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ARTICLE

An Assessment Model for a Standard Gill Net Incorporating Direct and Indirect Selectivity Applied to Walleye

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Abstract
Fisheries managers regularly use catch-per-effort (CPE) statistics and length-frequency distributions from standard gill-net surveys to inform future management activities. The data from these surveys is implicitly tied to the net's selectivity, and caution should be used when not accounting for selectivity. We combined indirect and direct methods for estimating the parameters of absolute selectivity by using data from Minnesota's standard gill-net surveys for Walleye *Sander vitreus*, enabling the estimation of density from CPE. The indirect piece used a state-wide gill-net database and generalized linear modeling to identify a set of possible shapes for the selectivity curves. The direct piece added information based on 94 mark–recapture experiments that were paired with standard gill-net surveys. The resulting statistical assessment model used a bi-lognormal-shaped selectivity curve that was geometrically similar for each mesh, and it estimated fishing intensity that differed substantially with mesh size. Applications of the selectivity model allow the estimation of Walleye density as CPE divided by absolute selectivity by length-bin. The estimated absolute selectivity for the Minnesota standard gill net increased with increasing Walleye length to a peak of 0.76 ha/net at 535 mm and then decreased to about 0.26 at about 800 mm (1.0 and 0.34 relative selectivities, respectively). Fishing intensity increased with mesh size, so the selectivity curves for the individual meshes and that for the standard gill net (5 meshes in series) differed substantially from the curves that have resulted from indirect selectivity models that have ignored size-dependent encounter probabilities and assumed equal contact probabilities for all meshes. We caution investigators that adjusting gill-net catch data with indirect selectivity models that assume equal contact probabilities for each mesh may introduce considerable bias to estimates of population abundance and length distributions.

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Walleye *Sander vitreus* populations in Minnesota lakes have been the primary focus of the fisheries surveys that have been conducted by the Minnesota Department of Natural Resources (MDNR) by using standard gill nets since the late 1930s (Moyle 1949). Fisheries managers use the catch-per-effort (CPE) statistics and length-frequency distributions from these surveys to inform decisions on stocking, fishing regulations, and harvest targets, with the assumption that changes in the gill-net indices adequately reflect changes in the populations.

Gill nets are highly size selective, and there are consequences that are associated with failing to address or misestimating selectivity. Frater and Stefansson (2019) tested the consequences of size selectivity in gill-net surveys on the growth curve parameter estimates via simulation, and they found that failure to address selectivity led to biases in understanding fish growth. Likewise, Thorson and Prager (2011) used simulations to demonstrate the importance of incorporating selectivity when doing a catch-curve analysis. Such examples have led researchers to integrate survey size selectivity into various population assessment analyses (e.g., Taylor et al. 2005; Xu et al. 2018).

There has been extensive research on methods for estimating gill-net selectivity. Hamley (1975) reviewed and summarized the early work on selectivity and noted that the exact definition of selectivity varies depending on what part of the capture process is being assessed (e.g., the proportion of fish that were caught for the total population or the proportion of the population that encountered the net). Several physical processes give rise to the selectivity curve of a gill net (often referred to as the total selectivity). Using the model that was expressed by Anderson (1998), we define selectivity here as a multiplicative process of the probability that a fish will approach a net (encounter), the probability that an approaching fish will then contact the mesh rather than detect and avoid it (contact), and the probability that a fish that contacts the mesh is retained (retention). Many mathematical descriptions of gill-net selectivity do not include possible avoidance based on mesh size or twine thickness (e.g., Hamley 1975).

Encounter probabilities have been assumed to be independent of fish size (or ignored), treated as power functions of fish size (Rudstam et al. 1984), or estimated through additional comparisons with statistical kill-at-age model estimates of abundance and size structure (Anderson 1998). Contact probabilities are likely to differ with mesh size. Hamley (1975) noted that the mesh construction of a gill net likely influences fish contact with the gill net, as twine thickness and hanging ratios affect the visibility of the net. The retention curve for each mesh describes the relative probability of capture for fish of various sizes after contacting that mesh. Many investigators use Baranov's (1977) assumption of geometric similarity and consider retention to be a function of the relative size of the fish and mesh; that is, the mean or mode and the spread of the retention curve are proportional to mesh size. The principle of geometric similarity suggests that the most vulnerable-sized fish for various meshes would be retained with equal probability (i.e., the retention curves for all mesh sizes have the same magnitude); however, that follows only if the expressions for probability of encounter and probability of contact are unimportant. Some authors further divide retention into initial capture and subsequent retention components (Regier and Robson 1966; Prchalová et al. 2011), a distinction that is important when considering the saturation of nets that are set for varying lengths of time, but this step is unnecessary here.

Ideally, one would estimate gill-net selectivity directly by sampling a population with a known abundance and size distribution; however, such information is difficult to obtain, as it would involve marking and releasing a large number of fish over a wide size range and a substantial gill-net effort afterwards. Therefore, such direct methods are rare. In a classic study, Hamley and Regier (1973) estimated selectivity and catchability for various meshes directly by repeatedly gillnetting a marked Walleye population. They found that selectivity by mesh was bimodal due to catch by wedging and by tangling and that catchability increased with mesh size. In a direct analysis, catchability is the fraction of the population of a given length that is caught in a unit of fishing effort (Ricker 1975). The most frequent method for estimating selectivity is via statistical kill-at-age models or virtual population analyses (Quinn and Deriso 1999). Using these methods, selectivities are derived from estimates for the population at age or length that is then assumed to be available for sampling by the net. These are also direct methods in the sense that they rely on data about the population that are beyond those that are obtained with the gill-net survey itself. These models incorporate kill-at-age estimates and auxiliary data, such as from standard gill-net surveys, to estimate population size and survey selectivities and catchabilities at age, and they may not address the selectivity of separate meshes. Given the data demands of the direct methods, many investigators use an indirect method to estimate relative selectivity with the goal of providing fisheries managers with a way to correct for some of the size selectivity of the gear.

In indirect analyses, relative selectivity estimates are made by examining how the catch of various lengths is distributed across different mesh sizes. Indirect methods have advantages in that the essential data is easily obtained when fishing with standard nets and statistical tools are readily available. Millar and Holst (1997) developed a statistical approach for estimating gill-net retention curves indirectly by using generalized linear modeling and maximum likelihood, assuming Poisson-distributed errors (termed the SELECT method).

Several assumptions are necessary for computing selectivities when an indirect analysis is used (Millar and Holst 1997; Anderson 1998). One must assume that similar-sized frequency distributions encounter each mesh. Another assumption that is often applied is that all meshes are equally likely to be contacted after being encountered. Alternative ideas that contact probabilities are proportional to mesh size or otherwise differ are rarely considered. Most applications of indirect methods to gill nets assume that after contact, the retention probabilities are equal for all meshes when they are expressed as a function of the relative size of the fish and the mesh (following the principle of geometric similarity). We will refer to the second assumption as one of equal contact probabilities (Anderson 1998), although similar ideas have been termed equal fishing power (Millar and Holst 1997) or equal fishing intensity (Brenden and Zhao 2012). The assumption that is made about contact probabilities influences the shape of the fitted retention curves and strongly drives the relative selectivity estimate of a standard net. Estimating the length distribution for the portion of the fish population that approaches or contacts the gill net rather than that for the population at large is perhaps the most important limitation of this modeling approach, as size-dependent approach rates are not estimable by SELECT methods (Anderson 1998). Therefore, due to the assumptions that are necessary for an indirect analysis, the selectivity that is estimated this way generally cannot be used to infer the size structure of a population.

A New Approach

A new approach is needed for testing assumptions and identifying models that may provide a more realistic description of the selectivities and length distributions for fish that approach nets, and other data sources would be essential. The foundation of the approach is based on a simple equation. If one assumes that encounter is dependent on fish size, contact is dependent on mesh size, and retention is dependent on both then the fundamental catch equation is as follows:

$$C_{L,M} = N_L \alpha_L \beta_M \gamma_{L,M} E_M, \tag{1}$$

where $C_{L,M}$ is the number of fish caught of length L with mesh M, N_L is the number of fish of length L, α, β, γ are the probability of encounter, contact, and retention per unit effort, respectively, and E_M is fishing effort with mesh M. After dividing through by lake area A (in hectares) and rearranging yields,

$$D'_L = \left(C_{L,M}/E_M\right)/\left(A \alpha_L \beta_M \gamma_{L,M}\right) = I_{L,M}/\varsigma_{L,M}, \tag{2}$$

where D'_L is the estimated density of fish of length L, $I_{L,M}$ is the CPE for fish of length L in mesh M, and $\varsigma_{L,M}$ is the absolute selectivity for fish length L in mesh M. The units of absolute selectivity are hectares/unit effort, so it is a measure of the effective area fished for fish of length L. Therefore, the relationship between density and absolute selectivity-adjusted gill-net CPE is assumed to be proportional. The absolute selectivity for fish length L in mesh M is

$$\varsigma_{L,M} = \left[s_{L,M}/\max\left(s_{L,M}\right)\right]\xi_M, \tag{3}$$

where $s_{L,M}$ is the selectivity curve for length-bin L in mesh M and ξ_M is the fishing intensity of mesh M for the most vulnerable size, here defined as the effective area fished (in hectares) by a unit effort of mesh M.

Indirect analyses that use a large set of gill-net catch data and the SELECT method can provide the initial parameters for the selectivity curve. The initial fishing intensity parameters can come from a direct analysis (e.g., derived from Hamley and Regier's (1973) catchability curves). These two sets of parameters can then be estimated numerically by minimizing an objective function that includes components on selectivity (indirect) and discrepancies between density observations and density predictions (direct).

This statistical assessment model approach combines indirect and direct analyses to estimate absolute selectivity that allows the prediction of density from CPE and describes how fish of a specific size are distributed among meshes. The structure of this approach is appropriate if encounter probabilities vary as a power function of fish size, (conditional) contact probabilities vary by mesh, and (conditional) retention probabilities follow the principle of geometric similarity and are reasonably approximated by using a parametric selectivity curve. The mathematical form of this process model simplifies to resemble, superficially, an indirect analysis model (a contact–retention selectivity model); however, the coefficients that define fishing intensity and the shape of the relative selectivity curve incorporate encounter effects and no longer correspond exactly to the contact and retention curves.

This statistical assessment model approach is analogous to statistical kill-at-age models. The latter age-structured models use the Baranov's catch equation, make assumptions on fishing selectivity, and recognize that the kill-at-age is measured with error (Quinn and Deriso 1999). Both model approaches estimate parameters in a likelihood framework. The statistical kill-at-age modeler uses information on the relative magnitudes of the variances associated with the kill and survey data sets to set appropriate weights for the objective function components during the model-fitting process, whereas the analyst using this statistical assessment modeling approach is uncertain of some of the observation and process error variances and is challenged to set weights.

Objectives

The objectives of this investigation were to estimate selectivity for Minnesota's standard gill net for Walleye and to determine the degree to which Walleye density was related to gill-net CPE. We evaluated whether the relationship between density and gill-net CPE was proportional and whether that relationship could be improved with the inclusion of environmental variables. Most importantly, we used multiple sources of data, including Walleye population estimates and gill-net surveys from many lakes, to construct a statistical assessment model (SAM) with parameters that were estimated numerically by minimizing an objective function and to determine the precision of those models for use in estimating Walleye density from standard survey data for gill-net CPE by length. We combined indirect and direct methods to estimate the parameters, including fishing intensity. Lastly, we compared the estimates of Walleye abundance and length distributions from the SAM with predictions from two existing models.

METHODS

Gill-net survey data source.— Moyle and Burrows (1954), Scidmore (1970), and the MDNR (1993) documented the procedures for using gill nets to conduct survey sampling in lakes in Minnesota. The gill nets are 76.20 m (250 ft) in length and 1.83 m (6 ft) in depth, consisting of five panels that are 12.24 m (50 ft) in length with 38-, 51-, 64-, 76-, and 102-mm stretch meshes each, with the following bar measures: 19.05, 25.4, 31.75, 38.1, and 50.8 mm (0.75, 1.0, 1.25, 1.5, and 2.0 in). Each mesh panel is constructed with a hanging ratio of 50% (1/2-basis). Initially Minnesota's standard survey gill nets were constructed with linen twine, and from the 1960s to the 1990s they were constructed with #69 (Denier/Ply: 210/3) twisted nylon twine for the three smallest mesh panels and #104 (210/4) twisted nylon twine for the two largest mesh panels. Recent nets have been constructed with two-strand twisted nylon twine for all meshes. From the mid-1990s to the 2000s the MDNR fish crews used both nylon twine types. In most cases, the gill nets were set in established locations that were perceived to be good Walleye habitat (i.e., effort was not randomly distributed and anoxic waters were avoided) at a time of year that has been standardized for the lake (most surveys were conducted from mid-June through mid-September and gill-net catchability may vary over this period). Each net was left in the water for approximately 24 h.

To design a tool that is applicable across a range of Walleye lakes, we used Walleye gill-net catch data that was pooled from hundreds of lakes that were surveyed by MDNR staff between 1984 and 2017. In these surveys, total fish lengths were measured to the nearest mm (or the nearest tenth of an inch from 1984 to 1992) and recorded by net and mesh panel ($N = 348{,}888$; $N = 11{,}052$ for 1984 to 1995; $N = 156{,}276$ for 1996 to 2006; and $N = 181{,}560$ for 2007 to 2017). We pooled these fish measurement data by mesh and 10-mm length-bins (the mid-points of the length-bins were used in the selectivity analyses). The use of the 10-mm bins minimized the analytical consequences of digit bias (human preferences for lengths ending in 0, 2, and 5 in this data set).

Indirect analyses.— We analyzed the pooled catch data from Walleye gill-net surveys that were conducted from 1984 to 2017 by using the SELECT method (Millar and Holst 1997). Five common gill-net retention curves were explored for potential use: normal with common spread, normal with spread proportional to mesh size, lognormal, bi-normal, and bi-lognormal. The bi-normal and bi-lognormal curves are composed of two normal or lognormal distributions to account for potential differences in wedging and tangling by fish length. We assumed that the meshes had equal contact probabilities, and we generally assumed geometric similarity between gill-net meshes (the normal retention curve with common or equal spread does not make that assumption). The retention curve with the lowest model deviance was selected for further use. We also examined whether a retention curve changed with the gill-net twine that was used by fitting equal contact probability models for the periods 1984 to 1995, 1996 to 2006, and 2007 to 2017. We compared these with otherwise similar models where the relative contact probabilities were fixed values that were proportional to the peak amplitudes of Hamley and Regier's (1973) curves. The SELECT modeling used Millar and Holst's (1997) approach via computer code written in R (SelnCurveDefinitions.R and NextGeneration.R obtained from https://www.stat.auckland.ac.nz/~millar/selectware/RNext/; R Development Core Team 2019).

A statistically good fit for a SELECT model does not mean that the assumptions were met. Any SELECT model may be multiplied by any arbitrary function of fish length to produce a new selectivity model that yields identically good expected catch values (Millar 1995; Millar and Holst 1997; Anderson 1998). There remains an infinite set of different models that provide identical expected catch estimates yet imply different length distributions approaching nets and different selectivities. Appendix 1 shows how this fundamental ambiguity applies for geometrically similar models.

Population estimate, gill-net survey data source, and regression models.— From 1965 to 2016, 94 mark–recapture experiments with paired standard gill-net surveys were completed on 44 lakes. The lakes ranged in size and productivity (Table 1). Walleye were often marked in the spring when the fish were spawning and vulnerable to capture via trap nets or electrofishing. T-bar anchor tags, disk dangler tags, or fin clips were the primary methods of marking the fish. The experiments often targeted specific sizes of fish or only mature fish; with the latter, we assumed that all fish that were greater than 356 mm (14 in) total length were mature. The fish were recaptured with a variety of methods (e.g., trapnetting, gillnetting, electrofishing, and angling). While the reported population estimates from the mark–recapture experiments were often made with the adjusted Petersen method or other methods (e.g., stratified Petersen, Schnabel's method or Schumacher estimates), we computed and used population estimates that were based on the adjusted Petersen method (Chapman–Petersen method; Ricker 1975). These mark–recapture-based population estimates are typical of many state agency data sets in that not all of the mark–recapture conditions were necessarily met (Ricker 1975) and the number of recaptures were sometimes low (Table 1), resulting in poor precision and possibly in unknown biases.

The population estimates were paired with standard gill-net survey data consisting of catch, catch rate (CPE), length frequency, and targeted CPE representing the same size of fish that were targeted by a mark–recapture population estimate (many mark–recapture surveys targeted Walleye that were greater than 256 mm [10 in] or 356 mm [14 in], so for most cases the targeted CPE was the sum of CPEs for fish of these sizes). Gill-net surveys that used the Minnesota lake survey sampling methods that are noted above were mostly conducted in the same year as were the associated mark–recapture experiment and the spring population estimate for the Walleye population in the lake; however, in some cases a previous fall gill-net survey or a following summer gill-net survey was conducted. Gill-net survey catch and CPE for each population estimate were used, and where the population estimates targeted a specific size of fish, a comparable targeted CPE was used (see the Supplement available in the online version of this article). The limits of these data generally did not allow the determination of selectivity curves for individual lakes. Unlike Hamley and Regier's (1973) effort, which repeatedly gillnetted a marked Walleye population, the Minnesota gill-net surveys were single gillnetting events at established locations that caught an insufficient number of marked Walleye by length to adequately estimate the gill-net selectivity for each paired mark–recapture experiment and standard gill-net survey.

Using the 94-observation data set, regression models were developed to predict Walleye density (fish/ha). Linear mixed-effects models were used to test for significant fixed effects on the response variable (fixed effects and response variables were log transformed). The influence of lake size (lake surface area in hectares), littoral area (ha), shoreline complexity (ratio of the shoreline length divided by the circumference of a circle of area equal to the surface area of the lake), lake mean depth (m), lake mean summer total phosphorus (TP) concentration (μg/L), lake mean Secchi disk depth (m), and targeted or total Walleye gill-net CPE were explored as fixed effects. Lakes were modeled as random effects due to dependencies between observations from the same lake (e.g., Walleye density estimates from the same lake are more likely to be related to each other than to estimates from mark–recapture experiments on different lakes). The approach of examining fixed effects, adding random effects, and using the Akaike information criterion (AIC) scores to select models follow the suggestions of Burnham and Anderson (2002) and Zuur et al. (2009). The linear mixed-model analyses were conducted using R (R Development Core Team 2019) and the LME function in the NLME R package (Pinheiro et al. 2019).

Statistical assessment model (SAM).— A statistical assessment model was created by combining aspects of

TABLE 1. Median, range, mean, and standard deviation of the lake attributes, mark–recapture population parameters, and observed Walleye catch from Minnesota standard gill nets.

Attribute or variable	Median	Range	Mean	SD
Lake size (ha)	292	57–123,665	5,341	17,695
Lake mean depth (m)	4.5	1.0–29.7	5.8	4.3
Summer mean total phosphorus (μg/l)	17	8.0–147	26	28
Mean Secchi disk depth (m)	3.1	0.5–6.0	3.0	1.3
Estimated Walleye population density (fish/ha)	12.6	1.0–67.6	15.9	13.4
Mark–recapture experiment				
Number of Walleye marked (M)	561	65–32,064	2,173	4,948
Catch or sample taken for census (C)	118	5.0–25,232	836	3,043
Number of recaptured marks (R)	16	1.0–242	35	51
Gill-net CPE (Walleye/net)	9.3	0.7–29.6	9.9	5.1
Targeted gill-net CPE (Walleye/net)	7.1	0.7–29.6	7.2	4.9
Targeted gill-net CPE/density	0.54	0.13–6.17	0.72	0.73
Gill-net sampling day of year	216	163–266	220	25

two initial analyses: the initial estimates for the coefficients of a selectivity curve from a SELECT model and the estimates for fishing intensity for each mesh. For the latter, the estimates for peak catchabilities from the figures in Hamley and Regier (1973) were obtained. We used the peak selectivity amplitudes from Hamley and Regier's (1973) Walleye wedging curves (in their Figure 7: 19.05 mm: 0.05; 25.4 mm: 0.12; 31.75 mm: 0.25; 38.1 mm: 0.43; and 50.8 mm: 1.00) to compute fishing intensity for each mesh size in our standard gill net. We also computed apical absolute selectivities from their peak catchability amplitudes (in their Figure 8, wedging peaks, absolute selectivity by mesh: 19.05 mm: 0.4; 25.4 mm: 0.8; 31.75 mm: 1.6; 38.1 mm: 2.8; and 50.8 mm: 7.6) to compare with the SAM-estimated selectivities by mesh.

A SAM was constructed by merging the indirect and direct analyses to estimate density from CPE. For this model, we assumed Baranov's geometric similarity (that density is directly proportional to CPE) and that conditions as outlined in the descriptions of equations (4)–(7) (below) were met. The SAM estimated fishing intensity for each mesh and a gill-net selectivity curve concurrently (see Appendix 2). The model had 10 parameters that were estimated numerically by minimizing an objective function (O): fishing intensity parameters (5), and selectivity-shape curve parameters (5). The objective function consisted of the following components:

$$O = O(S) + O(D) + O(d), \tag{4}$$

$$O(S) = \sum_{M,L}\left(c_{L,M}^{0.5} - \hat{c}_{L,M}^{0.5}\right)^2, \tag{5}$$

$$O(D) = \sum_{x}\left[\ln(D_x) - \ln(D'_x)\right]^2, \tag{6}$$

and

$$O(d) = \sum_{x,M}\left[\ln(D_x) - \ln(D'_{x,M})\right]^2, \tag{7}$$

where $O(S)$ is the objective function component for the indirect gill-net selectivity component using a least squares estimation (the square root transformation of the catches before the estimation procedure means that we are assuming independent catches that approximate a Poisson random distribution; see Anderson 1998; Hovgård et al. 1999; Hovgård and Lassen 2000), $O(D)$ is the sum of squares of discrepancies between mark–recapture density observations and the density that is modeled for the standard net, and $O(d)$ is a similar sum of squares using the densities that are modeled for each mesh. The objective function component weighting differences were moderately explored, and the final model assumed equal weights (minor changes to weighting resulted in negligible changes to the estimated parameters). The starting values that were used for the selectivity curve in the SAM included five coefficients for the bi-lognormal curve from the unequal-contact-probability SELECT analysis of the 1984 to 2017 data set of 348,888 Walleye. The five starting values for fishing intensity were based on peak wedging catchabilities from the figures in Hamley and Regier (1973). The parameters were estimated by minimizing the objective function by using the Solver routine in Microsoft Excel (Microsoft Corporation, Redmond, Washington). We explored parameter identifiable issues by rerunning the model-fitting process with a range of initial parameter values, assessing convergence, and comparing the resulting final parameter estimates.

The selectivity curve of the gill net by mesh and fish length was calculated by using equation (A.2.1). The absolute selectivity for fish length-bin L in mesh M, $\varsigma_{L,M}$ was calculated by equation (A.2.2) and the absolute selectivity for fish length-bin L, ς_L by equation (A.2.3). The relative selectivity by length-bin L for the standard gill net (S_L) was defined by using equation (A.2.4). Following Hovgård et al.'s (1999) methods, the predicted catch by length-bin L in mesh M for the statewide data set ($\hat{c}_{L,M}$; equation A.2.5) was the product of the absolute selectivity for fish length-bin L in mesh M and the relative number of fish that were available to any of the mesh sizes. For each lake survey, the SAM allowed the estimation of density by length-bin L as CPE divided by absolute selectivity (via equation A.2.6 by mesh and equation A.2.8 for the standard gill net), and these density at length-bin L estimates were summed (via equation A.2.7 by mesh and equation A.2.9 for the standard gill net) to produce lake estimates for Walleye density for the targeted size of fish in the mark–recapture experiments for each lake (usually for length-bins that were 356 mm [14 in] and greater).

The SAM was evaluated in several ways. First, we assessed its performance by examining the model-fitting statistics. Second, the uncertainty in the selectivity curve parameters and the Walleye density and population size estimates were estimated through simulations that included measurement error. Using the 94 mark–recapture experiments with paired standard gill-net surveys and the associated uncertainties, we generated 1,000 simulated 94-paired data sets and fitted the SAM to each simulated data set. Simulated gill-net CPE and mark–recapture population estimate data with a median equal to the observed was generated by multiplying the observed by a lognormal measurement error term. The assumed relative standard error (RSE; the standard error divided by the mean, expressed as a percentage) associated with gill-net CPE was based on sampling effort (15% if >20 nets, 20% if 11–20 nets, and 30% for ≤10 nets, derived from observations of numerous Minnesota gill-net surveys). The variance that was associated with the mark–recapture population estimate was computed by using the Chapman–Petersen equation (equation 3.8 in Ricker 1975). The variance associated with the gill-net length-frequency data was estimated assuming a multinomial distribution (Gerritsen and McGrath 2007). We evaluated the performance of the SAM based primarily on the uncertainties or confidence intervals of the parameter estimates.

Third, we examined the assessment and simulation model predictions for Walleye abundance and length distributions for two populations, Mille Lacs and Upper Red Lake in 2017. As these population estimates rely on gill-net surveys with large numbers of nets, these existing estimates have modest uncertainties (for 2017, the gill-net survey RSE was 10% for Mille Lacs and 9% for Upper Red Lake, and these variabilities were used in the simulation study). We compared the density predictions from the SAM with the existing population estimates. The Walleye population in Mille Lacs was estimated with a statistical kill-at-age model (Melissa Treml, MDNR, personal communication), and the Walleye population in Upper Red Lake had been estimated previously with a gill-net selectivity model (Anderson 1998; Tony Kennedy, MDNR, personal communication).

Lastly, we compared the relative (S_L) and absolute (ς_L) selectivities from the SAM to other gill-net selectivity models in the literature. We computed Hamley and Regier's (1973) selectivity curves for the mesh sizes that are present in Minnesota's standard gill net, using parameters in their Table 4 and their girth–length relationship, then scaling catchability to account for the change in the panel size of the mesh (proportionately to net area) and to account for changes in lake area (inversely to lake area). We compared these selectivities with those of the SAM. Anderson (1998) estimated selectivity for Minnesota's standard gill net, and we directly compared these estimates and those of absolute selectivity with those that were estimated by the SAM. We also computed the relative selectivities for Minnesota's standard gill net by using the estimated parameters from two models that used a bi-normal selectivity function (Vandergoot et al. 2011; Shoup and Ryswyk 2016) and compared them with the relative selectivities from the SAM.

RESULTS

There was considerable measurement error in the population estimates from the 94-observation mark–recapture data set (with an average coefficient of variation [CV] of about 20%). Gill-net CPE was also measured with considerable error (the survey RSE was often in the range of 10% to 30%). A linear regression model predicting ln density from ln gill-net targeted CPE had a slope of 0.78 (with intercept 0.99), whereas the reverse regression suggested a slope of 1.86 and a standard major axis regression slope of 1.21 (Figure 1). We modeled the relationship as a direct proportionality. The large disparity in the coefficients between the two models indicates substantial uncertainty in the proportionality of gill-net CPE and density. The inclusion of the environmental variables in the linear mixed-effects models did not appear to improve the relationship.

Of the five commonly used gill-net selectivity curves, the bi-lognormal shaped selectivity curve produced the lowest model deviance when it was applied to the Walleye gill-net catch data set from the pooled lake survey (Table 2; parameters in Table 3). The selectivity curve appeared to be unimodal and strongly skewed, as the tangling component was not sufficiently distinct to produce a separate mode. The predicted peak catches by mesh approximated the observed catch, and only the predicted modes for the 31.75 and 38.1 mm meshes were positively offset by about 10 mm from the observed mode. The selectivity curve may have changed with the change in the gill-net twine that was used (Figure 2). For four of the five bi-lognormal-shaped selectivity curve parameters, there were significant differences between the 1984–1995 period, a period with only the older twine, and the recent period, where a different twine was used in the construction of gill nets. The 1996–2006 period, a transition period when both types of gill nets were used, had intermediate parameter values. An incorrect assumption of equal contact probabilities, or changes of twine, may have contributed to the patterns in the residuals of the SELECT model (Figure 3). However, we continued with the bi-lognormal-shaped selectivity curve in our assessment model because our population

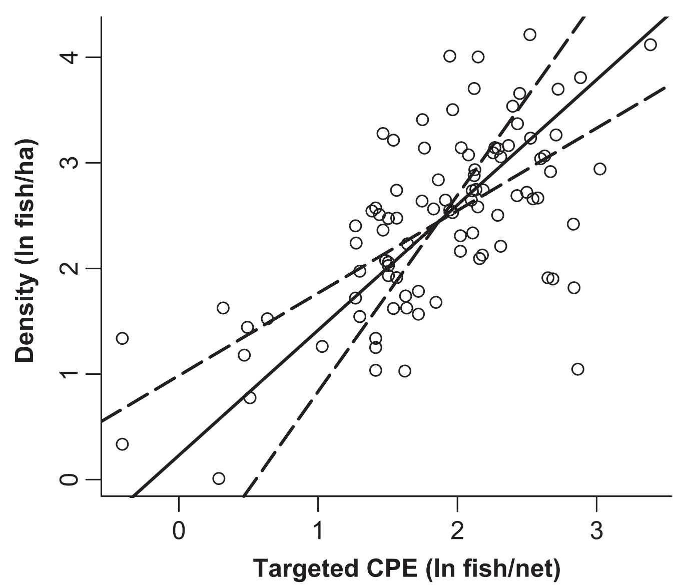

FIGURE 1. Walleye population density (fish/ha ln-transformed) as a function of ln-transformed gill-net targeted CPE. The two dotted regression lines bound the range of linear regression possibilities with the geometric regression slope equal to 1.2.

TABLE 2. The SELECT model deviance, number of estimated parameters, and degrees of freedom for five gill-net retention curves that were fitted to the observed Walleye catch from Minnesota standard gill nets from 1984 to 2017.

Model	Deviance	Number of parameters	df
Normal with common spread	112,376	2	302
Normal with proportional spread	160,921	2	302
Lognormal	78,612	2	302
Bi-normal	34,540	5	299
Bi-lognormal	18,915	5	299

estimates were made across the entire time span, and it was intractable to include more than one selectivity submodel.

The SAM produced an asymmetrical selectivity function (S_L) for the standard net gang of five meshes. It increased with increasing fish length to a peak at 535 mm and then decreased to about 0.34 at about 800 mm. The estimated absolute selectivity (ς_L) for the Minnesota standard gill net increased with increasing fish length to a peak of 0.76 ha/net at 535 mm and then decreased to about 0.26 at about 800 mm. The selectivity curves by mesh that were estimated by the SAM provided a reasonable fit to the observed Minnesota gill-net catches (Figure 4).

The SAM that incorporated the estimation of fishing intensity parameters indicated substantially different selectivity than either the SELECT model with the underlying assumption of equal contact probabilities or the SELECT model with Hamley and Regier's (1973) catchabilities did (Figure 5). The SAM indicated selectivities with more distinctive wedging and tangling components than were produced by the SELECT model assuming equal contact probabilities. The bi-lognormal-shaped selectivity curve parameters of the SAM changed little when measurement error was added in the simulations (Table 4), as the pooled gill-net survey data source was large ($N = 348{,}888$ Walleye were measured). The estimated fishing intensity and peak selectivity by mesh increased almost linearly with mesh size, and these values deviated from the catchabilities that were used in Hamley and Regier (1973) to initiate the analysis. The four smallest meshes had higher relative fishing intensities, and all of the meshes had lower peak selectivities than they reported. Because our assessment model followed the principle of geometric similarity, the relative amplitudes of the wedging and tangling pieces did not change with mesh size, unlike with the Hamley and Regier selectivity curve model. The estimated density had considerable error relative to the mark–recapture estimate (Figure 6). The median relative error was 6% and mean relative error 50% (with a median absolute relative error of 38% and median absolute relative error of 80%).

For the Walleye populations in Mille Lacs and Upper Red Lake, the SAM estimates for density and population size were similar to the results from existing stock assessment models, but the distributions by length were noticeably different. For Mille Lacs, the SAM predicted the population of fish greater than 356 mm in fall 2017 to be 840,000 (16.2 fish/ha), with an 80% probability distribution ranging from 760,000 to 1,030,000 (Table 5). The existing sex-specific statistical kill-at-age model that was used for the Mille Lacs population predicted a population of 772,000 (with an 80% probability distribution from Markov chain–Monte Carlo methods of ±3%) of fish larger than

TABLE 3. The SELECT model parameters for the bi-lognormal-shaped selectivity curves for Minnesota's standard gill net, assuming equal contact probabilities and unequal fishing intensity and approximating the pattern that was determined from Hamley and Regier (1973).

Parameter	Equal contact probabilities		Unequal contact probabilities	
	Estimate	SE	Estimate	SE
For 19.05-mm mesh				
Mode for the 1st curve	197.626	0.110	204.527	0.176
Standard deviation for the 1st curve	21.934	0.129	22.654	0.142
Mode for the 2nd curve	247.254	0.397	319.779	0.916
Standard deviation for the 2nd curve	84.767	0.454	109.779	0.782
Proportion factor	0.764	0.002	0.547	0.002
Relative fish size (total length/bar measure) at the mode of the lognormal selection curve 1 (μ_1)	2.339		2.374	
Standard deviation of the lognormal selection curve 1 (σ_1)	0.109		0.109	
Relative fish size (total length/bar measure) at mode of the lognormal selection curve 2 (μ_2)	2.563		2.821	
Standard deviation of the lognormal selection curve 2 (σ_2)	0.295		0.295	

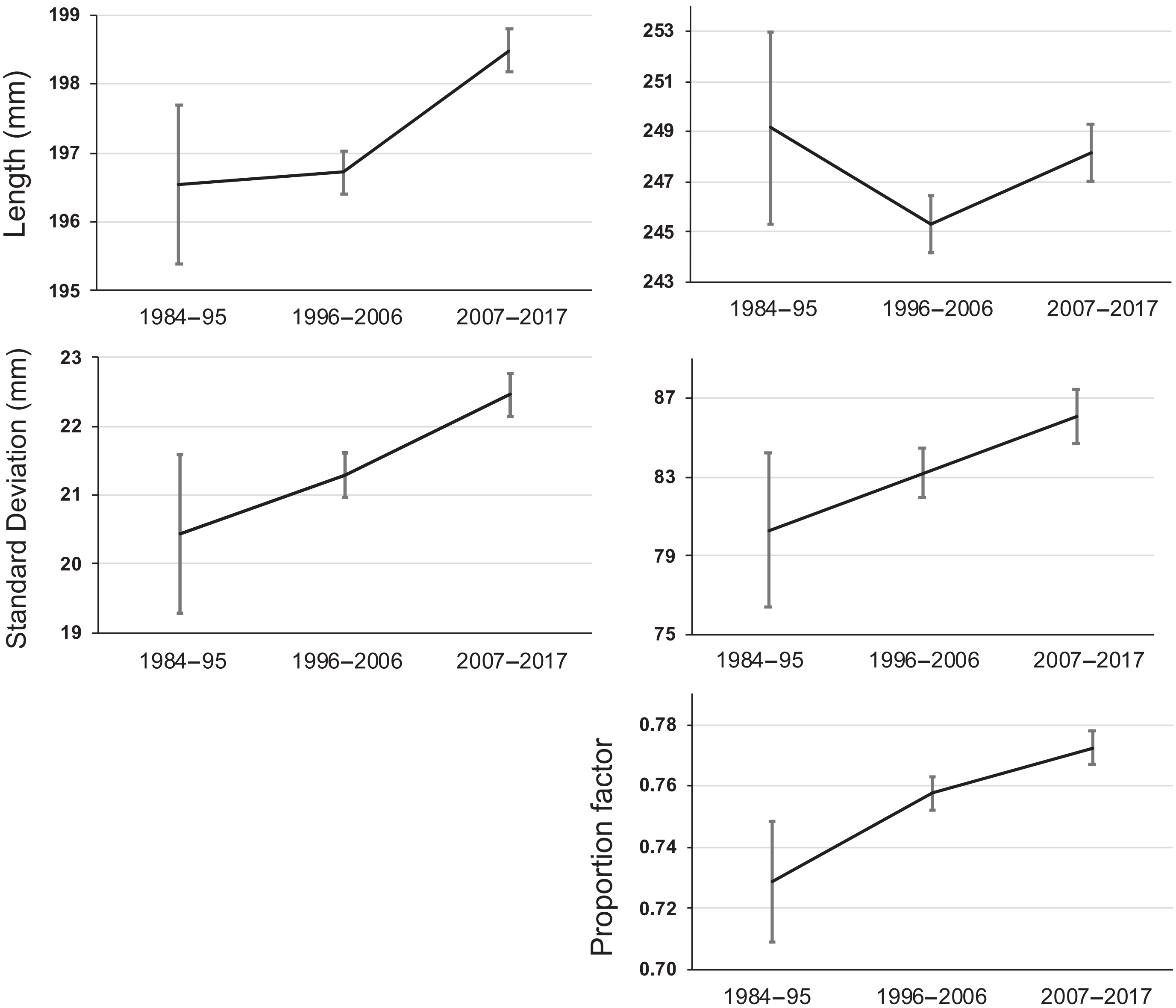

FIGURE 2. Bi-lognormal-shaped selectivity curve estimates for the three survey periods. The modal lengths for the 19.05-mm mesh for the wedging and tangling component curves (upper row), their standard deviations (middle row), and a proportion factor (*R*) controlling the relative heights of the two components (lower row) are shown. The error bars represent 2 SE.

356 mm, and the spring 2018 mark–recapture estimate was about 727,000 (SE = 75,000) fish (Tom Heinrich, MDNR, personal communication). For Upper Red Lake, the SAM predicted the population measuring greater than 356 mm to be 2,160,000 (44.7 fish/ha) with an 80% probability distribution ranging from 2,040,000 to 2,680,000. A gill-net selectivity model (Anderson 1998), currently used for Upper Red Lake, estimated a 2017 population size of 1,960,000 fish measuring >356 mm. For the two lakes, the SAM population estimates by length-bin had wide ranges for fish measuring between 356 and 480 mm, with a range of CVs for the length-bins in this size range for Mille Lacs of 14% to 22% and for Upper Red Lake 12% to 21%. The SAM estimated fewer fish in the small length-bins and more in the larger length-bins. The Mille Lacs statistical kill-at-age model estimate for Walleye had a 50% higher estimate for small fish (for total length-bins between 250 and 330 mm) and a 53% lower estimate for large fish (>560 mm) than the estimates from the SAM did; whereas the existing Upper Red Lake model had a 51% higher estimate for small Walleye (280 to 380 mm) and a 63% lower estimate for fish greater than 420 mm than the SAM did (Figure 7).

The SAM selectivity estimates were similar to other selectivity curves that have been reported in the literature

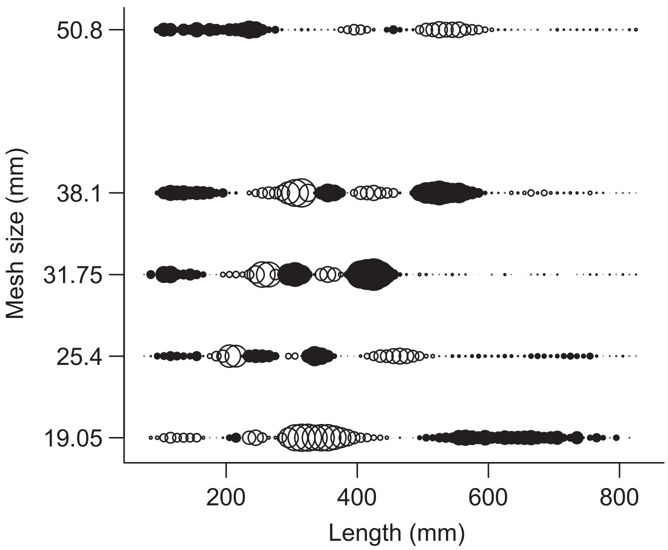

FIGURE 3. The residuals from fitting a bi-lognormal-shaped selectivity curve by mesh by using SELECT. The circle size is proportional to the residual value. Open circles are negative residuals, and solid circles are positive residuals.

for this net in peaking at some intermediate size, yet there were important differences in selectivities at length between the models. All of the models that were compared had irregular bell-shaped selectivity curves with relative selectivities (S_L) that declined to low values as the total length of Walleye increased beyond 600 mm (Figure 8). Two models (Vandergoot et al. 2011; Shoup and Ryswyk 2016) that used a bi-normal selectivity function assuming equal contact probability for all meshes had much higher relative selectivities for Walleye measuring less than 475 mm than the SAM did. Hamley and Regier's (1973) and Anderson's (1998) models had much lower relative selectivities for Walleye measuring < 475 mm than the SAM did. The assessment model's absolute selectivities for Walleye measuring between 200 to 375 mm were slightly higher than those that were estimated by Anderson (1998), and for fish measuring between 450 to 700 mm, the assessment model's absolute selectivities (ς_L) were considerably lower than both Hamley and Regier's and Anderson's estimates were. This means that for the same CPE-by-length data set, the SAM will estimate a lower number of small Walleye and a higher number of large Walleye than those models (see Figure 7 to compare the Anderson model and SAM population estimates for Upper Red Lake).

DISCUSSION

Our statistical assessment model combined an indirect gill-net selectivity model for Walleye based on a large statewide database (348,888 length and mesh records) and a direct analysis of 94 mark–recapture population estimates that are representative of a wide range of Walleye lakes in Minnesota. This was done in an attempt to address the issue of measurement error in both population and CPE estimates and overcome the limitations of indirect methods. Indirect model results are strongly dependent on the assumptions that are made about the relative contact probabilities of various meshes and cannot, by themselves, account for size-dependent encounter rates. In addition, indirect models are inherently ambiguous. Even when the retention curves follow strict geometrical similarity, there are many other models that produce identical predicted catch values. Therefore, the estimates of the probabilities

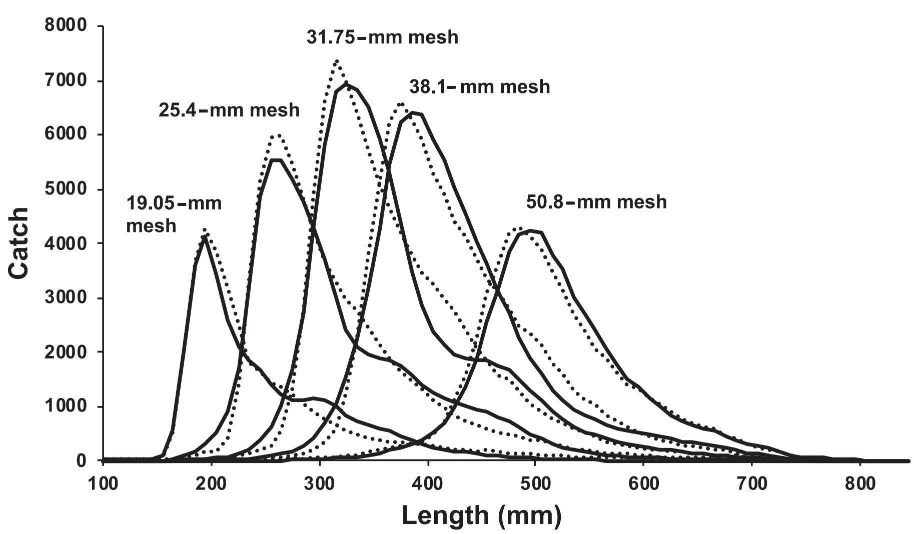

FIGURE 4. Observed catch (dotted lines) and predicted catch (solid lines) results from the statistical assessment model for Minnesota's standard gill net by mesh for the 19.05-, 25.4-, 31.75-, 38.1-, and 50.8-mm meshes.

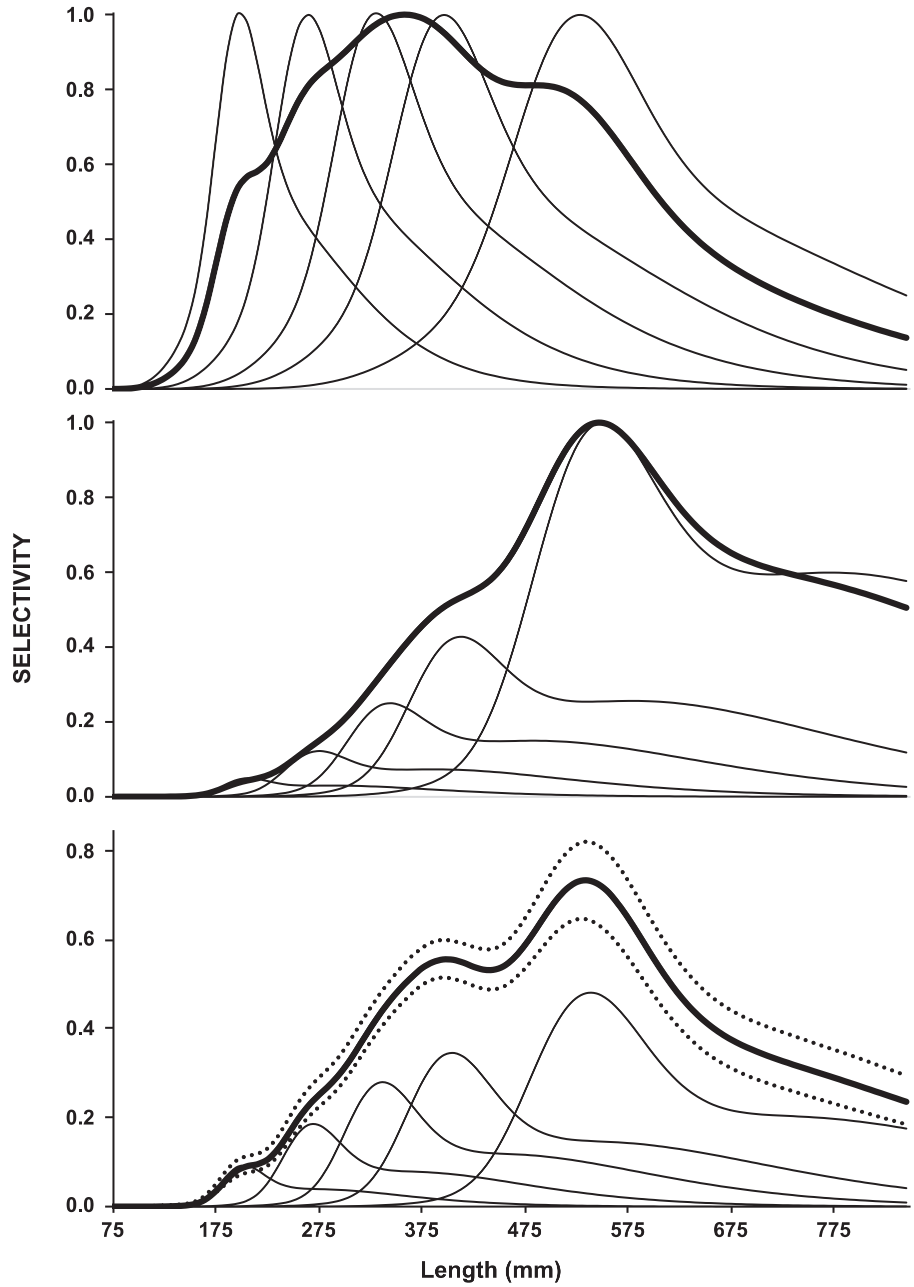

FIGURE 5. Walleye selectivity curves by fish total length (mm) for Minnesota's standard gill net (thick dark lines) from the SELECT model that assumes equal contact probabilities (upper panel, S_L), from the SELECT model that assumes unequal fishing intensity, approximating the pattern determined from Hamley and Regier (middle panel, S_L), and those derived by using the fishing intensity that was estimated with the statistical assessment model (lower panel, ς_L). Also shown are the selectivities of the mesh for the 19.05-, 25.4-, 31.75-, 38.1-, and 50.8-mm meshes (the thin lines; $s_{L,M}$ for the upper and middle panels and $\varsigma_{L,M}$ for the lower panel). The two dotted lines bound the 90% confidence interval of the median selectivity curve (ς_L) based on the statistical assessment model and 1,000 simulated data sets that incorporated measurement error.

of encounter, contact, or retention may not be realistic (Anderson 1998). These other geometrically similar indirect models are most easily visualized as those where selectivity has been multiplied by a power function of fish length. If encounter rates follow a power function of fish length, as estimated by Rudstam et al. (1984) and assumed by Spangler and Collins (1992), the effect can be incorporated to produce a catchability model, one which still produces identical predicted catches $\hat{c}_{L,M}$, though the fishing intensity and selectivity parts combine swimming speed with contact and retention, respectively (Appendix 1). If encounter rates are not power functions of length, then

TABLE 4. Results from the statistical assessment model. Percentile values are from the analysis of 1,000 simulated data sets that incorporated measurement error. The proportion factor scales the two lognormal distributions.

Parameter	Estimate	5th percentile	95th percentile
Bi-lognormal-shaped selectivity curve ($s_{L,M}$)			
Relative fish size (total length/bar measure) at the mode of the lognormal selection curve 1 (μ_1)	2.3587	2.3568	2.3630
Standard deviation of the lognormal selection curve 1 (σ_1)	0.1024	0.1019	0.1027
Relative fish size (total length/bar measure) at the mode of the lognormal selection curve 2 (μ_2)	2.7442	2.7315	2.7743
Standard deviation of the lognormal selection curve 2 (σ_2)	0.2715	0.2703	0.2723
Proportion factor (R)	0.6537	0.6210	0.6632
Fishing intensity, ξ_M by mesh bar measure (fishing power by mesh, F_m)			
19.05-mm mesh	0.0930 (0.1931)	0.0636	0.0960
25.4-mm mesh	0.1849 (0.3839)	0.1413	0.1849
31.75-mm mesh	0.2778 (0.5768)	0.2285	0.2730
38.1-mm mesh	0.3457 (0.7179)	0.2954	0.3441
50.8-mm mesh	0.4814 (1.0000)	0.4102	0.5218

our model more crudely coerces the fishing intensities and selectivity curves to approximate the combined effect of encounter, contact, and retention.

Although direct estimates of catchability and indirect estimates of selectivity use overlapping terminology, they are really estimating different things. Using direct data on the population at large may allow the estimation of absolute selectivity—the combined effects of the encounter, contact, and retention components. Indirect models only allow inferences about the length distribution of fish that encounter and contact the nets—and only if the assumptions about contact probabilities and form of retention curves are correct. They may be used to estimate the length distribution of the population at large only if encounter rates do not vary with fish size. Hamley (1975) and Ricker (1975) rejected the idea that contact probabilities were equal for the most vulnerable sizes of Walleye with respect to each mesh. Size-dependent encounter rates or unequal contact probabilities could increase the vulnerability of larger fish to larger meshes. Many researchers have estimated relative selectivity curves for Walleye for various standard gill nets' mesh sizes assuming equal contact probabilities (e.g., Irwin et al. 2008; Vandergoot et al. 2011; Shoup and Ryswyk 2016), and their results are inconsistent with those of Hamley and Regier (1973).

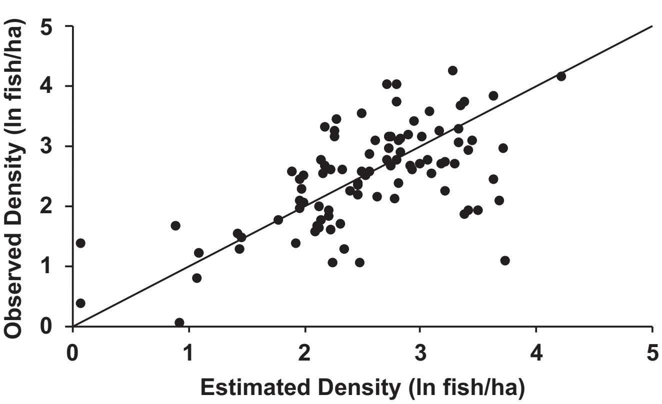

FIGURE 6. Walleye population density estimates from the mark–recapture experiments (observed, ln-transformed, fish/ha) and the estimated density from the statistical assessment model (equation A.2.9; ln-transformed). The line represents a 1:1 relationship.

Indirect models based on an underlying assumption of equal contact probabilities may provide good first approximations of selectivity for single meshes when the analysis is for a species that is caught principally by wedging—using a gill net with a small number of closely spaced mesh sizes. This may be because (1) the variation in encounter rates within the size range may be small, (2) variation in geometric shape of the fish may be small, (3) differences in detection and avoidance of meshes may be small, and (4) differences in twine or filament thickness may be small. Such applications may be useful to understanding gill-net fisheries. However, when applied across the wide range of mesh sizes, which is common in many standard nets, any assumptions of equal encounter rates, equal contact probabilities, and geometric similarity are likely not met. In particular, assumptions about contact probabilities strongly control the form of the selectivity curve for the entire standard net. To resolve the ambiguity that is inherent in indirect analysis and identify a realistic selectivity curve, testing against other data is critical.

Obtaining ancillary data is a challenge. Camera traps have provided some validation of retention curves (Grant et al. 2004a). Similar studies without a physical mesh in place could allow direct estimates of the length

TABLE 5. Population and density estimates for the fall of 2017 for Walleye measuring greater than 356 mm total length for the existing fisheries management models that were used for Mille Lacs and Upper Red Lakes compared with the statistical assessment model (SAM).

Lake and parameter model	Parameter estimate	Assessment model simulation					
		10th percentile	25th percentile	50th percentile	75th percentile	90th percentile	CV (%)
Mille Lacs–population							
Existing model	772,000						
SAM	840,000	760,000	820,000	890,000	960,000	1,030,000	12
Mille Lacs–density							
Existing model	14.9						
SAM	16.2	14.6	15.7	17.1	18.5	19.8	12
Upper Red–population							
Existing model	1,960,000						
SAM	2,160,000	2,040,000	2,180,000	2,330,000	2,500,000	2,680,000	11
Upper Red–density							
Existing model	40.6						
SAM	44.7	42.3	45.1	48.3	51.7	55.5	11

distribution of the fish encountering the virtual net. Obtaining improved abundance estimates that are based on a better understanding of catchability and gear selectivity likely requires the incorporation of variability of gear across space and time (e.g., Brun et al. 2011; Kraus et al. 2017). Askey et al. (2007) used a hierarchical Bayesian analysis of mark–recapture data and depletion gill-netting to estimate gill-net selectivity. They designed a model that allowed lake–year effects on the gill-net selectivity curve, but with an assumption that the lake-specific parameter values came from a general population. These and other statistical approaches that effectively use data across and within sampling units may provide additional information to lake fisheries managers who now often rely only on standard gill-net CPE statistics and length-frequency distributions that are uncorrected for gear selectivity when they are making decisions on stocking, fishing regulations, and harvest targets. Using statistical assessment models, analogous to statistical kill-at-age models, that incorporate mark–recapture, gill-net CPE, size structure, and other data is one step in that direction, and additional research about this approach seems appropriate.

The problem is not simply that contact probability and retention parameters may be statistically confounded (Millar and Holst 1997), as even when they are not confounded Brenden and Zhao (2012) found that parameter bias and uncertainty may result when these parameters are estimated simultaneously. However, Brenden and Zhao (2012) did not present results like those in our Figure 5 that would allow the reader to evaluate bias in the selectivity that is estimated for a standard net and bi-normal models may have local maxima in the likelihood surface. Our recommendation is to consider all assumptions as testable hypotheses and then test them or otherwise validate the model.

The combined SAM approach that we used was an attempt to address many of these issues while estimating the size distribution and density of the populations at large. The SAM effectively used data from multiple sources: standard gill-net survey data were compiled for the same-sized fish as were targeted in the associated mark–recapture population estimates. These statistics were assumed to have measurement error, and within a measurement-error model approach, the parameters were found by minimizing the residual sum of squares (Quinn and Deriso 1999). As with statistical kill-at-age analyses, making incorrect assumptions may lead to substantial biases in density-at-length estimates.

The shape of our estimated selectivity curve for Minnesota's standard gang resembles those of other direct analyses by Hamley and Regier (1973) and Anderson (1998) in that selectivity for small fish, or the smallest mesh, is much lower than that for larger Walleye (about 500–600 mm long), or the largest mesh. Our curve differs in this respect from those that were produced by indirect analyses (Shoup and Ryswyk 2016; Smith et al. 2017). This key difference could result if encounter rates are strongly size dependent, as indirect models provide no information about the encounter process, if the assumption of equal contact probabilities for all meshes in these indirect analysis is wrong, or both. Our fishing intensity coefficients combined elements of encounter and contact probabilities, but there is an assumption that encounter probabilities are a power function of fish size. Anderson's (1998) model included both a size-dependent encounter component and contact probabilities that increased with mesh size. The shape of our estimated curves for

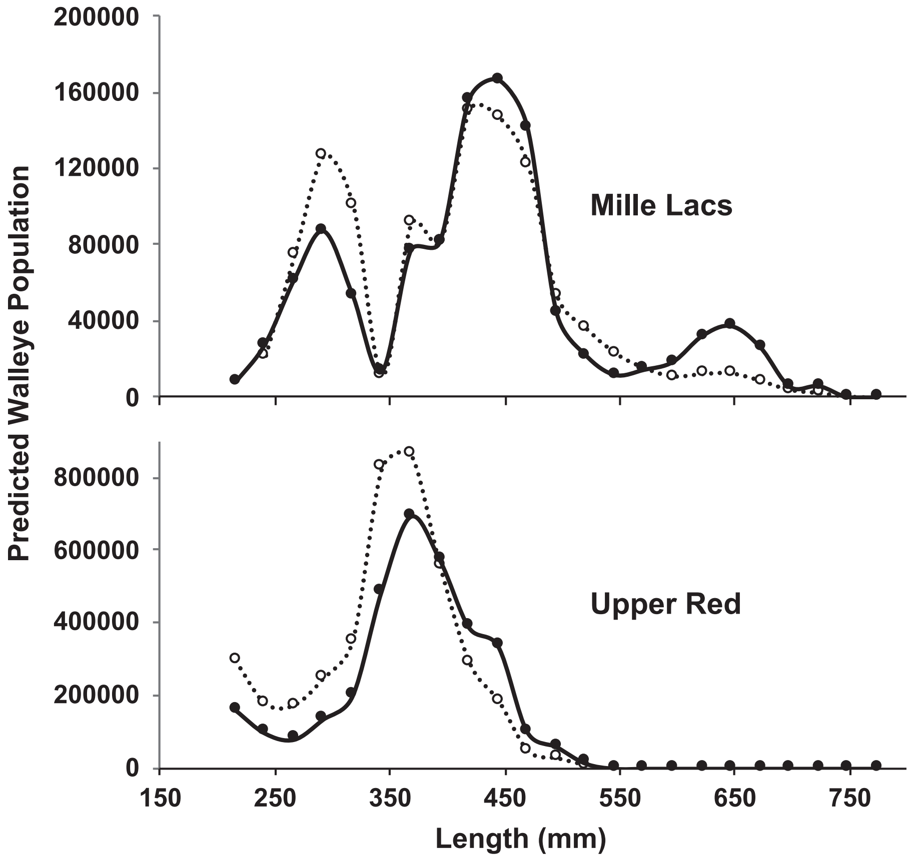

FIGURE 7. Walleye population abundance estimates by length-bin for Mille Lacs and Upper Red Lake for the fall of 2017 by using the statistical assessment model (solid line, closed circles; equation A.2.8) and the existing models for the fisheries (dotted lines, open circles). The lower bounds of the class length-bins that are presented are in inches from 8 to 30.

individual meshes was unimodal, strongly skewed, and conformed to the principle of geometric similarity, a pattern that is consistent with indirect estimates of retention curves (Anderson 1998; Shoup and Ryswyk 2016; Smith et al. 2017), unimodal length-frequency distributions of the catch in large survey programs (Henderson and Wong 1991), and observations with camera traps (Grant et al. 2004a). The addition of a size-dependent encounter function produced a slight bimodality in the selectivities of the smallest meshes in Anderson's model and in the selectivity curves that were not geometrically similar. We agree with Henderson and Wong (1991) inquestioning Hamley and Regier's (1973) conclusions about strongly bimodal Walleye selectivity curves. The selectivity curves that were estimated by the SAM provided a reasonable fit to the observed Minnesota gill-net catches. The deviations were likely because the assumption of geometric similarity was not fully met (Vandergoot et al. 2011).

The SAM estimates for the absolute selectivity of Minnesota's standard gill net for Walleye deviated from Hamley and Regier's (1973) and Anderson's (1998) models. Hamley and Regier's (1973) model estimated apical absolute selectivities by mesh for Dexter Lake (4 km^2) were much larger than those that were computed by our model (4–16 times that of our model). Hamley and Regier only made catchability estimates for one lake, and the pattern by mesh may be inaccurate, whereas our approach determined the estimates for absolute selectivities by mesh by using 94 mark–recapture experiments. However, each approach was limited by low Walleye catches in the smallest and largest meshes. The apical absolute selectivity for Minnesota's standard gill net was 4 times as great for Hamley and Regier's model and 3 times as great for Anderson's model than for our model, which means that our model would predict about 60% higher Walleye densities for each of the length-bins between 450 and 700 mm. The reasons for these differences are unclear. It is possible that Hamley and Regier's apical absolute selectivity is higher because they used a stratified random design for gill-net locations that may have included both good and poor Walleye habitat for the gill netting sites, whereas Minnesota generally uses established gill netting sites in good Walleye habitat. It is possible that Anderson's apical absolute selectivity is higher because it used estimates for the Walleye population in Mille Lacs from virtual population analyses that

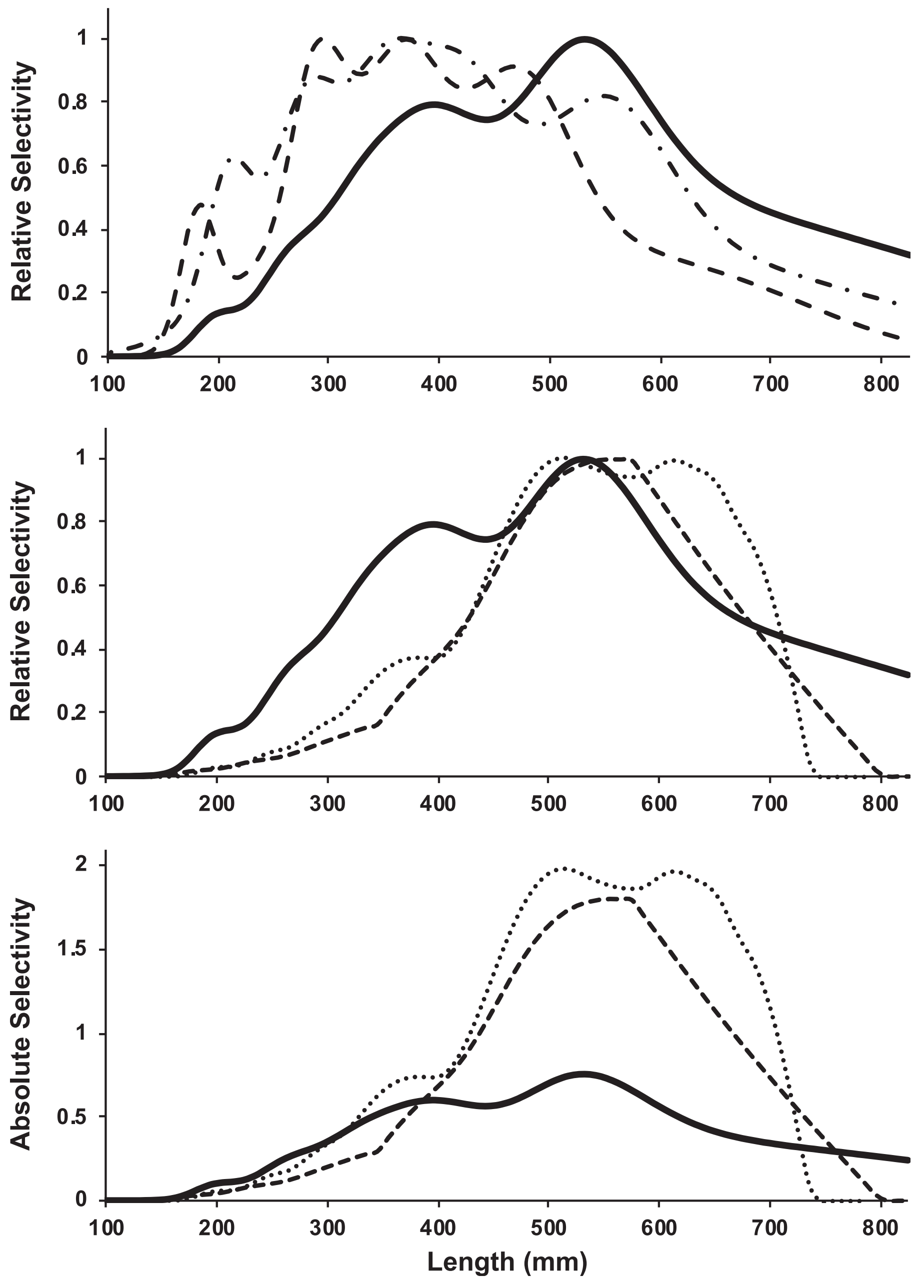

FIGURE 8. Estimated relative (S_L) and absolute selectivity (ς_L) by Walleye total length (mm) for Minnesota's standard gill net by using the statistical assessment model (dark line) compared with the other models. The top panel includes the relative selectivites from the models from Vandergoot et al. (2011), shown by the long dashed line, and Shoup and Ryswyk (2016), shown by the long dash-dot line. The middle and lower panels include selectivities from the models from Hamley and Regier (1973), shown by the dotted line, and Anderson (1998), shown by the dashed line.

may have underestimated the population at the time. It is also possible that our assessment model underestimated apical absolute selectivities due to underestimating fishing intensity for the largest meshes.

Gill-net selectivity is influenced by any size dependence in swimming speed and behavior, so estimating the selectivity requires some direct knowledge of fish abundance at length in the population at large. Minnesota's standard gill net appeared to be highly selective for larger-sized Walleye. The estimated relative selectivity curve (S_L) exceeded 0.75 for Walleye measuring between 365 to 595 mm in total length (Figure 8). The effects of this selectivity curve are evident in Figure 9, where both CPE and density are shown for two fisheries. The density estimate for small fish is much higher relative to the gill-net CPE of small fish (in particular note the Mille Lacs panel), whereas that for large fish relative to the gill-net CPE of large fish is subtle. Shoup and Ryswyk (2016) estimated selectivity for the North American standard gill net, which has three additional large meshes, and they reported much higher selectivities for small Walleye (<400 mm). The difference is largely because they assumed equal contact probabilities. When our assessment model with equal contact probabilities across meshes was applied, it resulted in length-frequency distributions suggesting that very few small fish were encountering the nets.

The differences in the length estimates for the Walleye populations in Mille Lacs and Upper Red Lake from our assessment model compared with their existing stock assessment models may provide fisheries managers with some insight on existing stock assessment modeling approaches. The Mille Lacs statistical kill-at-age model produced a sigmoidal relative selectivity curve with a value close to 1 for Walleye age-groups with mean lengths that are >560 mm, whereas our model curve increased with increasing individual fish length to a peak at 535 mm and then decreased to about 0.26 (or 0.34 relative selectivity) at about 800 mm (Figure 5). The Mille Lacs statistical kill-at-age model also estimated lower densities for many length-classes (most notably for the largest fish). These differences are meaningful, and they could be a result of model misspecification(s) in either model. For example, the SAM produced a particular pattern in fishing intensity; however, if this pattern was miss-specified then deviations from the true selectivity curve and population density at length would result. Similarly, alternate fishery selectivity and natural mortality patterns that are used within statistical kill-at-age models have to be carefully considered (Radomski et al. 2005; Punt et al. 2014). The difference in the estimates for population at length for Walleye in Upper Red Lake was simpler to understand. Here the existing gill-net selectivity model (Anderson 1998), as noted, has slightly lower catchabilities for small Walleye and higher for large Walleye than the SAM's catchabilities for the same fish lengths did.

The SAM estimated density and population at length with high uncertainties. To reduce uncertainties, gear selectivity investigators will need to directly estimate the number of fish at length in one or preferably many populations (e.g., Borgstrøm et al. 2010). We assumed that an adjusted gill-

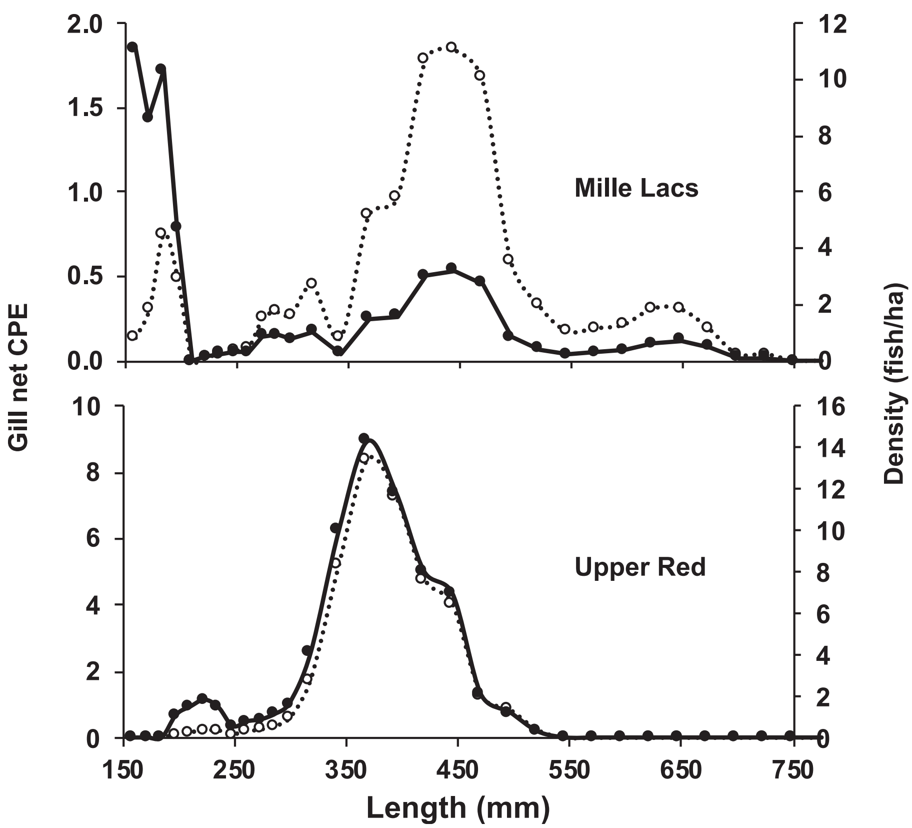

FIGURE 9. Walleye population density estimates by length for Mille Lacs and Upper Red Lake for the fall of 2017 by using the statistical assessment model (solid line, closed circles; equation A.2.8) and gill-net CPE data (dotted lines, open circles). The lower bounds of the class length-bins that are presented are in inches from 6 to 30.

net CPE for Walleye was directly proportional to density. Other investigators have found catchability to be a function of environmental variables. For Northern Pike *Esox lucius*, Pierce et al. (2010) reported that gill-net catchability was significantly related to a lake's mean depth and littoral area. For Rainbow Trout *Oncorhynchus mykiss*, Ward et al. (2012) found that catchability was a function of surface water temperature at the time of gill netting and proportion of littoral area within each lake. Walleye CPE varies by season, water temperature, site effects, dissolved oxygen, and feeding behavior (Grant et al. 2004b; Schmalz and Staples 2011), so an improved model could include these and other variables to reduce model uncertainty such as lake habitat characteristics, lake productivity, fish behavior, and gill netting conditions. Investigators will also need to recognize that gill-net surveys are inherently variable, and because precision in estimating model parameters is strongly dependent on variability in the data source, modest to high variability in density estimates will likely still be an issue.

There are several management implications of this work. First, we suggest that fisheries managers in Minnesota apply this SAM (equation A.2.8; Figure 5, lower panel) and several other models to make estimates of population abundance and size distributions (with confidence intervals based on simulations or bootstrapped data). Such estimates are likely to be the most precise (and potentially refutable) for Walleye that measure >356 mm and when the RSE of gill-net CPE is <30%. As shown with the Mille Lacs and Upper Red Lake examples, the 80% probability distribution of the predicted Walleye density by length-bins for fish measuring between 356 and 510 mm could be plus or minus 20% to 30%. Because our model is based on statewide data, it is likely to have some generality but the scatter of points in Figure 1 about the line of direct proportionality and the random lake effects in the models for statewide trends (Grant et al. 2004b; Bethke and Staples 2015) suggest that average catchability likely varies among lakes. The use of fixed net sites rather than randomized locations in Minnesota's standard surveys also contributes to such variation. The examination of multiple population estimates should encourage validation efforts. Some of these must be in the form of mark–recapture experiments with larger sample sizes, using individually marked fish and advanced statistical models rather than simple Chapman–Petersen analyses. Second, we suggest that researchers develop methods to directly estimate capture probability by size and test the assumptions of indirect selectivity models. Lastly, some management questions about trends and changes in stock status may be addressed by analyses of raw gill-net catch rates and size distributions (Grant et al. 2004b; Bethke and Staples 2015); however, questions about the abundance and size distribution of the populations require considering size selectivity and capture probability. Not addressing selectivity biases the estimates of vital statistics, and adjusting gill-net catch data with indirect selectivity models that assume equal contact probabilities for each mesh may introduce considerable bias to estimates of population abundance and length distributions.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Appendix 1: Other Geometrically Similar Select Models Provide Identical Fit to the Data

In the special case of geometric similarity, the selectivity of mesh M can be written as

$$S_M(l) = F_M \cdot r(l/m_M),$$

where F_M is the relative fishing power of the mesh and $r(l/m_M)$ describes retention as a function of the relative size of the fish and the mesh (i.e., the ratio of fish length l and mesh size m_M).

The SELECT models have been fit using a multinomial likelihood or as an equivalent log-linear model. For fish of a given length l, one expects the observed total catch of fish in length class L, $X_L = (c_{l,1}, c_{l,2},\ldots,c_{l,5})$ to be multinomially distributed across the five meshes, that is $X_L \sim Mult(n_L, \pi)$ with index n_L equal to the shared length-class total catch and parameter $\pi = (\pi_1, \pi_2, \cdots, \pi_5)$, where the elements of π are conditional probabilities and each π_M can be thought of as the proportion of the selectivity of the entire standard net (of fish in length-class L) contributed by mesh M, which can be written as a function of selectivity:

$$\begin{aligned}\pi_M &= P(M|l) = s_M(l)/\textstyle\sum_{M=1}^{5} s_M(l)\\ &= F_M \cdot r(l/m_M)/\textstyle\sum_{M=1}^{5} F_M \cdot r(l/m_M).\end{aligned}$$

One may produce other selectivity curves by multiplying the retention function by $(l/m_M)^d$ (a power function of relative size, for any real value of d) and multiplying each fishing power by $(m_M)^d$, then renormalizing to follow the convention that selectivities have a maximum value of one. The conditional probability of this new selectivity model is

$$\begin{aligned}\pi'_M = P'(M|l) &= F_M \cdot (m_M)^d \cdot r(l/m_M) \cdot (l/m_M)^d\\ &\quad /\textstyle\sum_{M=1}^{5} F_M \cdot (m_M)^d \cdot r(l/m_M) \cdot (l/m_M)^d,\end{aligned}$$

and it simplifies to equal that of the starting selectivity model. Therefore, the new selectivity model produces identical predicted catch values.

The expected catch in the log-linear approach is

$$E[c_{L,M}] = \lambda_L \cdot F_M \cdot r(l/m_M),$$

where λ_L may be viewed as a statistical nuisance parameter or as the relative abundance of fish of length l encountering each mesh. One may multiply the retention curve by $(l/m_M)^d$, the fishing power by $(m_M)^d$, and the relative abundance by l^{-d}; the expected catch is unchanged although relative abundance and selectivities have.In short, geometrically similar SELECT models may be multiplied as described with various values for d to produce an infinite set of other geometrically similar models that fit the data equally well.

Appendix 2: Model Equations that Were Used in the Statistical Assessment Model

A selectivity curve by length-bin L for mesh M (with mesh size m) as a function of fish length (l) assuming a bi-lognormal function:

$$\begin{aligned}s_{L,M} = &\frac{m_M}{l}\exp\left(\mu_1 - \frac{\sigma_1^2}{2}\right) \cdot R\exp\left\{\frac{-[\ln(l/m_M) - \ln(\mu_1)]^2}{2\sigma_1^2}\right\}\\ &+ \frac{m_M}{l}\exp\left(\mu_2 - \frac{\sigma_1^2}{2}\right) \cdot (1-R)\exp\left\{\frac{-[\ln(l/m_M) - \ln(\mu_2)]^2}{2\sigma_2^2}\right\},\end{aligned} \tag{A.2.1}$$

where μ_1, μ_2, σ_1, σ_2, and R are the parameters describing the relationship.

Absolute selectivity for fish in length-bin L for mesh M, adjusted for fishing intensity (ξ_M):

$$\varsigma_{L,M} = [s_{L,M}/\max(s_{L,M})]\xi_M \tag{A.2.2}$$

Absolute selectivity for the standard gill net for fish in length-bin L:

$$\varsigma_L = \textstyle\sum_M \varsigma_{L,M} \tag{A.2.3}$$

Relative selectivity curve for the standard gill net for fish in length-bin L:

$$S_L = \varsigma_L/\max(\varsigma_L) \tag{A.2.4}$$

Predicted catch for fish in length-bin L and mesh M:

$$\hat{c}_{L,M} = \varsigma_{L,M}\left[\textstyle\sum_M (\varsigma_{L,M} c_{L,M})^{0.5}/\textstyle\sum_M \varsigma_{L,M}\right]^2 \tag{A.2.5}$$

Estimated fish density for lake survey x, length-bin L, and mesh M:

$$D'_{x,L,M} = I_{x,L,M}/\varsigma_{L,M} \tag{A.2.6}$$

Estimated fish density for lake survey x and mesh M for size range targeted by population estimate:

$$D'_{x,M} = \textstyle\sum_{L=b} D'_{x,L,M} \tag{A.2.7}$$

Estimated fish density for lake survey x and length-bin L for standard gill net (i.e., all meshes):

$$D'_{x,L} = I_{x,L}/\varsigma_L \quad \text{(A.2.8)}$$

Estimated fish density for lake survey x for standard gill net for size range targeted by population estimate:

$$D'_x = \sum_{L=b} D'_{x,L} \quad \text{(A.2.9)}$$

Observed fish density by lake survey x:

$$D_x = \frac{N_x}{A_x} \quad \text{(A.2.10)}$$

Observed fish density by lake survey x apportioned by length-bin L based on selectivity:

$$D_{x,L} = (D'_{x,L}/D'_x)D_x \quad \text{(A.2.11)}$$

Fishing intensity for the standard gill net for lake survey x:

$$\xi_x = I_x/D_x \quad \text{(A.2.12)}$$

TABLE A.2.1. List of symbols.

Symbols and definitions	
A_x	Lake area occupied by the population of mature fish in lake x (i.e., lake size in ha)
b	Starting length-bin of targeted size for mark–recapture experiment in lake x
$c_{L,M}$	Observed number of fish caught for length-bin L in mesh M (in the statewide data set)
$\hat{c}_{L,M}$	Predicted number of fish caught for length-bin L in mesh M (for the statewide data set)
D_x	Observed estimated density of fish in lake survey x from mark–recapture experiment across targeted sizes
$D'_{x,L,M}$	Estimated fish density of fish in lake survey x for length-bin L in mesh M
$D'_{x,L}$	Estimated fish density of fish in lake survey x by length-bin L
$D'_{x,M}$	Estimated fish density of fish in lake survey x for size range targeted by population estimate in mesh M
D'_x	Estimated fish density of fish in lake survey x for size range targeted by population estimate
E_M	Fishing effort with mesh M
F_M	Fishing power of mesh M of gill net (relative measure; range 0 to 1)
I_x	Observed gill-net CPE of sizes targeted by population estimate in lake x
$I_{x,M}$	Observed gill-net CPE for lake survey x in mesh M
$I_{x,L,M}$	Observed gill-net CPE for lake survey x for length-bin L for mesh M
N_x	Observed estimated abundance of fish in lake survey x from mark–recapture experiment
R	Proportion factor for scaling the two lognormal distributions
$s_{L,M}$	A bi-lognormal shaped selectivity curve for length-bin L in mesh M
S_L	Relative selectivity for the standard gill net for length-bin L normalized to maximum of 1
ξ_M	Fishing intensity of mesh M of gill net (i.e., ha per unit effort for the most vulnerable size; used in estimating density from CPE)
ξ_x	Fishing intensity of standard gill net for lake survey x (i.e., targeted CPE/density; ha per unit effort)
$\varsigma_{L,M}$	Absolute selectivity for length-bin L in mesh M adjusted for fishing intensity of mesh M
ς_L	Absolute selectivity for length-bin L for the standard gill net adjusted for fishing intensity
μ_1	Mean of log-normal selection curve 1
μ_2	Mean of log-normal selection curve 2
σ_1	Standard deviation of the log-normal selection curve 1
σ_2	Standard deviation of the log-normal selection curve 2