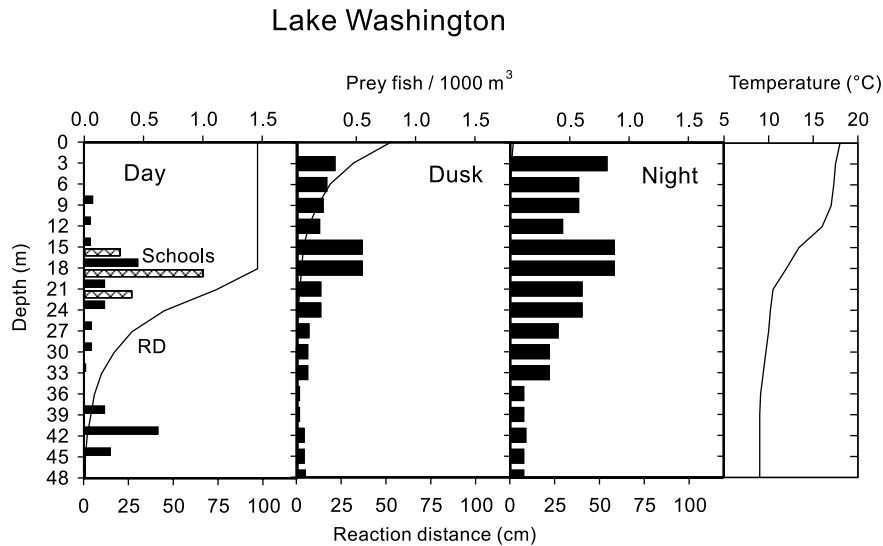


Fig. 5. Diel depth distribution of prey fish (5–10 cm) in Lake Washington in July 1992 during the day, dusk, and night. Densities of individual targets are indicated by solid bars, and schooling longfin smelt and juvenile sockeye salmon are represented on a relative scale by cross-hatched bars. The line represents the decline in RD of piscivores to prey with depth during each diel period. The vertical temperature during this period is also shown.



surface to 18 m and then declined rapidly to 1 cm at 48 m. Schools dispersed at dusk, with peaks in target density (0.13–0.27 target/1000 m³, longfin smelt) occurring at 0–3 and 15–18 m depths (0.55 targets/1000 m³; predominantly juvenile sockeye salmon mixed with some longfin smelt, Beauchamp et al. 1992). Midcrepuscular RD_z declined exponentially from 53 cm at the surface to 0 cm at 30 m. At night, targets were more abundant (0.10–0.86 target/1000 m³) but maintained the bimodal depth distribution observed during dusk. The nocturnal RD_z ranged from 2 to 0 cm from the surface to 9 m. The modal depth of piscivorous rainbow trout was 1 m throughout the diel cycle but ranged from 0 to 13 m (Warner and Quinn 1995). Piscivorous cutthroat trout occupied 5–25 m with a modal depth at 15 m (Beauchamp et al. 1992; Beauchamp 1994).

In Strawberry Reservoir during late June 1996, no schools of prey fishes (juvenile cutthroat trout or kokanee) were detected in limnetic regions during daylight, and relatively low densities of individual fishes (0.5 target/1000 m³) were concentrated in 0–2 m (Fig. 6). During daylight, RD_z was only 18 cm from the surface to 17 m and then declined to 10 cm at 23 m. Fish densities increased at dusk with peak densities of 1.4 targets/1000 m³ and at night with peak densities of 2.4 targets/1000 m³ in the 2–5 m depth stratum. The midcrepuscular RD_z declined from 10 cm at the surface to 0 cm at 20 m. The nocturnal RD_z for piscivores declined gradually from 6 cm at the surface to 2 cm at 23 m. Predatory-sized cutthroat trout ranged from 0 to 11 m throughout epi- and meta-limnetic waters but were most concentrated in 0–2 m during this period (Baldwin 1998).

Fig. 6. Diel depth distribution of prey fish (5–12 cm) in Strawberry Reservoir in June 1996 during the day, dusk, and night. Densities of individual targets are indicated by solid bars. No schooling was evident during daylight. The line represents the decline in RD of piscivores to prey with depth during each diel period. The vertical temperature during this period is also shown.

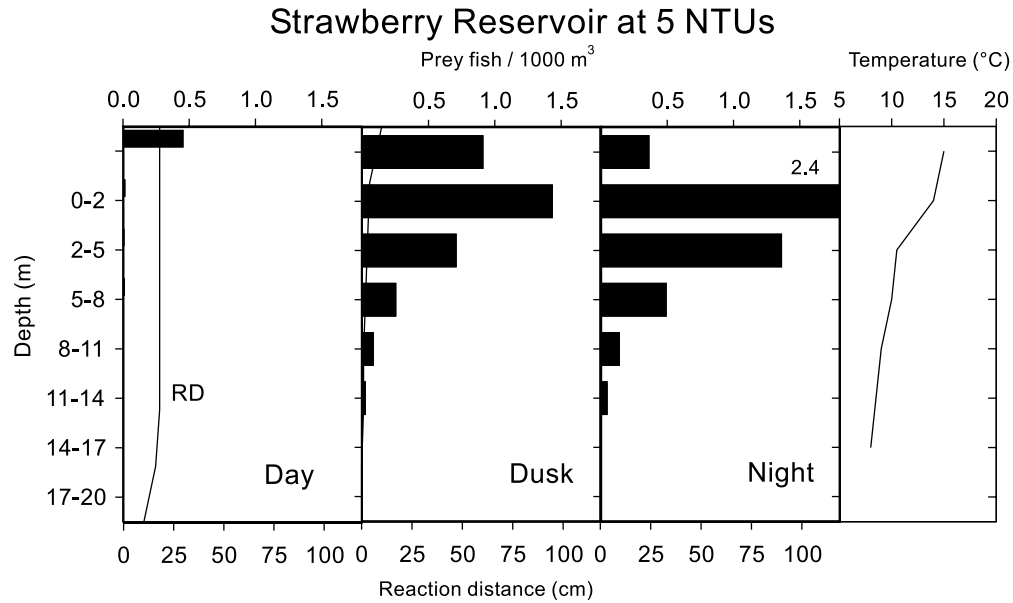
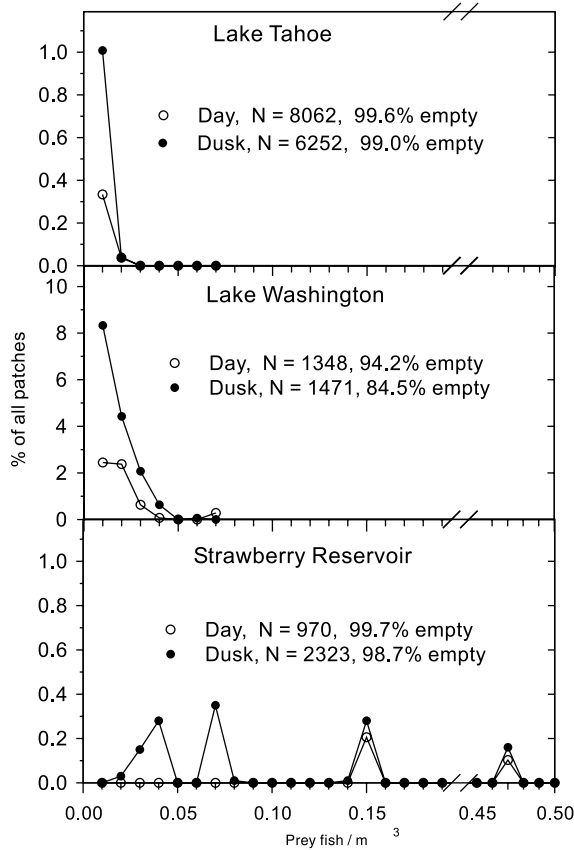


Fig. 7. Percentage of patches containing different densities of prey fish during daylight and crepuscular hydroacoustic transects in each lake. The patches represent 25-m segments of the transects. Total number of patches and the percentage of empty patches are displayed for day and crepuscular periods in each lake. Note that the vertical scale is 10 times larger for Lake Washington than for Lake Tahoe and Strawberry Reservoir.



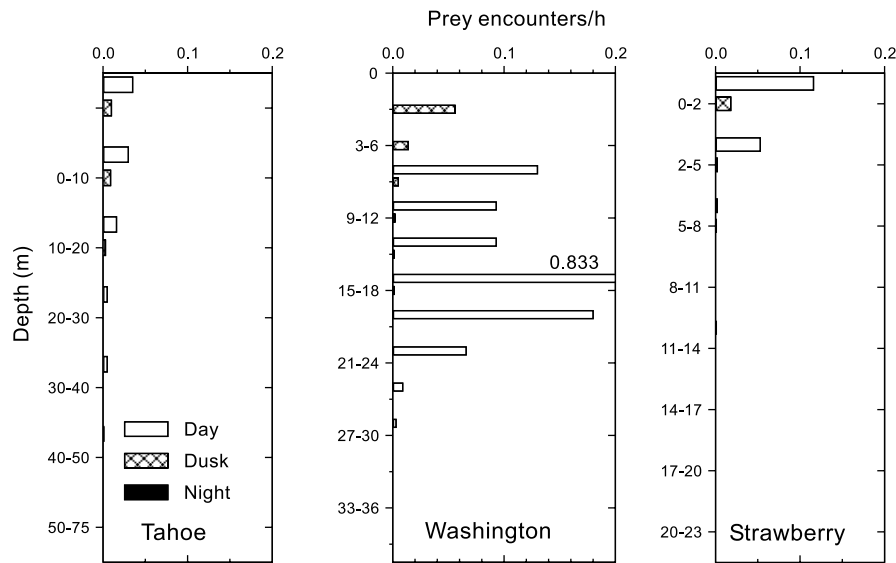
The horizontal distribution of prey fishes was extremely patchy in all three systems. The majority (84.5–99.7%) of 25-m-long patches were empty, but the frequency of non-empty patches was consistently higher during crepuscular periods than during daylight (Fig. 7). Lake Washington showed both a larger percentage of nonempty patches and higher patch densities than Lake Tahoe. Higher-density patches were found in Strawberry Reservoir but at much lower frequencies than in Lake Washington. The maximum patch density of prey fishes was 500–2000 times greater than the mean density at their modal depth for all daytime and crepuscular transects in Lake Tahoe, 100–150 times greater in Lake Washington, and 1000–3000 times greater in Strawberry Reservoir.

Diel changes in depth-specific prey encounter rates

Diel foraging opportunities differed considerably in magnitude and by depth among the three lakes. In all waters, prey encounters were relatively rare, with maximum rates ranging from 0.035/h in Lake Tahoe to 0.833/h in Lake Washington and 0.116/h in Strawberry Reservoir (Fig. 8). Piscivores could encounter prey fishes for longer periods over a greater range of depths in waters with higher transparency. During summer stratification in Lake Tahoe, piscivores should encounter the most prey fish in 0–30 m depths during daylight (0.016–0.035 prey fish/h), with much reduced encounters during crepuscular periods (0.003–0.010 prey fish/h) and no measurable visual encounters at night (<0.001 prey fish/h). When considering the horizontal patchiness of prey, piscivores would randomly encounter 0.16 nonempty patches/h during daylight, 0.35/h during crepuscular periods, and 0.1/h at night.

In Lake Washington, piscivores could encounter 5- to 10-cm prey fish in 9–30 m depths during daylight, with maximum encounter rates of 0.833 prey fish/h in 15–18 m (Fig. 8). Encounter rates declined at dusk, with peak encounter rates at 0–6 m (0.014–0.056 prey fish/h). Encounter rates

Fig. 8. Diel encounter rates predicted for piscivores foraging at depth in Lake Tahoe, Lake Washington, and Strawberry Reservoir. Daylight encounter rates extend to 0.833 prey/h at 15–18 m in Lake Washington.



were negligible at night. When considering the horizontal patchiness of prey, piscivores would encounter 1.4 non-empty patches/h during daylight, 3.6/h during crepuscular periods, and 1.8/h at night.

In Strawberry Reservoir, piscivores could encounter 5- to 12-cm prey fish (juvenile cutthroat trout and kokanee) during daylight, with maximum encounter rates of 0.116 prey fish/h in 0–2 m, declining to 0.001 prey fish/h at 14 m (Fig. 8). Encounter rates declined at dusk, with peak encounter rates of 0.018 prey fish/h in 0–2 m, declining to 0.001 prey fish/h at 8 m. Encounter rates were negligible at night over all depths. When considering the horizontal patchiness of prey, piscivores would encounter 0.15 nonempty patches/h during daylight, 0.22/h during crepuscular periods, and 0.50/h at night.

Comparison of model predictions with independent estimates of piscivory

The model predicted that piscivores would encounter more than enough prey fish biomass to satisfy the growth rates and diet compositions observed in each of the systems. Despite the increasing density of prey fishes from Lake Tahoe to Lake Washington to Strawberry Reservoir, we predicted that piscivory should be low in Lake Tahoe and Strawberry Reservoir but higher in Lake Washington. These predictions agreed qualitatively with the estimated consumption of fish prey (grams prey fish per gram predator) by piscivores from these waters during the summer (Beauchamp 1990; Beauchamp et al. 1992; Thiede 1997; Baldwin 1998) (Fig. 9). The estimated daily consumption of fish prey represented 2% of the prey fish biomass encountered in Lake Tahoe, 24% in Lake Washington, and 2% in Strawberry Reservoir. Invertebrates supplemented the diets in all cases, representing 90% of the diet by weight for lake trout in Lake Tahoe, only 29% of the diet for rainbow and cutthroat trout in Lake Washington, and 95% of the diet for cutthroat trout in Strawberry Reservoir.

Sensitivity analysis

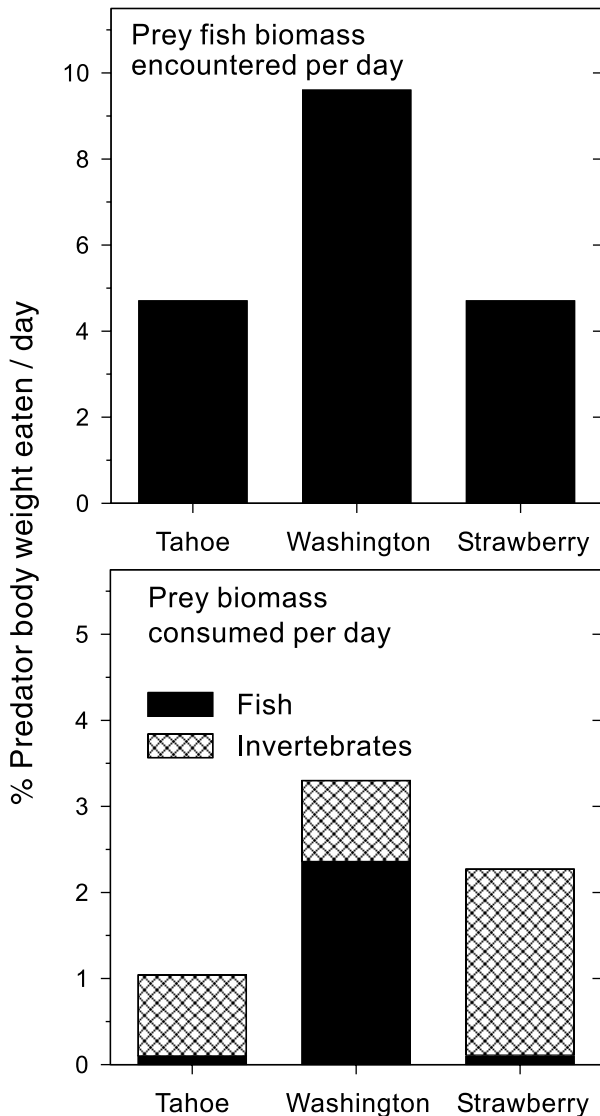
Since encounter rates are estimated by overlaying time-

and depth-specific search volumes on corresponding ambient prey densities, the relative sensitivity of the model to each of the lake-specific inputs can be evaluated analytically. Encounter rates at any depth or time will vary as a 1:1 correspondence to changes in swimming speed or prey density (e.g., a 10% increase in either variable will result in a 10% increase in encounter rate). The model is much more sensitive to changes in RD, since search volume is proportional to RD^2 . Moreover, RD varies as complex functions of light and turbidity. RD increases rapidly with increasing light to a threshold and then remains constant at all light levels above SIT (Henderson and Northcote 1985; Vogel and Beauchamp 1999). Sensitivity analysis indicated that search volume was more sensitive than RD to changes in light and turbidity, and both search volume and RD were more sensitive to changes in turbidity than to changes in light. A 10% reduction or increase in light level changed RD by -4.9 or 4.6% , respectively, and changed search volume by $\pm 9.5\%$. Whether above or below SIT, a 10% reduction or increase in turbidity changed RD by 7.0% or -5.9% , respectively, and changed search volume by 14.5 or -11.5% , respectively. A $\pm 10\%$ variation in the constant 12.034 lx ($77.9 \mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) resulted in an equal $\pm 10\%$ variation in RD. A $\pm 10\%$ variation in the light dependence coefficient (0.4747) resulted in a -10 or 12% change in RD, whereas a $\pm 10\%$ change in the turbidity dependence coefficient (-0.624) resulted in changes in the opposite direction of $\pm 4\%$. Results of the Monte Carlo simulations for the collective error propagation of eq. 8 resulted in an overall average CV of 17.2% across all light and turbidity levels with no trends in CV related to either factor. The results of the individual parameter perturbation and Monte Carlo simulations indicated that RD was moderately sensitive to parameter error and somewhat less sensitive to measurement errors for the input variables light and turbidity.

Discussion

The visual foraging model predicted that piscivory should

Fig. 9. Comparison of predicted daily biomass of prey fish encountered by piscivores, with estimates of biomass of prey consumed in Lake Tahoe (Thiede 1997), Lake Washington (Beauchamp 1994), and Strawberry Reservoir (Baldwin 1998). Prey biomasses were reported as percentages of predator body weight to adjust for differences in predator and prey sizes among the lakes.



be low in Lake Tahoe and Strawberry Reservoir but much higher in Lake Washington, despite the increasing density of prey fishes from Lake Tahoe to Lake Washington to Strawberry Reservoir. The predicted encounter rates were sufficient to satisfy the observed growth rates of piscivores in all three systems, and our predictions qualitatively agreed with the biomass of prey fish observed in the diet of piscivores during the summer in all three lakes. Whether estimating encounter rates from average depth-specific prey densities or from the frequency of nonempty patches, the same pattern emerged: the opportunity and importance of piscivory were greatest in Lake Washington and considerably less in both Lake Tahoe and Strawberry Reservoir.

A general prediction of this model was that fish consump-

tion should be highest for pelagic piscivores in waters of intermediate productivity. Encounter rates are determined by the product of search volume and prey density. When transparency is caused by organic rather than mineral turbidity, transparency will decline with increasing productivity, whereas prey fish production should increase. In low-productivity lakes, transparency and light penetration are high, search volumes are at or near maximum, but prey fish densities are low. Since RDs are asymptotic, search volumes do not increase in proportion to increased transparency once light exceeds SIT. Thus, prey encounters should be low because search volumes cannot increase enough to compensate for the low prey densities. Pelagic prey encounters should be maximized in lakes of intermediate productivity because search volumes remain near maximum, while prey densities increase. As lakes become more productive, prey densities do not increase fast enough to compensate for the rapid decline in search volume. This interaction between prey density and search volume could explain some of the shifts in fish communities along productivity gradients that were reported by Persson et al. (1991); they reported that the proportion of pelagic piscivores in the total fish biomass peaked in systems of intermediate productivity.

This approach provides a framework for examining ecological trade-offs confronting both predator and prey species. When temporally and spatially explicit encounter rates are combined with predator abundance and distribution data, the foraging opportunity (prey encounter rate in numbers or grams of prey per hour) and predation risk (number of encounters with predators per hour) associated with specific time and depth cells could be quantified. Predator abundance or distribution data are often lacking, in which case the model would only estimate the relative risk or foraging opportunity associated with each time and depth cell as hourly encounters per predator in each cell. Therefore, this model can be used to make predictions about diel vertical migration or horizontal distribution patterns of prey, based solely on predation risk, or it could be linked with data or predictions from other models (e.g., Stockwell and Johnson 1997) regarding the distribution or foraging opportunity of prey.

Earlier works on planktivorous fish distributions assumed that predation risk helped determine diel distribution patterns of prey (Eggers 1978; Wurtsbaugh and Li 1985; Clark and Levy 1988; Levy 1990, 1991; Appenzeller and Leggett 1995) but rarely provided data on the diet, distribution, or density of predators or a quantitative measure of predation risk as a function of time and space (but see Clark and Levy 1988). By linking a mechanistic foraging model with empirical data on diel distribution and density from hydroacoustic transects, the approach described here provides a framework for integrating the effects of biotic and abiotic factors into predictions of the trophic dynamics of a limnetic community under a variety of conditions. The foraging model could be integrated into spatially explicit models for fish growth (e.g., Brandt et al. 1992) to examine the implications of various spatial and temporal changes in foraging opportunities and predator distribution for its growth potential.

This work represents the first known development, application, and initial test of a visual foraging model for pelagic piscivores. Eggers (1977) and Aksnes and Giske (1993) presented theoretical models for visually feeding zooplank-

tivorous fish and more general visual foragers, respectively. These models required numerous parameters that would not be routinely available, and they primarily focused on zooplanktivore–zooplankton systems (Gerritsen and Strickler 1977; Confer et al. 1978; Hairston et al. 1983; Wright and O'Brien 1984). Breck (1993) described important differences between the visual systems required by fish feeding on zooplankton versus those feeding on larger, more mobile prey fishes, which occur at much lower densities than zooplankton (e.g., 0.000 001–10 fish/m³ compared with 0.1–100 000 crustacean zooplankton/m³). He warned against extrapolating from acuity-based zooplanktivore foraging models to piscivore systems because gross overestimates of RD would result. RDs required of piscivores are great enough that increased backscattering over these distances and the consequent declining contrast between the prey, and its background (Loew and McFarland 1990; Guthrie and Muntz 1993), cause RDs to asymptote much sooner than would be predicted from an acuity-based model. Our goal was to develop a piscivore model constructed from a much reduced set of parameters that subsumed many of the mechanisms modeled explicitly by the theoretically derived models of Eggers (1977) and Aksnes and Giske (1993). Furthermore, for the model to be readily applicable to new waters, lake-specific inputs (e.g., light extinction, turbidity, diel prey fish density distributions) needed to be acquired either with relative ease, economy, and timeliness or from reasonable values inferred from behavioral or physiological principles. Previous models of this sort have rarely been tested against field observations (but see Wright and O'Brien 1984).

By estimating temporally and spatially explicit search volumes, we can gain insight into the scale at which piscivores experience patchiness. For example, we estimated that a lake trout in Lake Tahoe could swim 1062 m/h and search 3863 m³/h at midday but swim 846 m/h and search only 100–500 m³/h at dusk. This has implications for how we measure prey density so that these estimates and their variability correspond to the foraging capabilities of predators. Hydroacoustics and ultrasonic telemetry will play important roles in this area. With current hydroacoustic technology, the spatial resolution of prey densities can be acquired at a precision of ≤ 1 m in the vertical dimension and by individual or fixed numbers of pings to achieve the desired precision in the lateral dimension (e.g., Nero and Magnuson 1989; Schael et al. 1995). Seasonal and diel movement and distribution patterns of piscivores can be obtained by ultrasonic telemetry to examine factors that influence how piscivores perceive and operate in their environment.

The estimates for search volume are based on several critical assumptions. The model assumes that RD represents the radius of a piscivore's visual field; however, prey might be detected at greater distances than RD measured in laboratory experiments. If prey detection distances DD exceed RD, then search volumes would be underestimated by the model, biased in proportion to $(RD^2 - DD^2)/DD^2$. Since the encounter rate predictions exceeded observed consumption rates, we assume that differences between DD and RD are probably less important than changes in capture success as a function of prey size (Juanes 1994; Christensen 1996; Mason et al. 1998), light (Petersen and Gadomski 1994), turbidity, or

other factors. Diel swimming speed estimates were obtained from both laboratory and telemetry studies. Swimming speed is typically underestimated by telemetry studies due to the inability to record continuous fine-scale movements. Laboratory estimates might not represent natural swimming speeds due to influences imposed by the experimental arena. However, the reasonably close agreement between the laboratory and telemetry estimates enhanced our confidence in the values that we used in the model.

The predicted biomass of prey fish encountered exceeded the consumption rates required to satisfy the summer growth rates observed for predators in all three lakes. Encounter rates do not necessarily equate to consumption rates (Savitz and Bardygula 1989; Christensen 1996). Therefore, when translating encounter rates into predation rates, encounters will need to be discounted by varying probabilities of attack and capture success as a function of diel period, light intensity (Petersen and Gadomski 1994), size (Juanes 1994; Christensen 1996), or schooling/nonschooling status (Magurran and Pitcher 1987; Pitcher and Parrish 1993). Therefore, one of the next logical steps will be to develop capture success relationships, probably from experiments in large laboratory tanks or enclosures in lakes. Spatial and temporal changes in prey encounter rates form the basis for hypotheses regarding the expected distribution and movement patterns of predators and for whether predators could or should switch to alternative prey as prey availability or environmental conditions change. Moreover, deviations from predicted movement and distribution patterns could reveal additional factors that contribute significantly to the diet and distribution patterns of predators and prey (e.g., temperature, dissolved oxygen).

The performance of this model over a relatively broad range of trophic conditions should encourage refinement and application of this approach to more waters and to a wider range of species where interactions between cruising piscivores and prey fishes would be expected in limnetic regions. The current model represents an early version of work in progress. Considerable refinement is expected, and this will be driven by the types of questions posed and the accuracy and precision required by new objectives.

As more species-specific parameters are generated for this model, we can begin to evaluate interspecific differences in the abilities of predators to exploit different prey species under varying environmental conditions. Of particular interest will be the generality of the model parameters among taxa. Will a generic model suffice for all pelagic piscivores, or will we need to generate unique parameters for each order, family, genus, or species? Despite its development from laboratory experiments on largemouth bass, a predominantly littoral, sit-and-wait predator, the model performed reasonably well against data from laboratory trials with lake trout, except that prey size had no effect on RD by salmonid predators, and maximum RD was shorter for salmonid predators (Vogel and Beauchamp 1999).

As the demand to manipulate predator or prey populations increases, so does the need to predict the effects of these changes on the structure and function of existing aquatic communities. As environmental conditions in a watershed change, the trophic dynamics of the food web could change significantly due to shifts in productivity and transparency of

the lake or reservoir. A visual foraging model for top predators should improve our predictive capability by providing a tool for estimating the expected proportional contribution of fish prey to the diet, based on temporal changes in prey fish density distributions and the optical conditions of the water body.

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