Modeling Target Strength Distributions to Improve Hydroacoustic Estimation of Lake Trout Population Size

HARRY J. CROCKETT*

Colorado Division of Wildlife, 317 West Prospect Street, Fort Collins, Colorado 80526, USA

BRETT M. JOHNSON

*Department of Fishery and Wildlife Biology, Colorado State University, 1474 Campus Delivery,
Fort Collins, Colorado 80523, USA*

PATRICK J. MARTINEZ

Colorado Division of Wildlife, 711 Independence Avenue, Grand Junction, Colorado 81505, USA

DAN BRAUCH

Colorado Division of Wildlife, 300 West New York Avenue, Gunnison, Colorado 81230, USA

Abstract.—Many management agencies use hydroacoustic surveys to estimate pelagic prey fish abundance and population trends. It would be desirable to simultaneously assess piscivore population size and predation demand. However, multiple sources of variation in target strength complicate the target strength–fish size relationship, impairing managers' ability to distinguish the echoes of predators and prey. This uncertainty may substantially bias population size estimates, especially for piscivores that are greatly outnumbered by other species. We used an in situ estimate of target strength variance combined with fish length-frequency distributions to estimate the distribution of target strengths for prey-sized kokanee *Oncorhynchus nerka* and piscivorous lake trout *Salvelinus namaycush* in Blue Mesa Reservoir, Colorado. Comparison of the resulting lake trout population size estimates with those obtained from an intensive mark–recapture study showed that this approach substantially improved the precision and accuracy of hydroacoustic estimates. This technique may be especially useful in systems having relatively few species or species with discrete size-classes, as is the case for many western U.S. reservoirs.

Hydroacoustic surveys are a desirable means of estimating fish abundance because they are more efficient, less invasive, and less selective than other sampling methods (MacLennan and Simmonds 1992). Extensively used in marine fisheries stock assessment, hydroacoustic sampling is also being applied increasingly to lakes and reservoirs (e.g., Yule and Luecke 1993; Beauchamp et al. 1999; Luecke et al. 1999; Johnson and Martinez 2000; Ruzycki et al. 2001). Many such waters in the western USA and elsewhere contain a species mix that includes a piscivorous top predator in combination with important sport or native prey species. Examples include the lake trout *Salvelinus namaycush* and kokanee *Oncorhynchus nerka* assemblage in Blue Mesa Reservoir (BMR), Colorado (Johnson and Martinez 2000), lake trout and native cutthroat trout *O. clarkii* in Yellowstone Lake, Wyoming (Ruzycki et al. 2003), and Bear Lake, Utah (Ruzycki et al. 2001), and lake trout, kokanee, and

Utah chub *Gila atraria* in Flaming Gorge Reservoir, Utah (Yule and Luecke 1993).

Maintenance of prey stocks in the presence of a long-lived, efficient predator such as lake trout requires frequent assessments of both populations. Hydroacoustics would be well suited for this purpose if predators could be distinguished from prey with confidence. However, the use of hydroacoustics to estimate abundance of individual species in natural systems is challenging because the size distribution of the species of interest often overlaps with that of other species present. Even when there is little or no overlap among species, size differences can be obscured by the substantial variability in target strengths that may be obtained from fish of a given length (Rose and Leggett 1988; Gunderson 1993).

Target strength (TS), expressed in decibels (dB), is calculated as 10 × the $\log_{10}$ transformation of an acoustic scatterer's backscattering cross section (σ_{bs}), which is in turn a function of the intensity of backscattered sound relative to the intensity of the incident sound wave (Brandt 1996; MacLennan et al. 2002). Love (1971, 1977) provided equations for

* Corresponding author: harry.crockett@state.co.us

converting TS to fish length based on data pooled from ex situ measurements on multiple species; since then, a great deal of research has been devoted to the TS–fish length relationship (MacLennan and Simmonds 1992, Simmonds et al. 1992, and Brandt 1996 provide reviews). Temporal variation in TS may arise from behavioral and physiological factors, including fish orientation, swimming behavior, and responses to pressure changes due to vertical migration (Foote 1980a, 1980b, 1991; Ona 1990; Mukai and Iida 1996). Further influences on TS include environmental noise (e.g., waterborne and vessel noise, plankton, and echoes from adjacent fish), physical properties of sound waves (constructive and destructive interference among echoes), and system error, such as incomplete correction of beam pattern effects (Ransom et al. 1999). The combined effect of all these factors is that TS varies among conspecific fish of identical size and on a ping-to-ping basis within an individual fish track, thereby blurring distinctions between fish of different sizes.

Despite progress toward species identification using response spectra across a range of frequencies (Simmonds and Copeland 1989; Simmonds and Armstrong 1990) or echo properties other than intensity (summarized in Brandt 1996), no technique has emerged as sufficiently robust for general survey use (Rose 1992; Ransom et al. 1999). Similarly sized fish of different species can be distinguished if they are very distinct physiologically (e.g., possessing versus lacking a swim bladder; Foote 1980b) or highly segregated behaviorally (Rudstam and Johnson 1992). In many lake and reservoir systems, however, the pelagic fish are all physiologically similar, belong to one or a few families, and are aggregated rather than segregated behaviorally because they either prey upon each other or compete for a common food resource. In such situations, manufacturers of high-end hydroacoustic equipment still offer the rule of thumb that to be reliably distinguished, one species must average twice the mean length of the other (P. Nealson, Hydroacoustic Technology, Inc. [HTI], personal communication), a requirement that limits the utility of hydroacoustics as a rapid assessment tool for predator–prey evaluations.

To overcome this constraint in estimating the abundance of piscivorous-sized ($\geq$425 mm) lake trout in BMR, we estimated TS variance directly, determined the size distributions of both lake trout and kokanee (the predominant prey species), and predicted the TS distribution for each species based on the contributions of fish size and TS variance. We used the predicted lake trout TS distribution to account for the effect of TS variance on the number of fish appearing to be of piscivorous size, and we used the corresponding kokanee TS distribution to estimate the percentage of nontarget individuals that were misidentified as the species of interest. Concurrently, we developed a second, independent estimate for the same piscivorous lake trout population from an extensive mark–recapture study led by the Colorado Division of Wildlife (CDOW). A goal of our study was to determine whether such an approach could enhance the utility of hydroacoustics for rapid assessments.

Our research was immediately motivated by a management controversy: egg take and angler harvest were down in BMR's economically important kokanee fishery, and lake trout piscivory was among the suspected causes of the declines. Initial hydroacoustic estimates of piscivorous lake trout numbers were alarmingly high (Johnson and Martinez 2000), lending support to this hypothesis. However, BMR also supports a trophy lake trout fishery, having produced a series of state records within the past 6 years, so it was essential to substantiate lake trout population size estimates before considering aggressive management actions to reduce their numbers.

Methods

Study site.—Blue Mesa Reservoir lies near Gunnison, Colorado, and impounds water of the Gunnison River and several significant tributaries. This reservoir, the largest in Colorado, is about 32 km long and has a surface area of 3,700 ha, a maximum depth of 96 m, and a storage capacity of 1.16×10^9 m^3. The reservoir includes three distinct basins: Iola (originating at the Gunnison River inlet), Cebolla (downstream of Iola), and Sapinero (Figure 1).

The fishery is dominated by kokanee, which typically constitute over 70% of angler harvest as estimated by creel surveys (D.B., unpublished data) and about 90% of the pelagic fish captured in vertical gill nets (B.M.J., unpublished data). The kokanee stock is maintained by hatchery propagation. Lake trout were stocked originally in the early 1960s and intermittently thereafter until 1992. There is abundant evidence of consistent natural lake trout reproduction (D.B., unpublished data; B.M.J., unpublished data). Other reservoir species include the rainbow trout *O. mykiss*, brown trout *Salmo trutta*, white sucker *Catostomus commersonii*, and longnose sucker *C. catostomus*.

Mark–recapture of lake trout.—In the spring (May–June) of 2000–2002, CDOW conducted intensive mark–recapture efforts using 60×2 m monofilament horizontal gill nets. The mesh size (4.5-cm stretch) was chosen to target lake trout larger than or equal to 425 mm total length (TL), which is the size that corresponds to the onset of piscivory in BMR lake
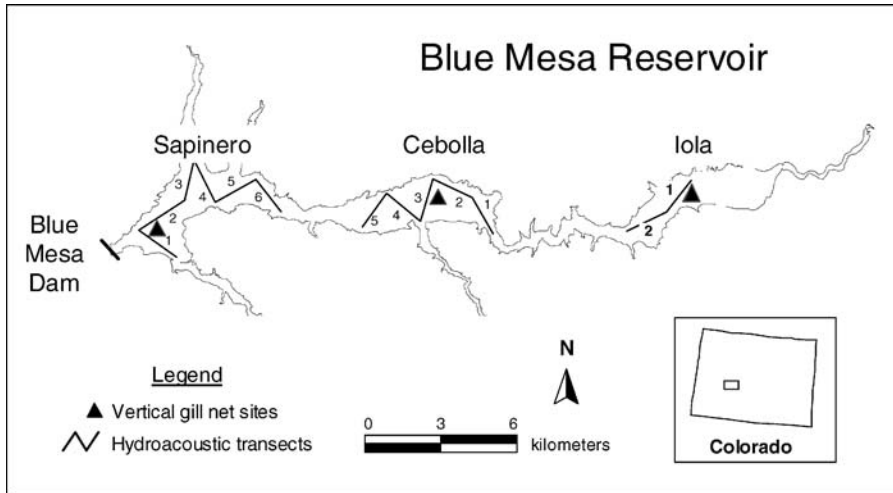
FIGURE 1.—Map of Blue Mesa Reservoir near Gunnison, Colorado, where the hydroacoustic target strength and actual length-frequency distributions of kokanee and lake trout were assessed.

trout (Johnson and Martinez 2000). To reduce mortality, we limited soak times to 45 min and avoided setting nets at depths greater than 36.5 m; the majority of nets were set at 18 m or less. Captured lake trout were examined for marks, tagged with individually enumerated cinch-up tags, batch marked as a means of estimating tag loss, and released. Length, weight, and additional relevant data were recorded for lake trout and for all bycatch.

Netting was conducted from ice-out until early summer, when lake trout are often particularly mobile and found in shallower water than at most other times of year (Martin and Olver 1980; D.B., unpublished data). Sampling effort was distributed roughly equally across the three basins. Within each basin, the method of determining net locations was similar: at least one net was set on every bar with a relatively flat bottom and at a depth of no more than 25 m. The depth constraint was imposed to reduce sampling mortality caused by air bladder distention. To maximize the number of fish marked, we set additional nets in "hot spots" that had yielded the highest catch per unit effort of lake trout on the first pass.

An additional netting session was conducted in October–November 2001. At this time of year, lake trout move into shallower water to spawn. Methods for the fall netting effort were the same as for the spring except that net locations were randomized. We used a geographical information system (GIS) to grid each basin into 100-m^2 cells and to identify all suitable cells, which were defined as those having a slope of no more than 0.2 and a depth no greater than 25 m. A subset of these cells was then selected at random for netting.

Hydroacoustic surveys.—On 5 and 6 August 2002, the reservoir was surveyed by means of a 200-kHz echosounder (Hydroacoustic Technology, Inc. [HTI]; Model 243) with a bow-mounted, split-beam transducer; the transducer had a 15° nominal beam width (defined at the half-power points). Thirteen transects followed a zigzag pattern that was established by CDOW in accordance with recommended methods (MacLennan and Simmonds 1992; Simmonds et al. 1992; Ransom et al. 1999) and that was used in several previous studies (Johnson et al. 1997; Johnson and Martinez 2000; see Figure 1). At the time of the survey, the entire eastern portion of Iola Basin was less than 5.5 m deep and for safety reasons could not be sampled. The survey was conducted at night, during the new-moon phase, when fish are generally most widely dispersed (Ransom et al. 1999). Targets were identified as fish by HTI's proprietary tracking algorithms; tracking parameters (Table 1) were recommended by the manufacturer as suitable for BMR and were further identified as appropriate by a sensitivity analysis (Hardiman et al. 2004). The hydroacoustic gear was calibrated before data collection by means of a tungsten carbide calibration sphere.

Concurrently with the hydroacoustic survey (5–7 August), standardized experimental vertical gill nets (Powell 1981) were set overnight for one night in each of the three basins. These nets consisted of six 1.5-m-wide, vertical panels that had bar mesh sizes of 1.3, 1.9, 2.5, 3.2, 3.8, and 5.1 cm. The nets extended from the surface to within a few meters of the bottom.

Gill-net locations were standardized in previous studies and were chosen to allow sampling of pelagic

TABLE 1.—Target selection parameters used to discriminate fish targets from noise in a hydroacoustic survey of Blue Mesa Reservoir, Colorado, in August 2002. Parameters were input to proprietary tracking algorithms in Echoscape signal processing software (Hydroacoustic Technology, Inc.).

Parameter	Value	Description
Ping gap	5	Maximum time (in pings) between echoes from one fish
Minimum pings	5	Minimum number of pings comprising a fish track
Velocity	5.0	Maximum expected fish velocity (m/s)
Change in range	0.2	Maximum change in range (m/ping)
Expansion exponent	0.2	Changes rate at which tracking window expands with each missed echo

areas that were representative of those surveyed hydroacoustically. Length, weight, species, and depth were recorded for all gillnetted fish.

Estimation of lake trout population size from mark–recapture data.—We developed Cormack–Jolly–Seber (CJS) models for model selection, as this structure is well suited to open populations (Lebreton et al. 1992; Franklin et al. 2000). The CJS models directly estimate apparent survival (ϕ_i) and capture probability (p_i). Apparent survival represents the probability that an individual in the population at sampling occasion i remains alive and available for recapture at occasion $i+1$. In the present study, emigration was assumed to be negligible. Capture probability is the probability that a marked individual is captured during occasion i. When strictly interpreted, both parameters apply only to marked individuals; inference to the entire population is only warranted if the study's design and conduct support fundamental model assumptions (Williams et al. 2002).

We developed an a priori set of variables and their hypothesized effects on the estimated parameters (Table 2) to generate a candidate set of models. For model selection, we held the parameter of greatest interest fixed at high dimensionality (i.e., p_t) while comparing alternative parameterizations of ϕ. Once a preferred parameterization of ϕ was identified, it was held fixed and the process was repeated for p. Akaike's information criterion corrected for small-sample bias (AIC$_c$) was used to select the most parsimonious models at each step in the process (Burnham and Anderson 2002). This step-down approach generally followed that advocated by Lebreton et al. (1992) except that model selection was based solely on AIC$_c$ rather than on likelihood ratio tests (Burnham and Anderson 2002). Eleven models were compared at each step of the analysis.

Goodness of fit was evaluated before modeling began. We used TEST2 in the program RELEASE (Burnham et al. 1987) to estimate the overdispersion parameter $\hat{c}$ (deviance/df) for the most general model (model ϕ_t, p_t). Fisher's maximum likelihood method was used for estimating model parameters and their standard errors (Lebreton et al. 1992; Burnham and

Anderson 2002). Each model was structured in general linear form; in other words, the "real" parameters, $\phi_{i...k}$ and $p_{i...k}$, were reparameterized as a vector of slopes, $\beta_{i...k}$. This reduced the number of parameters and rendered effects easily interpretable but did not constrain ϕ and p estimates between 0 and 1. The linear logistic function was used to impose this constraint and provide maximum likelihood estimators (MLEs) of the real parameters, that is,

$$\hat{\phi}_i = \frac{\exp(\hat{\beta}_0 + \hat{\beta}_1 \cdots + \hat{\beta}_k)}{1 + \exp(\hat{\beta}_0 + \hat{\beta}_1 + \hat{\beta}_k)}. \quad (1)$$

All of the aforementioned processes were facilitated by the use of the program MARK (White and Burnham 1999).

Population size $\hat{N}$ was estimated by $n_i/\hat{p}_i$, where n_i is the number of individuals captured on the ith occasion; "population" in this case denotes lake trout that are large enough to be at risk of capture, roughly those of piscivorous size (≥ 425 mm). Recruitment to this population occurs as individuals attain this size and thus become susceptible to capture during the course of the study. We based the estimate on the fall 2001 capture occasion because it was randomized. A related model type, the Jolly–Seber model, estimates N directly but is prone to bias, particularly when sample sizes are relatively small (White et al. 1982). Thus, it was better to use the more-restricted CJS model and derive estimates of $\hat{N}$, although $\hat{N}$ is consequently not an MLE. The variance of $\hat{N}$ was estimated by

$$\hat{\text{var}}(\hat{N}) = \left(\frac{\partial n_i}{\partial p_i}\right)^2 \times \text{var}(\hat{p}_i). \quad (2)$$

Modeling TS distributions for prey and piscivores.—We assumed that a fish's TS was best estimated by the mean σ_{bs} from the echoes comprising its track, as is true under many conditions (Burczynski and Johnson 1986; Dawson and Karp 1990; Simmonds et al. 1992; Ehrenberg and Torkelson 1996). Target strength was thus estimated as

$$\text{TS} = 10 \times \log_{10}(\overline{\sigma_{bs}}), \quad (3)$$

where TS is expressed in decibels with a reference pressure of 1 μPa. The variance of TS was estimated

TABLE 2.—Modeled hypotheses about potential effects on apparent survival (ϕ_i) and capture probability (p_i) of lake trout in Blue Mesa Reservoir (BMR), Colorado. The symbols ϕ_1, ϕ_2, and ϕ_3 represent the intervals between capture occasions p_1 and p_2, p_2 and p_3, and p_3 and p_4, respectively. Capture occasion p_1 occurred in May–June 2000, p_2 in May–June 2001, p_3 in October–November 2001, and p_4 in May–June 2002. Capture probability during p_1 is by definition nonestimable for the Cormack–Jolly–Seber model. To correct for different interval durations, we scaled all ϕ_i estimates by exponentiating by interval length (i.e., ϕ^L; White and Burnham 1999); this step is not reiterated for each effect in the discussion below.

Effect	Description
Hypotheses about effects on ϕ_i	
$\phi.$	$\phi_1 = \phi_2 = \phi_3$. Given the forage availability and good condition of lake trout in BMR, the survival rate might be uniformly high.
ϕ_{Length}; ϕ_{Weight}	ϕ_i is a function of individual fish size (length or weight) at first capture. The potential life span of lake trout exceeds the time they have been in BMR, so mortality from old age is probably not a factor. However, larger individuals might be subject to differential angler harvest. Quadratic and cubic functions of length and weight were also fitted.
ϕ_{Winter}	$\phi_1 = \phi_3$; ϕ_2 is higher because fish do not experience a winter during that interval. Winter is probably not environmentally stressful for BMR lake trout, but they might experience significant mortality due to ice fishing, about which no creel data were available.
$\phi_{Release\ condition}$	ϕ_i is a function of individual fish condition when released after capture. Individuals released in poorer condition might have a lower survival rate.
$\phi_{Length+winter}$	Encompassed the additive effect of these two variables, used to indirectly assess effect of angler harvest (if hypotheses about harvest described above are correct).
ϕ_t	$\phi_1 \neq \phi_2 \neq \phi_3$. Apparent survival is different for each interval due to stochastic variation or systematic effects that were not included in the above models or that were not detected because of insufficient sample size.
ϕ_{Trend}	Apparent survival rate changes over time as a linear trend. There was some suggestion that angler harvest might be increasing, so this possibility was modeled.
Hypotheses about effects on p_i	
$p.$	$p_2 = p_3 = p_4$. Fish were behaviorally susceptible to capture in spring and fall; if netting intensity was sufficient on all occasions, p_i might emerge as uniform.
p_{Fall}	$p_2 = p_4$; p_3 is different due to random selection of fall net locations (p_3 expected lower) or different fish behavior in fall versus spring (effect on p_3 unknown).
p_{Effort}	p_i is a function of effort, measured as total net soak time per capture occasion. If the relationships of p_i and effort were linear, this would imply that the underlying $p_2 = p_3 = p_4$.
p_{Length}; p_{Weight}	p_i is a function of individual fish size (length or weight) at first capture. This models the effect of net selectivity.
p_t	$p_2 \neq p_3 \neq p_4$. Capture probability is different for each interval due to stochastic variation or systematic effects that were not included in the above models or that were not detected because sample size was insufficient.

using the delta method for estimating the variance of a transformed variable (Seber 1982; Burnham et al. 1987), namely,

$$\hat{var}(TS) = \left[\frac{\partial}{\partial\sigma_{bs}}(10 \times \log_{10}\sigma_{bs})\right]^2 \times var(\sigma_{bs}). \quad (4)$$

All conversions between TS and fish TL were made with Love's equation for dorsal aspect (Love 1971), namely,

$$TS = 19.1 \times \log_{10}(L) - 0.9 \times \log_{10}(f) - 62.0, \quad (5)$$

where L is the length of the fish (cm) and f is the frequency of transmitted sound (kHz). In this study, the frequency was fixed at 200 kHz, so the equation simplifies to

$$TS = 19.1 \times \log_{10}(L) - 64.07. \quad (6)$$

In BMR (Johnson et al. 1996), few kokanee reach 425 mm (−33.0 dB), the size of the smallest piscivores in this study, so we initially estimated piscivore population size only for targets of at least −33.0 dB. A second estimate again used targets of at least −33.0 dB but also excluded all targets less than 20 m deep (sensu Johnson

and Martinez 2000), the approximate depth where water temperature is 10°C in the BMR in August. This temperature preference for lake trout is well documented (Martin and Olver 1980; Stewart et al. 1983; Sellers et al. 1998; Madenjian and O'Connor 1999).

The observation that neither of these estimates excluded kokanee whose size was "inflated" by TS variance compelled us to model their TS distribution to determine the apparent maximum length of kokanee. For any cohort of fish, such as an age-class, this distribution is a function of the length-frequency distribution compounded by the TS variation. We determined mean lengths of kokanee age-classes and the associated variances from the August vertical gill-net sample. Comparison with otolith aging data from previous cohorts (Stockwell and Johnson 1999) validated the age classification of kokanee by the length-frequency method. To estimate sampling variance, we obtained the TS variance for each tracked fish from equation (4) and calculated from these the grand mean variance and standard error ($\overline{SE}$), the positive root of the grand mean variance. We assumed that

errors were normally distributed around the TS and that the set of standard errors from all tracked fish therefore had a mean of 0 and a standard deviation equal to $\overline{SE}$. Across all tracked fish, TS and its standard deviation were uncorrelated ($R^2 = 0.013$). Thus, the magnitude of sampling variance is independent of fish size, and its contribution to the observed TS may be represented as additive:

$$TS = 19.1 \times \log_{10}(L) - 64.07 + \varepsilon, \qquad (7)$$

where L is distributed as (mean, SD of measured age-3 kokanee TLs [cm]) and ε is distributed as (0, $\overline{SE}$ [dB]).

We simulated TS for 100,000 age-3 kokanee; for L, we inserted a value that was randomly drawn from the distribution of age-3 kokanee TLs, and for ε we inserted a value that was randomly drawn from the distribution of TS standard errors. From the resulting TS distribution, we determined the 99th-percentile TS for age-3 kokanee. For application to our hydroacoustic survey data, any target that exceeded the threshold was provisionally considered to be a lake trout. The 99th percentile was chosen as the threshold that eliminated the most prey targets while still allowing estimation of a significant component of the piscivore population. We conducted the same analysis for age-2 kokanee to ensure that a negligible percentage of them could appear large enough to exceed the threshold.

We expected an analogous effect of TS variance on lake trout; in other words, some lake trout that were actually smaller than the length corresponding to the threshold TS would appear to exceed it, and vice versa. To estimate the relative error in each direction, we simulated lake trout TS in the same fashion as kokanee TS except that the distribution of lengths L_i conformed to the observed lake trout size structure. To determine the relative abundance of lake trout that were too small to be fully recruited to the gill nets, we apportioned netted lake trout to age-classes based on otolith-determined ages of lake trout recently taken from BMR (134 otoliths representing 14 age-classes; P.J.M., unpublished data), and we used the slope of the resulting catch curve ($R^2 = 0.90$) to back-calculate the abundance of ages 1–4 (age-0 fish were not considered). For these age-classes, length was assumed to be evenly distributed around the mean length at age. Target strength error amounts were randomly sampled from the TS error distribution and added to lengths, as before.

Converting target counts to population size.—Boat locations were recorded every 5 s by means of a Global Positioning System unit. Bottom depth was recorded for every ping. Based on these data and the effective beam width, the volume sampled was calculated trigonometrically for each 5-s interval and was summed to obtain each transect's sampled volume (v_i). Transect volumes were parsed into 1-m depth strata, and targets exceeding the piscivore size threshold were binned by these strata. Counts were divided by strata volumes to obtain densities (thereby effectively weighting targets by volume sampled), which were then averaged to yield the mean piscivore density (d_i) for each transect. Volume-weighted densities were summed to obtain mean observed densities ($\bar{d}_j$) for each of the reservoir's three basins ($j = 1$–3). We stratified by basin to increase precision, because we suspected that density would differ markedly across basins. The variance of basin mean density was estimated by

$$\mathrm{v\hat{a}r}(\bar{d}_j) = \frac{\sum_{i=1}^{k_j} v_i \times (d_{ij} - \bar{d}_j)^2}{v_{Sj}(k_j - 1)}, \qquad (8)$$

where k_j = the number of transects in basin j; v_{Sj} = the total volume sampled in basin j ($= \sum_{i=1}^{k_j} v_i$).

Using a combination of GIS and hydroacoustic depth data, we determined that Iola, Cebolla, and Sapinero basins contained roughly 10, 25, and 65%, respectively, of total reservoir volume and that these proportions remained nearly constant across the range of reservoir levels that occurred during the survey months. Whole-reservoir volumes on survey dates, available from the U.S. Bureau of Reclamation, made it possible to calculate basin volumes and to estimate whole-reservoir mean density, that is,

$$\hat{\bar{D}} = \frac{\sum(v_{Bj} \times \bar{d}_j)}{V}, \qquad (9)$$

where V = the whole-reservoir volume and v_{Bj} = the volume of basin j. Whole-reservoir estimates of N and its variance are thus calculated as

$$\hat{N} = V \times \hat{\bar{D}} \qquad (10)$$

and

$$\mathrm{v\hat{a}r}(\hat{N}) = V^2 \times \mathrm{var}(\hat{\bar{D}}). \qquad (11)$$

For equation (11), the variance of $\hat{\bar{D}}$ is estimated by

$$\mathrm{v\hat{a}r}(\hat{\bar{D}}) = \frac{\sum[v_{Bj}^2 \times \mathrm{v\hat{a}r}(\bar{d}_j)]}{V^2}. \qquad (12)$$

As above, the population estimated by N encompasses lake trout of piscivorous size.

To evaluate indirectly the possibility that bottom-oriented lake trout might be masked by the bottom echo, we determined distance from the bottom for every piscivore-sized target in the August survey. We reasoned that if many lake trout were undetectable due to their proximity to the bottom (≤ 1.5 m given the

tracking parameters), a fairly high percentage of those that were observed should appear just outside the bottom window.

Results

Experimental Gillnetting

In the three nights of experimental gillnetting conducted concurrently with hydroacoustic surveys, we caught 125 kokanee and 8 individuals belonging to species other than kokanee, substantiating the expectation that kokanee represented the vast majority of pelagic fish. Apparent age-classes of kokanee were easily discernible (Figure 2). The mean TL of 46 apparently age-3 fish was 399 mm (SD = 21 mm), which corresponds closely to the values (mean = 406 mm; SD = 18 mm) obtained by Stockwell and Johnson (1999) for age-3 kokanee (ages known from otoliths) on the same DOY. A Q–Q plot confirmed normality of the distribution (Ott 1993).

Hydroacoustic Estimates and TS Distribution Modeling

The initial estimated $\hat{N}$ based on targets of at least −33.0 dB was 15,727 (SE = 4,582). Imposing the greater than 20-m depth criterion lowered the estimate by 4,601 (Figure 3).

The mean TS standard error for all tracked fish ($\overline{SE}$) was 3.42 dB. Modeling of the TS distribution of age-3 kokanee using $\overline{SE}$ and the empirical length distribution reported above yielded a 99th-percentile TS of −30.62 dB (SE = 0.04; Figure 4), corresponding to a TL of 564 mm. A negligible percentage (0.02%) of modeled age-2 kokanee had larger TS values, so no further increase in the age-3 threshold was necessary. When the

FIGURE 3.—The top panel shows the number of piscivorous lake trout in Blue Mesa Reservoir, Colorado, estimated by four methods: (left to right) target strength (TS; $\geq$ −33.0 dB) observed at all depths during a hydroacoustic survey on 5–6 August 2002; TS ($\geq$ −33.0 dB) at depths greater than 20 m; a Lincoln–Petersen (L–P) estimate calculated from recapture of marked individuals 425 mm TL or larger, captured during 2000–2002; and a Cormack–Jolly–Seber (CJS) estimate calculated from the same mark–recapture data. The bottom panel shows the estimated number of piscivorous lake trout larger than 564 mm based on TS and on the recapture of marked fish. In both panels, error bars represent 95% confidence intervals (CV = coefficient of variation).

−30.62-dB threshold was applied to the hydroacoustic survey data, 57 tracked fish exceeded the threshold, resulting in a piscivore estimate of 2,073 (SE = 1,026; Figure 3). On average, piscivore tracks were comprised of 9.8 echoes (541 total pings).

Modeling of the lake trout TS distribution indicated that 2.79% of all age-1 or older lake trout would be smaller than the threshold but would appear larger (i.e., TL $\leq$ 564 mm but TS exceeding −30.62 dB; Figure 5). Conversely, 2.43% would exceed the threshold but would appear smaller, for a net underestimate of 0.36%, or seven individuals among the estimated 2,073 piscivores. We deemed this a negligible source of error.

The distances of piscivore targets from the bottom were widely distributed (Figure 6). The median distance from the bottom was 12.8 m. Volume weighting proved to have little effect on the distribution because most fish, regardless of their distance from
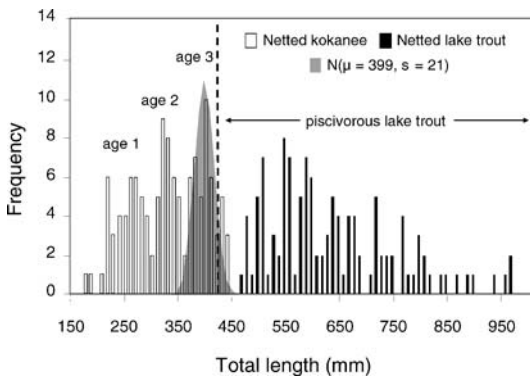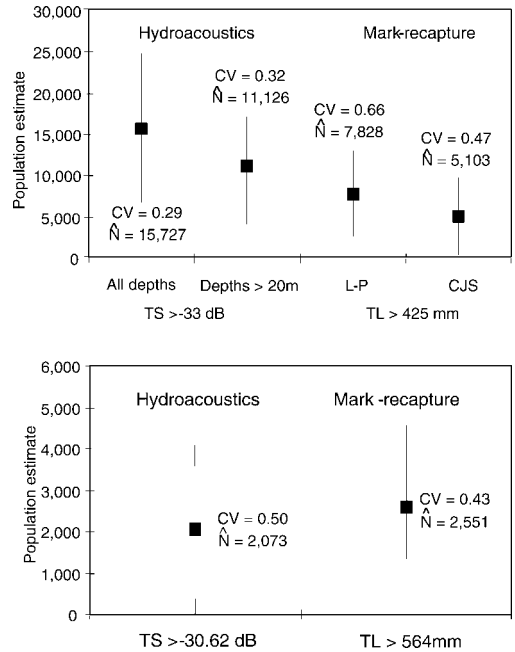

FIGURE 2.—Length-frequency distributions of kokanee caught in experimental vertical gill nets on 5–7 August 2002 and lake trout caught in horizontal gill nets on 20 April–23 May 2002 in Blue Mesa Reservoir, Colorado. The shaded region shows a normal distribution with the observed mean and SD for age-3 kokanee length.
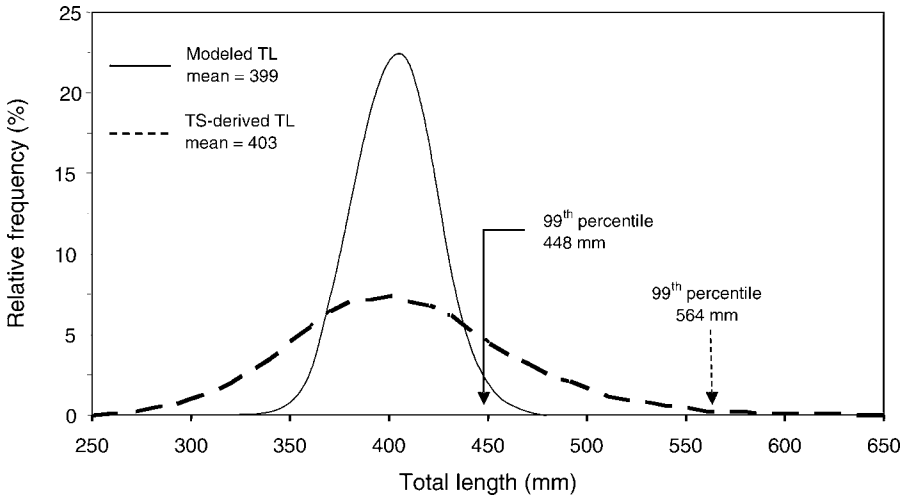
FIGURE 4.—Modeled total lengths of 100,000 age-3 kokanee based on the kokanee size distribution determined in Blue Mesa Reservoir, Colorado, during August 2002; the modeled lengths of the same fish as seen in hydroacoustic sampling (TS = target strength) are superimposed.

the bottom, were observed in strata that were sampled with similar effort.

Modeling of Mark–Recapture Data

A total of 939 lake trout were captured over the course of the mark–recapture study (Table 3). Overall tag loss rate was low to negligible (one fish, or 0.1%, had lost its tag). Goodness-of-fit tests of the most general CJS model (ϕ_t, p_t) indicated no evidence of overdispersion or structural lack of fit (TEST2 χ^2 = 0.17, df = 1; $\hat{c}$ = 0.49); thus, a c-value of 1 was used in subsequent analyses. The model receiving the most support represented ϕ as a function of weight and p as

a function of time; that is, capture probability was different for each netting occasion (Table 4). This model received 27.6% of the AIC_c weight; the difference in AIC_c values (ΔAIC_c) between this model and the next-best-supported model was 1.46. Several models had ΔAIC_c less than 2.0, indicating that they were all reasonable candidates; therefore, a model-averaged parameter estimate was calculated by weighting each model's estimate by its AIC_c weight and summing the weighted estimates. The variance of model-averaged parameter estimates was estimated by
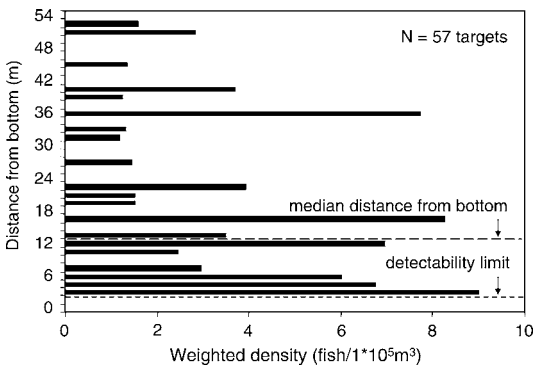

FIGURE 5.—Density-weighted distribution of piscivore (lake trout) distances from the bottom in Blue Mesa Reservoir, Colorado, during a hydroacoustic survey conducted on 5–6 August 2002.
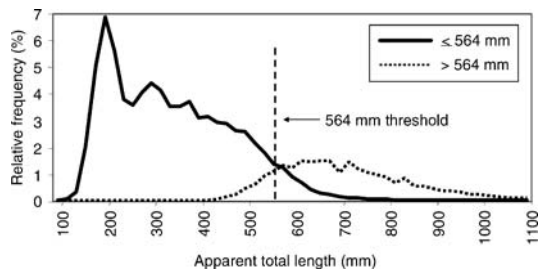

FIGURE 6.—Modeled total lengths of 15,283 lake trout as seen in hydroacoustic sampling (apparent TL), based on the lake trout size distribution in Blue Mesa Reservoir, Colorado, during 2001–2002. The 564-mm threshold represents the 99th-percentile TL of age-3 kokanee in August 2002 hydroacoustic sampling. The two distributions represent lake trout with actual TLs ≤564 mm and >564 mm, respectively; the values on the x-axis are apparent TLs given the sampling variance.

TABLE 3.—Release–recapture array for individually marked lake trout captured in horizontal gill nets in Blue Mesa Reservoir, Colorado, during May 2000–June 2002. A total of 939 lake trout were captured; total released ($\Sigma\ R_i$) plus mortalities exceeds 939 because R_i for each occasion (i) includes recaptures (j) from all previous occasions.

i	R_i	j 2	3	4	Mortalities	Total soak time (min)
1 (Spring 2000)	270	19	3	5	61	9,455
2 (Spring 2001)	327		4	10	49	8,492
3 (Fall 2001)	68			3	30	6,608
4 (Spring 2002)	155				21	5,421

$$\hat{var}(\hat{\bar{\theta}}) = [\sum w_i \sqrt{var(\hat{\theta})_i + (\hat{\theta}_i - \hat{\bar{\theta}})^2}]^2, \quad (13)$$

where $\hat{\bar{\theta}}$ is the model-averaged parameter estimate, θ_i are the parameter estimates from individual models, and w_i are the models' AIC_c weights. Burnham and Anderson (2002) define this quantity as unconditional variance in that it is not conditional upon a particular model (although it is conditional upon the candidate model set).

The estimated N was 5,103 (SE = 2,412), which was much lower than either of the initial hydroacoustic estimates (Figure 3). A Lincoln–Petersen estimator calculated for purposes of comparison yielded $\hat{N}$ equal to 7,828; the coefficient of variation for this estimator was 0.66 versus 0.43 for the CJS estimator. For comparison with the hydroacoustic estimate from targets of at least -30.62 dB, the CJS estimate was repeated based on only 564-mm and larger lake trout ($N = 66$) captured in fall 2001. Parameter estimates

were again averaged to obtain $\hat{N}$ equal to 2,551 (SE = 1,095; Figure 3).

Discussion

This study afforded an uncommon opportunity to compare hydroacoustic estimates of predator abundance with those from a rigorous mark–recapture study, allowing us to investigate the sources, direction, and magnitude of bias in a hydroacoustic estimate.

In the mark–recapture study, analytical practices, including a likelihood-based approach to model parameter estimation and the use of AIC_c to select best-approximating models, are supported by strong theory (Burnham and Anderson 2002). Randomized net locations and netting in multiple seasons facilitated identification of time-specific capture heterogeneity, which is often an important source of bias (White et al. 1982). Cormack–Jolly–Seber models can also underestimate population size if there is individual capture heterogeneity (Gilbert 1973; White et al. 1982); however, models that included size- or release-condition-specific capture probability received very little support ($\Delta AIC_c > 10$) in this study. Thus, use of the mark–recapture estimates as benchmarks is justifiable.

The initial hydroacoustic estimate of piscivore abundance was over three times that obtained by mark–recapture. The fact that application of the 20-m minimum depth criterion lowered the initial estimate by nearly 30% strongly suggests that many kokanee targets were being included, as thermal constraints probably prevented most lake trout from appearing above that depth. Because kokanee routinely appear

TABLE 4.—Results of selection of models representing hypotheses about apparent survival (ϕ_i) and capture probability (p_i) of lake trout in Blue Mesa Reservoir, Colorado. Selection was based on Akaike's information criterion corrected for small-sample bias (AIC_c). Models having AIC_c differences (ΔAIC_c) less than 2 have substantial empirical support. Models with ΔAIC_c greater than 10 are excluded. The number of estimated parameters (K) is also given. See Table 2 for more information about the models listed.

Model	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	K
$\phi_{Weight}2, p_t$	370.76	0	0.28	1.00	6
$\phi_{Weight}3, p_t$	372.22	1.46	0.13	0.48	7
$\phi_{Weight}2, p_{t+Weight}$	372.59	1.82	0.11	0.40	7
$\phi_{Weight}2, p_{Length+effort+fall}$	372.66	1.90	0.11	0.39	7
$\phi_{Weight}2, p_{t+length}$	372.66	1.90	0.11	0.39	7
ϕ_{Weight}, p_t	373.36	2.60	0.075	0.27	5
$\phi_{Length}3, p_t$	373.69	2.93	0.069	0.23	7
$\phi_{Length}2, p_t$	374.45	3.69	0.044	0.16	6
ϕ_{Length}, p_t	375.45	4.69	0.026	0.096	5
$\phi_{Weight}2, p_{Fall}$	375.71	4.95	0.023	0.084	5
$\phi_{Weight}2, p_{Length+fall}$	377.63	6.87	0.0090	0.032	6
ϕ, p_t	377.84	7.08	0.0080	0.029	4
$\phi_{Release\ condition}, p_t$	377.95	7.19	0.0076	0.028	5
ϕ_{Winter}, p_t	379.78	9.02	0.0030	0.011	5
ϕ_{Trend}, p_t	379.78	9.02	0.0030	0.011	5
$\phi_{Length+release\ condition}, p_t$	380.01	9.25	0.0027	0.0098	6

below 20 m in BMR (Hardiman et al. 2004), it is reasonable to assume that the second estimate was similarly inflated by kokanee. By contrast, the hydroacoustic estimate for lake trout above the 99th-percentile threshold of kokanee TS was within 20% of the CJS estimate for nominally the same-sized subset of lake trout, and the confidence intervals almost entirely overlapped.

Strong agreement with the mark–recapture estimate suggests that the exclusion of almost all targets that potentially were misidentified kokanee removed the major source of bias in the hydroacoustic estimate. However, three other potential sources of bias require consideration: (1) targets within the bottom window could go undetected, biasing the estimate downward; (2) the TS–length equation could introduce a systematic bias in either direction; and (3) predators could appear smaller or larger than their true size owing to TS variance, which would cause them either to be mistaken as prey or inappropriately classified as large piscivores.

Lake trout are demersal in other locations (Luecke et al. 1999; D. Yule, U.S. Geological Survey, Lake Superior Biological Station, unpublished data), but the distribution of piscivore distances from the bottom in this survey suggests that this was not the case in BMR. There was some apparent concentration of piscivores in the strata immediately above the bottom window, raising the possibility that others may have gone undetected within it. Given the irregular distribution of targets' distances off the bottom and a median distance of 12.8 m, it seems unlikely that a large percentage remained undetected. Further, the mean distance from the bottom at which lake trout were captured in vertical gill nets during 1994, 1995, and 2002 was 17.2 m (B.M.J., unpublished data).

As with all hydroacoustic population size estimation procedures, our method assumes that the equation relating TS to fish length is accurate. The primary shortcoming of general TS–length regressions, such as Love's (1971) equation, is that they do not account for physiological, behavioral, and environmental influences on TS, most of which are "parochial" (Fleischer et al. 1997). For this reason, in survey situations where a mean TS is needed to scale integrated echoes from dense schools, it is considered theoretically optimal to estimate mean TS in situ from individuals in low-density areas (Rose 1992; Gauthier and Rose 2001a). This approach has no direct application to systems like BMR, where (1) fish are widely dispersed at night, (2) TS is measurable for all fish, and (3) density is best estimated by echo counting. Alternatively, a number of species-specific equations have been developed (e.g.,

Foote 1987), but most are for commercial marine species and no standard equation for freshwater salmonids has emerged. Although Love's (1971) experiments did not include salmonids, the dorsal-aspect equation is suitable for a variety of species (e.g., Warner et al. 2002) and continues to be employed in salmonid surveys (Goyke and Brandt 1993; Thiesfield et al. 1999; but see Hartman and Nagy 2005 on the perils of "borrowing" species-specific equations).

We assumed that any systematic bias affected equal-sized kokanee and lake trout similarly given their phylogenetic similarity. If so, the results would be acceptable because we were primarily interested in the number of targets that exceeded a threshold rather than the exact size of fish represented by the threshold. The correspondence of our hydroacoustic estimate with the benchmark estimate from mark–recapture suggested that Love's (1971) equation provided a reasonably accurate conversion, but our method of parsing TS variance could be used with any TS equation.

For lengths of age-3 kokanee, the experimental gill nets provided an unbiased distribution, which was corroborated by comparison with the size structure in other years (Stockwell and Johnson 1999) and with the bycatch from horizontal gillnetting in the present study (D.B., unpublished data). To examine the fit of our predicted error distribution (mean $= 0$, SD $= \overline{\text{SE}}$) to the survey data, we subtracted each tracked fish's mean σ_{bs} from the values of each echo comprising the track and transformed the results into decibels (Figure 7). Note that actual statistics for each tracked fish (mean and SD) were calculated in the linear domain and then transformed; here, we express error from individual echoes in decibels only so as to evaluate the distribution's suitability for generating values of ε used in the simulation of fish TS. Although the transformed errors are not normally distributed (Kolmogorov's $D < 0.01$), this nonnormality results from a higher-than-expected percentage of observations being close to zero coupled with an elongated left tail (an asymmetry that would be expected given a symmetrical distribution of nontransformed errors, which is implied, though not prescribed, by use of the mean σ_{bs} to estimate fish size). Our assumption of normality is therefore conservative in that it overestimates the amount by which error can increase the TS of a given target. We do not know the generalizability of this result, although both the literature and personal observation furnish related examples (Gauthier and Rose 2001b; P.J.M., unpublished data). In any case, the ability to model errors as normal is merely convenient; one could fit a function to almost any error distribution.

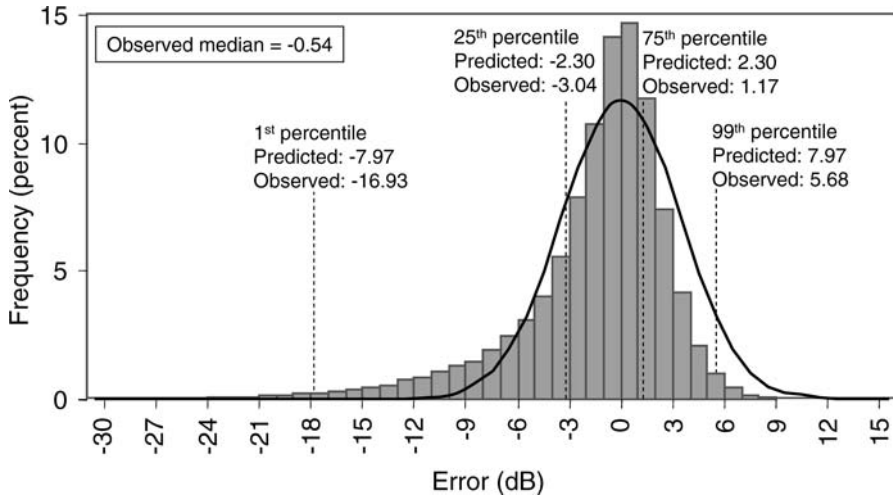A general goal of this study was to assess the value

FIGURE 7.—Distribution of target strength errors (bars) versus a normal prediction line from all fish that were tracked during a hydroacoustic survey of Blue Mesa Reservoir, Colorado, on 5–6 August 2002.

of hydroacoustics for rapid assessment of predator–prey relationships in simple fish communities, such as those encountered in many western U.S. reservoirs. To that end, we discriminated between predator and prey by establishing a threshold rather than by using a more elaborate means of separating the composite TS distribution function, such as Bayesian procedures (e.g., Hammond and Swartzman 2001). The method upon which we settled is analytically and computationally simpler but has two potential drawbacks: (1) the predator estimate is susceptible to bias if predators that are smaller than the threshold but appear larger outnumber those that exceed the threshold but appear smaller, or vice versa; (2) the predator estimate excludes the portion of the population that falls below the threshold size.

In this study, modeling of the predator TS distribution indicated that the numbers of predators erroneously classified on either side of the threshold were essentially offsetting. The likelihood of this being true in other systems should increase as the threshold size increases, because the modes of size distributions tend to meld in older ages, particularly in populations of long-lived fishes with consistent recruitment. However, due to the uncertainty added by error variance, this outcome cannot be assumed and the predator size for which it will be true cannot be predicted informally. It is therefore essential to determine the predator TS distribution, and this requires a thorough characterization of predator size structure. Considerable sampling effort may be required to develop a trustworthy length-frequency distribution

for relatively rare predators, thereby obviating some of the efficiency that makes hydroacoustic assessment attractive.

The ramifications of excluding smaller predators from hydroacoustic abundance estimates are similarly system specific. Blue Mesa Reservoir was well suited for our approach because the pelagic zone can reasonably be viewed as a two-species system and because kokanee have few and well-defined age-classes with low variances. Both conditions favor sharper differentiation between species than would be possible with a more complex species assemblage. In a system having multiple prey species of overlapping size, one could still determine a probability density function for the aggregated prey lengths and thereby estimate maximum prey TS. If nonpiscivorous fish—either additional species or prey individuals that have escaped the predation window—equal the largest predators in size, our approach would be unworkable because addition of TS error would yield a threshold exceeding the largest TS observed. Conversely, if the predator–prey size disparity is large, targets may be fully distinguishable without further effort to resolve them. However, piscivores generally consume prey items that are 20–45% of their length (Keeley and Grant 2001). For lake trout preying upon salmonids, the ratio is often 20–35% (Yule and Luecke 1993; Ruzycki et al. 2003). Thus, a manager considering our method would have to assess local biological conditions to determine whether a population size estimate for only larger fish is useful. We suspect that it often is, because the relative sizes of predators and prey play

a functional role in their relationship. For example, Johnson and Martinez (2000) found that prey salmonids in BMR (primarily kokanee) comprise about 30% of the diet of lake trout smaller than 600 mm but make up nearly 80% of the diet of lake trout larger than 600 mm. As a result, larger-sized lake trout accounted for a disproportionate amount of the total prey biomass consumed, despite being outnumbered by their smaller counterparts. The population size estimate for all lake trout larger than 564 mm accounted for enough of the consumption demand to afford a useful minimum consumption estimate. Finally, a researcher willing to accept less certainty about abundance could lower the threshold on predicted prey sizes (e.g., to the 95th percentile) and could thereby increase sample size and then use known prey or predator length-frequency distributions to "back out" the inappropriate targets. Arguably, a benefit of our approach is that the prey size confidence level quantifies the uncertainty, making explicit such trade-offs between accuracy and precision.

At BMR, modeling the distribution of prey TS values established a threshold prey TS that afforded a fourfold increase in the number of identifiable lake trout relative to the rule of thumb (2 × length), and commensurate improvement in the width of confidence intervals was made. The resulting estimate showed very good agreement with a rigorous mark–recapture estimate of the same-sized fish, and the levels of precision were comparable. Although predators that are below the threshold are inevitably excluded, the resulting estimate was adequate for the purpose of estimating minimum consumption demand by lake trout. Further, it could be used in conjunction with the empirical length-frequency distribution to estimate the size of the entire population. These results suggest that in suitable systems, sound predator population size estimates may be obtained efficiently by means of hydroacoustics without sacrificing rigorous discrimination of predator targets.

References

Beauchamp, D. A., C. M. Baldwin, J. L. Vogel, and C. P. Gubala. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. Canadian Journal of Fisheries and Aquatic Sciences 56(Supplement):128–139.

Brandt, S. B. 1996. Acoustic assessment of fish abundance and distribution. Pages 385–432 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Burczynski, J. J., and R. L. Johnson. 1986. Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (Oncorhynchus nerka). Canadian Journal of Fisheries and Aquatic Sciences 43:1776–1788.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Bethesda, Maryland.

Dawson, J. J., and W. A. Karp. 1990. In situ measures of target strength variability of individual fish. ICES (International Council for the Exploration of the Sea) Cooperative Research Report 189:264–273.

Ehrenberg, J. E., and T. C. Torkelson. 1996. Application of dual-beam and split-beam target tracking in fisheries acoustics. ICES Journal of Marine Science 53:329–334.

Fleischer, G. W., R. L. Argyle, and G. L. Curtis. 1997. In situ relations of target strength to fish size for Great Lakes pelagic planktivores. Transactions of the American Fisheries Society 126:786–794.

Foote, K. G. 1980a. Effect of fish behavior on echo energy: the need for measurements of orientation distributions. ICES (International Council for the Exploration of the Sea) Cooperative Research Report 39:193–201.

Foote, K. G. 1980b. Importance of the swimbladder in acoustic scattering by fish: a comparison of gadoid and mackerel target strengths. Journal of the Acoustical Society of America 67:2084–2088.

Foote, K. G. 1987. Fish target strengths for use in echo integrator surveys. Journal of the Acoustical Society of America 82:981–987.

Foote, K. G. 1991. Summary of methods for determining fish target strength at ultrasonic frequencies. ICES Journal of Marine Science 48:211–217.

Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Gauthier, S., and G. A. Rose. 2001a. Diagnostic tools for unbiased in situ target strength estimation. Canadian Journal of Fisheries and Aquatic Sciences 58:2149–2155.

Gauthier, S., and G. A. Rose. 2001b. Target strength of encaged Atlantic redfish (Sebastes spp.). ICES Journal of Marine Science 58:562–568.

Gilbert, R. 1973. Approximation of the bias in the Jolly–Seber capture–recapture model. Biometrics 29:501–526.

Goyke, A. P., and S. B. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. Transactions of the American Fisheries Society 122:870–883.

Gunderson, D. R. 1993. Surveys of fisheries resources. Wiley, New York.

Hammond, T. R., and G. L. Swartzman. 2001. A general procedure for estimating the composition of fish school clusters using standard acoustic survey data. ICES Journal of Marine Science 58:1115–1132.

Hardiman, J. M., B. M. Johnson, and P. J. Martinez. 2004. Do predators influence distribution of age-0 kokanee in a Colorado reservoir? Transactions of the American Fisheries Society 133:1366–1378.

Hartman, K. J., and B. W. Nagy. 2005. A target strength relationship for striped bass and white perch. Transactions of the American Fisheries Society 134:375–380.

Johnson, B. M., and P. J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:115–131.

Johnson, B. M., J. D. Stockwell, and K. Bonfantine. 1997. Ecological effects of reservoir operations on Blue Mesa Reservoir. U.S. Bureau of Reclamation, Progress Report, Grand Junction, Colorado.

Johnson, B. M., M. J. Wise, B. Herwig, G. Szerlong, D. Faber, and B. Byall. 1996. Ecological effects of reservoir operations on Blue Mesa Reservoir. U.S. Bureau of Reclamation, Progress Report, Grand Junction, Colorado.

Keeley, E. R., and J. W. A. Grant. 2001. Prey size of salmonid fishes in streams, lakes, and oceans. Canadian Journal of Fisheries and Aquatic Sciences 58:1122–1132.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Love, R. H. 1971. Dorsal-aspect target strength of an individual fish. Journal of the Acoustical Society of America 46:746–752.

Love, R. H. 1977. Target strength of an individual fish at any aspect. Journal of the Acoustical Society of America 62:1397–1403.

Luecke, C., M. W. Wengert, and R. W. Schneidervin. 1999. Comparing results of a spatially explicit growth model with changes in the length-weight relationship of lake trout (Salvelinus namaycush) in Flaming Gorge Reservoir. Canadian Journal of Fisheries and Aquatic Sciences 56(Supplement):162–169.

MacLennan, D. N., and E. J. Simmonds. 1992. Fisheries acoustics. Chapman and Hall, London.

MacLennan, D. N., P. G. Fernandes, and J. Dalen. 2002. A consistent approach to definitions and symbols in fisheries acoustics. ICES Journal of Marine Science 59:365–369.

Madenjian, C. P., and D. V. O'Connor. 1999. Laboratory evaluation of a lake trout bioenergetics model. Transactions of the American Fisheries Society 128:802–814.

Martin, N. V., and C. H. Olver. 1980. The lake charr, Salvelinus namaycush. Pages 205–277 in E. K. Balon, editor. Charrs: salmonid fishes of the genus Salvelinus. Dr W. Junk, The Hague, The Netherlands.

Mukai, T., and K. Iida. 1996. Depth dependence of target strength of live kokanee salmon in accordance with Boyle's law. ICES Journal of Marine Science 53:245–248.

Ona, E. 1990. Physiological factors causing natural variations in acoustic target strength of fish. Journal of the Marine Biological Association of the United Kingdom 70:107–127.

Ott, R. L. 1993. An introduction to statistical methods and data analysis, 4th edition. Wadsworth, Belmont, California.

Powell, T. 1981. Standardized fish sampling procedures for lakes and reservoirs. Colorado Division of Fish and Wildlife, Fort Collins.

Ransom, B. H., T. W. Steig, S. V. Johnston, J. E. Ehrenberg, T. C. Torkelson, and P. A. Nealson. 1999. Using hydroacoustics for fisheries assessment. Hydroacoustic Technology Incorporated, Seattle, Washington.

Rose, G. A. 1992. A review of problems and new directions in the application of fisheries acoustics on the Canadian East Coast. Fisheries Research 4:105–128.

Rose, G. A., and W. C. Leggett. 1988. Hydroacoustic signal classification of fish schools by species. Canadian Journal of Fisheries and Aquatic Sciences 45:597–604.

Rudstam, L. G., and B. M. Johnson. 1992. Development, evaluation, and transfer of new technology. Pages 507–524 in J. F. Kitchell, editor. Food web management: a case study of Lake Mendota. Springer-Verlag, New York.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23–37.

Ruzycki, J. R., W. A. Wurtsbaugh, and C. Luecke. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah–Idaho. Transactions of the American Fisheries Society 130:1175–1189.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd edition. Macmillan, New York.

Sellers, T. J., B. R. Parker, D. W. Schindler, and W. M. Tonn. 1998. Pelagic distribution of lake trout (Salvelinus namaycush) in small Canadian Shield lakes with respect to temperature, dissolved oxygen and light. Canadian Journal of Fisheries and Aquatic Sciences 55:170–179.

Simmonds, E. J., and F. Armstrong. 1990. A wideband echosounder: measurements on cod, saithe, herring, and mackerel from 27 to 54 kHz. ICES (International Council for the Exploration of the Sea) Cooperative Research Report 189:381–387.

Simmonds, E. J., and P. J. Copeland. 1989. Species recognition: results from a wide-band echo-sounder 27–54 kHz. Proceedings of the Institute of Acoustics 11:54–60.

Simmonds, E. J., N. J. Williamson, F. Gerlotto, and A. Aglen. 1992. Acoustic survey design and analysis procedure: a comprehensive review of current practice. ICES (International Council for the Exploration of the Sea) Cooperative Research Report 187.

Stewart, D. J., D. W. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout: application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681–698.

Stockwell, J. D., and B. M. Johnson. 1999. Field evaluation of a bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 56(Supplement):140–151.

Warner, D. M., L. G. Rudstam, and R. A. Klumb. 2002. In situ target strength of alewives in freshwater. Transactions of the American Fisheries Society 131:212–223.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, New Mexico.

White, G. C., and K. P. Burnham. 1999. Program MARK—survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.

Yule, D. L., and C. Luecke. 1993. Lake trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. Transactions of the American Fisheries Society 122:1058–1069.