Estimating walleye (Sander vitreus) density, gear catchability, and mortality using three fishery-independent data sets for Oneida Lake, New York


Abstract: We used three long-term data sets (gill nets, trawls, and adult population estimates) for walleye (Sander vitreus) to simultaneously estimate density, gear catchabilities, and mortality using an age-structured, nonlinear model. Model constraints included a fixed natural mortality rate and age- and gear-specific but time-invariant catchabilities. Trawl catchability decreased with age, whereas gillnet catchability increased towards a maximum by age-4. A sensitivity analysis was conducted to investigate how the information content of the different data sets influenced parameter estimates. Estimated catchability values were relatively robust to changes in data weighting. Estimated gillnet catchability values were fairly consistent with those derived from more conventional methods. An additional mortality term was added to reflect double-crested cormorant (Phalacrocorax auritus) predation, and vulnerabilities associated with angling and cormorants were calculated using independent length frequency information. Estimated subadult mortality increased and the influence of fishing mortality slightly decreased during recent years when double-crested cormorants were abundant and more restrictive size limits were in place. Walleye density in Oneida Lake (New York, USA) in the last decade is estimated to be approximately half of that before 1990.

Résumé : Nous utilisons trois banques de données à long terme (récoltes au filet maillant et au chalut, estimations de la population adulte) pour déterminer simultanément, à l’aide d’un modèle non linéaire structuré en fonction de l’âge, la densité, la capturabilité aux divers engins et la mortalité du doré (Sander vitreus). Les contraintes du modèle incluent un taux de mortalité naturelle fixe et des capturabilités spécifiques à l’âge et à l’engin, mais invariables dans le temps. La capturabilité au chalut diminue avec l’âge, alors que la capturabilité au filet maillant augmente pour atteindre un maximum à l’âge de quatre ans. Une analyse de sensibilité a servi à vérifier comment le contenu informatif des banques de données influence l’estimation des paramètres. Les valeurs estimées de capturabilité sont relativement robustes au changements de pondération des données. Les valeurs de capturabilité au filet maillant s’accordent généralement avec celles obtenues par des méthodes plus conventionnelles. Nous avons ajouté un terme de mortalité pour tenir compte de la prédation par les cormorans à aigrettes (Phalacrocorax auritus); des vulnérabilités associées à la pêche sportive et aux cormorans ont été calculées à l’aide d’information indépendante sur les fréquences de longueurs. La mortalité estimée des subadultes a augmenté et l’influence de la mortalité due à la pêche a diminué au cours des dernières années, alors que les cormorans à aigrettes étaient abondants et que des limites de taille plus restrictives ont été appliquées à la pêche. Nous estimons que la densité des dorés dans le lac Oneida (New York, E.-U.) durant la dernière décennie était d’environ la moitié de celle d’avant 1990.

[Traduit par la Rédaction]

Introduction

A common objective of traditional fisheries catch-at-age models is to use observed catch statistics to estimate both population abundance and exploitation rates through time (Hilborn and Walters 1992). Virtual population analysis (or cohort analysis) uses backwards projections to estimate previous abundance levels, whereas integrated analysis (or statistical catch-at-age analysis) estimates abundances for all ages during the initial year and for the age at first recruitment for all subsequent years to then project the population forward through time (Haddon 2001). A key component of
The ability of a sampling gear to capture organisms can depend on several factors. Anderson (1998) describes encounter, contact, and retention components of multifilament gill nets. These components are influenced by the size of the fish relative to that of the mesh, the visibility of the net, as well as the swimming speed and activity level of a fish. For example, swimming speed tends to increase with fish size, leading to increased encounter probability. Likewise, larger mesh sizes have a less visible surface, which increases contact probability, while larger fish can also be entangled in small mesh sizes. Combined, these effects suggest that gill-net catchability should increase with fish size even if the maximum retention probabilities of various mesh sizes are the same (Hamley 1975; Rudstam et al. 1984; Grant et al. 2004). In contrast, trawl catchability likely decreases with fish size because increased swimming speed at larger sizes should improve the ability of fish to avoid the gear (Wardle 1983). In addition, trawl catchability can be affected by water clarity (Nielsen 1983; Buijse et al. 1992), towing speed, and trawl material and construction (Wardle 1983). Variation in behavior, activity periods, and habitat preference among life stages of fish can further bias catches in most gears (Willis et al. 1985; Rudstam and Johnson 1992). In the case of these and other sampling approaches, gear biases and sampling variability can cause catch data to misrepresent the abundance of different age groups or size classes. As such, it is necessary to account for these differences in gear catchability to effectively compare age-specific estimates across sampling techniques.

We developed an estimation model that simultaneously uses all available long-term data for walleye in Oneida Lake to obtain a maximum likelihood estimate of the population while following multiple age groups over time. Specifically, our objectives were to synthesize the three fishery-independent, long-term data sources for Oneida Lake walleye to (i) derive an internally consistent and age-specific assessment of walleye density across nearly 50 years of data collection, (ii) estimate age-specific catchability values for both an active and a passive sampling gear, and (iii) evaluate possible changes in walleye mortality associated with an increase in abundance of a predator — the double-crested cormorant *Phalacrocorax auritus*.

Based on the available data and estimated parameters, it was not possible to allow the model to estimate a separate mortality rate for each year. However, we do expect a change in walleye mortality over time based on changing conditions in Oneida Lake. During the early 1990s, the establishment of zebra mussels (*Dreissena polymorpha*) (possibly combined with decreased nutrient loading) led to increased water clarity and photic zone depth in Oneida Lake (Idrisi et al. 2001), causing shifts in lower level trophic dynamics and enhanced littoral macrophyte growth (Mayer et al. 2002; Zhu et al. 2006). At the same time, the abundance of double-crested cormorants on Oneida Lake has increased, introducing a new source of predation on subadult walleye (VanDe Valk et al. 2002; Rudstam et al. 2004; Coleman et al. 2005). Rudstam et al. (2004) documented increased mortality of ages 1–3 walleye in the 1990s (based on trawl catches) and argued that cormorants were a major cause of the decline in the walleye population in Oneida Lake during this time. In addition, size limits for anglers...
have changed over time in the lake, likely contributing to differences in fishing mortality. Therefore, we decomposed mortality into three components: natural mortality, cormorant mortality, and fishing mortality. An instantaneous natural mortality was calculated from independent data (see Materials and methods) and fixed over all ages and years, whereas cormorant and fishing mortality were estimated and their influence varied with the proportion of vulnerable fish present in an age group. For fishing mortality, this proportion is a function of the angling regulation (size limit) imposed in specific years. The vulnerability of various ages to cormorant mortality also was based on fish size but only occurred during years after 1990, the year Rudstam et al. (2004) suggested cormorant predation had become noteworthy. In addition to creating a more realistic, time-dependent mortality, this allowed us to further test the conclusion of Rudstam et al. (2004) that subadult mortality in Oneida Lake walleye had increased since 1990.

We used a nontraditional, age-structured, nonlinear population dynamics model to estimate age-specific gear catchabilities, mortality rates, and the density (number ha\(^{-1}\)) of multiple age classes of walleye using input data from all three long-term data sets for walleye in Oneida Lake. The sensitivity of the catchability estimates to the selected weighting of the three data sources or to the fixed natural mortality rate was then investigated. We also compared gear catchability-at-age estimates from the model with both direct measures from the adult population and a gillnet relative selectivity curve constructed with traditional methods using the length distribution of the catch in individual mesh sizes.

Materials and methods

Description of study site

Oneida Lake has the largest (207 km\(^2\)) surface area of any lake entirely in New York State and is one of the most studied freshwater ecosystems in North America (Adams and Hankinson 1928; Mills et al. 1978; Forney 1980). In addition to offering long-term data series on multiple trophic levels ranging from algae to top predators, Oneida Lake provides important recreational and economic resources to much of central New York and the northeastern USA. Walleye and yellow perch (\textit{Perca flavescens}) are the most sought after sport fishes, and both species are important components of the Oneida Lake food web (Forney 1980; Mills and Forney 1988). Nearly every spring, larval walleye are stocked into Oneida Lake soon after hatching, and most captured walleye fry are believed to be of hatchery origin (Houde and Forney 1970; Forney 1975, 1980).

Indices of walleye abundance

Gillnet catch data for walleye are available for all years from 1958 to 2003 except for 1974. In each year, multifilament gill nets were used to sample 15 fixed sites in a standardized sequence from June through September. At each site, two nets (300 ft \(\times\) 6 ft depth; 1 ft = 0.3048 m) were set on bottom and allowed to fish overnight for approximately 12 h. Each net consisted of two gangs of six 25-ft panels with mesh size (as stretch mesh) that ranged from 1.5 inches to 4 inches at 0.5-inch increments (1 in = 25.4 mm). From 1963 through 1967, gillnet sampling was conducted using one white net and one colored (red, green, or black) net. During other years, two white nets were used at each site. Each year, scales were removed from all or a subsample of captured walleye for age determination, and these data were combined across sites and used to determine the annual age distribution for the total catch. The gillnet catch data were combined across mesh sizes and sampling locations so that annual total catch-at-age values could be used as an input data set for the estimation model.

Walleye abundance in Oneida Lake has also been assessed with a summer–fall bottom trawl survey at 10 standardized sites since 1961. Each site was sampled weekly for about 15 consecutive weeks. The bottom trawl had a 5.5 m footrope, and each haul sampled approximately 0.1 ha of bottom surface area with a transect length of approximately 280 m (see Nielsen 1983 for more details). Trawl catch data were combined across sites within a year. To facilitate comparisons with population estimates, we converted total trawl catches to catch per hectare swept (henceforth referred to as trawl CPUE). As for gill nets, trawl CPUE-at-age was used as an input data set. During 7 years, age-7 walleye were not specifically identified in the ageing process for trawl-caught fish. Instead, they were included as part of an age-7 and older group. These few lumped-age estimates were not used as trawl input data for the estimation model (see below).

Since 1958, the population size of adult walleye has been periodically estimated using mark–recapture methods (\(N = 21\) years). Unlike the long-term data sets from trawl and gillnet sampling, the mark–recapture population estimates are for adult fish only. During early spring (usually April), adult walleye were collected in trap nets near Scriba Creek by the Oneida Fish Cultural Station staff, Constantia, New York, and near Shackelton Point by personnel from the Cornell Biological Field Station. Individual walleye were marked (12 000 – 26 000 per year) using a year-specific fin clip. Occasionally, additional walleye were captured and marked at other locations using trap nets and electrofishing surveys; however, these collections usually contributed less than 20\% of the total number of marked fish. Throughout the summer and fall, recaptures were collected primarily using electrofishing and large trawls (with approximately equal effort in all areas of the lake), but occasionally using gill nets and trap nets (during 1958–1960). For the years when mark–recapture methods were employed, population estimates were calculated for each age group of adult walleye using Bailey’s (1951) modification of the Petersen formula (additional details for Oneida Lake in VanDeVelk et al. 2002) and used as an input data set for the estimation model.

Parameter estimation

We used AD Model Builder software (Otter Research Ltd., Sydney, British Columbia) to construct and perform nonlinear estimation procedures. Based on the relative availability of the three input data sources, the estimation model followed age-1 through age-7 and an aggregate age-8 and older category of walleye during the period 1958 through 2003. We used the model to evaluate age-specific catchability values for both sampling gears. The few missing trawl values and the missing gillnet catch from 1974 were not
used in model estimation; their contribution to the likelihood was eliminated using a matrix of weighting factors (0 or 1). Age-0 data were not included in the estimation model because of the very low catchability of this age class in gill nets as well as known high variability in annual mortality due to the vulnerability of this age class to cannibalism (Chevalier 1973). Estimated parameters included age-specific catchability values for the trawl and gill net separately, an instantaneous fishing mortality rate, an instantaneous mortality rate reflecting double-crested cormorant predation, and an initialization vector (including age-1 recruitment) of walleye density (number ha$^{-1}$). Parameters were initialized and estimated as loge values.

We used available walleye survival and harvest data to calculate a fixed instantaneous natural mortality rate and an initialization value for instantaneous fishing mortality. Annual measures of adult walleye survival and angler harvest were available during 1958, 1959, 1997, and 2002 (Forney 1967; VanDeValk et al. 2005b; Table 1). Annual survival measures (Table 1) were calculated as an average of two independent methods (VanDeValk et al. 2005b), one based on decreased population size over time and the other based on the ratio of different year-specific marks (see Ricker 1975). The corresponding instantaneous total mortality rates were then partitioned to instantaneous fishing ($F$) and instantaneous natural mortality ($M$) rates by setting the ratio of $F$ to $M$ equal to the ratio of number harvested by angling to number lost to natural mortality, using estimates of survival and angler harvest for years when these data were available (Table 1). Next, these values were averaged over years (Table 1), and an instantaneous natural mortality rate of 0.101 was applied to all age classes in the estimation model. The calculations used to determine $M$ were based on data for adult walleye, but we felt that it was reasonable to also apply this rate to subadults because throughout most of the sampled period, we expect that late-year age-1 and age-2 walleye would have few predators as they outgrow the size-selective piscivorous fish present (Chevalier 1973), and anglers harvest few walleye at these young ages (VanDeValk et al. 2005a). As part of a sensitivity analysis (described below), we also reran the model using either one-half or twice the calculated value of $M$. Likewise, an $F$ parameter was initialized at 0.242 (but then estimated by the model) based on data for these years (Table 1).

Cohorts were modeled to follow an exponential decline with time:

\[(1) \quad N_{i,j+1} = N_{i,j} \exp(-Z)\]

where $N_{i,j}$ is the density (number ha$^{-1}$) of a cohort during year $i$ at age $j$, $N_{i+1,j+1}$ is the density of the same cohort during the following year, $Z$ is an instantaneous annual mortality rate (all sources), and $t$ represents a 1-year time step. The density parameters for the initial year (1958) and the age-1 recruitment parameters were estimated on the loge scale and, for the efficiency of the algorithm, as an overall mean coupled with bounded deviations. Density was initialized with a value of 33.1 based on the average catch of age-1 walleye in the trawl and a previous trawl-catchability estimate for adult walleye.

For both the gill net and trawl, we assumed catchability was age-specific but remained constant across years. The annual age-specific catches for both gears were estimated from the predicted population density of walleye and the age-specific catchability scalar:

\[(2) \quad C_{i,k} = N_{i,j} q_{i,j,k}\]

where $C_{i,k}$ is the predicted catch at age-$j$ of walleye in the $k$th sampling gear during year $i$, $N_{i,j}$ is the estimated density (number ha$^{-1}$) of age-$j$ walleye in the lake during year $i$, and $q_{i,j,k}$ is the estimated age-specific catchability for that gear. The reported catchability-at-age estimates for the gill net do not range from 0 to 1 because the gillnet data are on the scale of annual total catch-at-age, while the mark-recapture population estimates for adult age classes are density values (number ha$^{-1}$). The trawl catchability-at-age values do range from 0 to 1, but only because the area swept by the combined 10 trawls in the standard survey happens to equal 1 ha, the same area as used for density values.

The estimation of parameters was driven by a nonlinear estimation procedure, which arrived at a set of parameter values that minimized a concentrated form of the negative log-likelihood by simultaneously minimizing the differences between the observed and predicted values for gillnet catches, the trawl CPUE, and the adult mark-recapture population estimates (the objective function). We used concentrated forms of the negative log-likelihood functions for normal and lognormal distributions to characterize these re-

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**Table 1.** Adult (age-4 and older) walleye (*Sander vitreus*) survival, abundance, and angler exploitation data used to select initialization values for mortality parameters.

<table>
<thead>
<tr>
<th>Year</th>
<th>Annual survival</th>
<th>Adult abundance</th>
<th>Angler harvest</th>
<th>$Z$</th>
<th>$F$</th>
<th>$M$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1958</td>
<td>0.87</td>
<td>1 035 000</td>
<td>106 000</td>
<td>0.139</td>
<td>0.110</td>
<td>0.030</td>
</tr>
<tr>
<td>1959</td>
<td>0.46</td>
<td>960 800</td>
<td>449 000</td>
<td>0.777</td>
<td>0.672</td>
<td>0.104</td>
</tr>
<tr>
<td>1997</td>
<td>0.80</td>
<td>251 900</td>
<td>35 400</td>
<td>0.223</td>
<td>0.157</td>
<td>0.066</td>
</tr>
<tr>
<td>2002</td>
<td>0.79</td>
<td>345 900</td>
<td>9 587</td>
<td>0.236</td>
<td>0.031</td>
<td>0.205</td>
</tr>
</tbody>
</table>

**Note:** Instantaneous total mortality rates ($Z$) were partitioned to instantaneous fishing ($F$) and instantaneous natural mortality ($M$) rates by setting the ratio of $F$ to $M$ equal to the ratio of number harvested by angling to number lost to natural mortality using independent estimates of walleye survival and angler harvest.
lationships between observations and predictions. For example, the traditional form of the full negative log-likelihood for the normal distribution was reduced to a concentrated form (e.g., \([-\ln L]\)) by replacing \(\sigma^2\) with its maximum likelihood estimate and simplifying:

\[
[-\ln L] = \frac{n}{2} \ln \left( 2\pi \sum \frac{\sum (\text{obs} - \text{pred})^2}{N} \right) + \frac{n}{2}
\]

where \(\text{obs}\) is the observed measure and \(\text{pred}\) is the predicted measure of age-\(j\) walleye in Oneida Lake during year \(i\). The mark–recapture data were fit assuming normal error (above), whereas the gillnet and trawl data were fit assuming lognormal error. Lognormal errors were selected for the sampling gear data because of skewness in their residuals when a normal likelihood was used (lognormal likelihood places less influences on extreme values). Because of a few age-specific cases where no fish were caught, we added a minimal value for each gear type (added value was equal to half of the minimum observed value: 0.5 for gill nets and 0.02 for trawl CPUE) to both the observed and predicted values before taking their natural logs. The objective function was the sum of the three separate, concentrated, negative log-likelihood functions, which were specific to each of the input data sets, after weighting coefficients were applied.

Weighting coefficients are usually applied to the different components of the likelihood to characterize the degree to which the separate sets of information should contribute to the overall parameter estimation. In our case, the data for adult walleye density and trawl CPUE were both input into the model as number per hectare; however, the sampling area of the passive gill net was unknown. Differences in the unknown age-specific catchabilities of the passive and active gears also add to the complexity. We applied weighting coefficients to the concentrated log-likelihood functions so that the importance of fitting predicted values to the observed data was approximately equal across the three data sets. To further assess the sensitivity of the catchability estimates to our assumptions, we re-estimated the model parameters under three alternative weightings. In each case, we adjusted the weighting coefficient of the likelihood component of an input data set by a factor of 10, which allowed that data set to dominate the influence of the parameter estimation over the other two. Further, we also examined the sensitivity of the catchability estimates to the assumed fixed natural mortality rate by re-estimating these values using either one-half or twice the calculated value of instantaneous natural mortality.

To evaluate the effects of double-crested cormorant predation on the dynamics of the walleye population, we split the estimation of mortality into two time periods (1958–1989 and 1990–2003). To do this, we added an additional mortality term to the second time period to reflect predation associated with double-crested cormorants. Because age-specific vulnerability to harvesters (either anglers or cormorants) is likely to change over time, we calculated the proportion of each walleye age group that was vulnerable to either anglers or double-crested cormorants using annual total-length-at-age values back-calculated from fish caught in gillnet collections, when the number observed by age category exceeded five, and specified thresholds of vulnerability (e.g., annual angler size limits and a maximum consumable size for cormorants). For the few years when observed catch-at-age was less than five, we calculated an average vulnerability proportion using surrounding years that had the same recreational size limit in effect. This way, the annual vulnerability proportions for angling reflected the effects of that year’s minimum length limit for angler harvest from Oneida Lake. Prior to 1975, no minimum size limit was in place, so we assumed that anglers would not have harvested walleye that were less than 12 inches (305 mm). In 1979 and 1980, the minimum length limit was 12 inches, and it was increased to 18 inches (457 mm) from 2001 to 2003. For all other years, the minimum length limit was 15 inches (381 mm). We did not attempt to account for changes in the creel limit. For the age-specific vulnerabilities associated with predation from double-crested cormorants, we similarly used the observed length-at-age values and assumed simply that double-crested cormorants were only capable of consuming walleye less than 360 mm (J. Coleman, Cornell University, Department of Natural Resources, Ithaca, NY, 194853, USA, personal communication, 2006).

The proportion vulnerable was calculated annually and used to weight the influence of the estimated instantaneous mortality rates across age classes. Using fishing mortality as an example, an age group \((N_j)\) can be separated into vulnerable \((V_j)\) and invulnerable \((R_j)\) components as

\[
N_j = V_j + R_j
\]

Fishing mortality then is only applied to the vulnerable portion of the population, whereas natural mortality is applied to both components. Therefore

\[
N_{j+1} = [(V_j) e^{-F} + R_j] e^{-M}
\]

The calculated proportion of each age class vulnerable to either estimated mortality rate was year specific (described above). Using this approach, only two instantaneous mortality parameters (representing fishing and double-crested cormorant predation) were estimated in the model, but the influence of both estimated instantaneous mortality parameters on each age class changed over time in relation to observed fish size.

**Relative selectivity of gillnet mesh sizes**

For comparisons with age-specific estimates of gillnet catchability produced by the estimation model, we calculated relative selectivity curves for walleye based on length distributions of more than 2145 walleye captured in different mesh sizes of the Oneida Lake gill nets (from 1986–1992; data from Forney et al. 1994). We assumed that the maximum selectivity is the same for each mesh size. Maximum selectivity has often been found to occur at a constant ratio of fish girth to mesh perimeter (Hamley 1975). When fish girth is a linear function of length (as is the case for walleye; Henderson and Wong 1991; Forney et al. 1994), this is equivalent to assuming that the modal fish length (the length of maximum retention probability) is a linear function of the mesh size; therefore, the selectivity curves can be es-
estimated directly from the length distribution. Following Hamley (1975) and Wulff (1986), we used a skew normal curve to estimate the length-based relative selectivity of each mesh size for each length bin:

$$S_{l,m} = \exp \left( -\frac{\lambda_{l,m}^2}{2} \left[ 1 - k \frac{\sigma_m^3}{2 \lambda_{l,m}^3} \right] \right)$$

where relative selectivity ($S_{l,m}$) was determined for forty-eight, 1 cm length bins ($l$) ranging from 10 through 57 cm for each of the six mesh sizes ($m$, as bar mesh in mm). In eq. 6, $k$ is an estimated skewness constant and

$$\lambda_{l,m} = \frac{L_l - L_{0,m}}{\sigma_m}$$

where $L_l$ is the length associated with the $l$th length bin (cm), and both the modal length of fish captured by mesh size $m$ ($L_{0,m}$, total length in mm) and the standard deviation of that mesh ($\sigma_m$) are linear functions of the mesh size:

$$L_{0,m} = a + bm$$

$$\sigma_m = cm$$

where parameters $a$, $b$, and $c$ are constants. The four parameters ($a$, $b$, $c$, and $k$) were estimated using a maximum likelihood function (Wulff 1986) to be 3.2, 0.97, 0.13, and 0.19, respectively.

Only length bins with more than 10 fish were included in the likelihood calculations. These calculations produced a selectivity curve for each of the mesh sizes, which were then summed to produce an overall selectivity curve for the Oneida Lake gill net. Because we assumed the height of the selectivity curves to be constant, this combined curve does not account for size-based changes in swimming speed or activity. Actual selectivity for a given size group of Oneida Lake walleye in the combined standard gill nets also includes a probability of an individual encountering and contacting the net (see Rudstam et al. 1984 or Anderson 1998). This encounter probability may be size dependent.

Results

Indices of walleye abundance

Gillnet effort was constant for all 45 available years, and the annual total catch of walleye in gill nets ranged from 75 to 836. The average percentage of the annual total gillnet catch of walleye that was aged was 96% (range = 66%--100%). Although the catch of age-1 walleye in gill nets was typically lower than that for older ages of a cohort, strong year classes of walleye typically produced large catches at age-1. Trawl effort ranged from 113 to 272 hauls per year (mean = 153) from 1961 to 2003. Trawl CPUE typically declined as the cohort aged, and catches were highest for age-1 walleye for 29 of 37 complete cohorts (data for age-1 to age-7).

Mark–recapture techniques produced age-specific absolute abundance estimates for adult walleye (age-4 and older) for 21 nonconsecutive years. Based on the mark–recapture estimates, the lowest density of adult walleye occurred in 1974; however, the five most recent surveys (performed in 2-year intervals since 1995) produced the next five lowest density estimates for the adult population.

Parameter estimation

The estimation model produced parameter values for the catchability of an active and a passive sampling gear, walleye mortality, and density by age group in the absence of fishery harvest data (Table 2). Three long-term indices of walleye density were synthesized to estimate these previously unknown parameters for walleye in Oneida Lake and aided our understanding of the development of the population over time and our sampling of it.

Age-specific estimates of trawl catchability decreased from age-1 to the aggregate age-8 and older category (Fig. 1a). The estimated values for gillnet catchability were lowest for age-1 and peaked for ages 4–6 (Fig. 1b). To assess the effects of the weighting coefficients applied to the input data sources, the model was rerun with each input data (gillnet catch-at-age, trawl CPUE, and adult density) set allowed to dominate the objective function. The plotted forms of the estimated age-specific catchability values for both the gill net and trawl were approximately the same but shifted upward for most age classes when more weight was alternatively given to the gear-specific data sets (Fig. 1). Likewise, the catchability estimates for adult walleye were unchanged when the calculated value for natural mortality was either halved or doubled. However, the catchability values for young walleye were more sensitive to this natural mortality value (Fig. 1). To serve as additional reference points for comparison with model estimates, catchabilities of adult walleye in gill nets and trawls were also calculated using the absolute abundance measures from mark–recapture of older walleye. These values also suggested a decreasing trend in catchability of walleye with age in bottom trawls and in gill nets from age-4 to older fish (Fig. 1). For gill nets, these direct calculations were based on the total annual catch-at-age of adult walleye collected at the 15 standard sites and should not be expected to range between 0 and 1 because the annual gillnet survey samples an unknown area of the lake. These decreasing trends in calculated gillnet catchability were expected, in part, because older fish are reaching sizes larger than the peak size selectivity of the largest mesh sizes used in our survey nets.

All ages were affected by the same fixed natural mortality rate. We allowed the instantaneous fishing and cormorant mortality parameters to be functions of fish size and size limits. The model estimated an annual instantaneous fishing mortality rate of 0.327 on vulnerable age classes. Depending on the size limit imposed in different years, the influence of this fishing mortality rate varied. As an example, the average fishing mortality affecting age-5 walleye was 0.327 before the 15-in size limit was put into place (1975), compared with 0.228 when the size limit was 15 in and 0.089 when the size limit was 18 in. Double-crested cormorants were not present on Oneida Lake in large numbers until the early 1990s; therefore, we assumed that walleye in the model were not vulnerable to the mortality parameter reflecting double-crested cormorants until after 1990. During this period, the instantaneous cormorant mortality rate was estimated to be 0.347 on fully vulnerable age-1 fish, while only a portion of other ages were considered vulnerable based on
Table 2. Loge-scale parameter estimates and associated linear approximations of the standard deviations shown in parentheses for walleye (Sander vitreus) densities and age-specific gear catchabilities.

(a) Age-1 density.

<table>
<thead>
<tr>
<th>Year</th>
<th>xxx0</th>
<th>xxx1</th>
<th>xxx2</th>
<th>xxx3</th>
<th>xxx4</th>
<th>xxx5</th>
<th>xxx6</th>
<th>xxx7</th>
<th>xxx8</th>
<th>xxx9</th>
</tr>
</thead>
<tbody>
<tr>
<td>1958-1959</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>3.67 (0.05)</td>
</tr>
<tr>
<td>1960s</td>
<td>3.37 (0.09)</td>
<td>3.11 (0.13)</td>
<td>2.85 (0.12)</td>
<td>3.16 (0.13)</td>
<td>3.12 (0.1)</td>
<td>3.59 (0.07)</td>
<td>2.97 (0.14)</td>
<td>1.11 (0.2)</td>
<td>2.66 (0.16)</td>
<td>3.58 (0.07)</td>
</tr>
<tr>
<td>1970s</td>
<td>-0.06 (0.24)</td>
<td>1.43 (0.19)</td>
<td>3.99 (0.05)</td>
<td>-0.13 (0.23)</td>
<td>0.99 (0.2)</td>
<td>0.80 (0.2)</td>
<td>3.43 (0.17)</td>
<td>0.55 (0.22)</td>
<td>3.64 (0.16)</td>
<td>1.65 (0.19)</td>
</tr>
<tr>
<td>1980s</td>
<td>1.30 (0.19)</td>
<td>2.94 (0.15)</td>
<td>3.60 (0.1)</td>
<td>2.61 (0.15)</td>
<td>2.38 (0.14)</td>
<td>2.50 (0.12)</td>
<td>2.49 (0.14)</td>
<td>1.22 (0.19)</td>
<td>3.68 (0.15)</td>
<td>1.44 (0.21)</td>
</tr>
<tr>
<td>1990s</td>
<td>1.84 (0.24)</td>
<td>2.00 (0.23)</td>
<td>3.55 (0.2)</td>
<td>1.43 (0.25)</td>
<td>2.23 (0.23)</td>
<td>2.03 (0.24)</td>
<td>2.42 (0.22)</td>
<td>1.59 (0.23)</td>
<td>2.29 (0.22)</td>
<td>2.50 (0.22)</td>
</tr>
<tr>
<td>2000-2003</td>
<td>2.51 (0.22)</td>
<td>2.21 (0.3)</td>
<td>3.12 (0.35)</td>
<td>2.39 (0.49)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

(b) Initial density.

<table>
<thead>
<tr>
<th>Year</th>
<th>Age-2</th>
<th>Age-3</th>
<th>Age-4</th>
<th>Age-5</th>
<th>Age-6</th>
<th>Age-7</th>
<th>Age-8+</th>
</tr>
</thead>
<tbody>
<tr>
<td>1958</td>
<td>1.5 (0.21)</td>
<td>1.16 (0.26)</td>
<td>3.73 (0.03)</td>
<td>-0.99 (0.49)</td>
<td>1.98 (0.14)</td>
<td>0.42 (0.53)</td>
<td>1.39 (0.25)</td>
</tr>
</tbody>
</table>

(c) Age-specific catchability (q_x).

<table>
<thead>
<tr>
<th>Gear type</th>
<th>Age-1</th>
<th>Age-2</th>
<th>Age-3</th>
<th>Age-4</th>
<th>Age-5</th>
<th>Age-6</th>
<th>Age-7</th>
<th>Age-8+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gill net (q_G)</td>
<td>0.65 (0.12)</td>
<td>1.45 (0.11)</td>
<td>1.88 (0.11)</td>
<td>1.98 (0.1)</td>
<td>1.84 (0.1)</td>
<td>1.98 (0.1)</td>
<td>1.74 (0.11)</td>
<td>1.61 (0.11)</td>
</tr>
<tr>
<td>Trawl (q_T)</td>
<td>-1.13 (0.13)</td>
<td>-1.50 (0.13)</td>
<td>-1.66 (0.12)</td>
<td>-1.89 (0.12)</td>
<td>-1.99 (0.12)</td>
<td>-2.06 (0.13)</td>
<td>-2.22 (0.14)</td>
<td>-2.60 (0.14)</td>
</tr>
</tbody>
</table>

Note: All parameters were originally estimated on a loge scale. The values for loge density are presented first by decade for age-1 fish and then for the remaining ages for 1958 only (the initial year included in the analysis). Next, loge age-specific (age-1 through 8+) catchability values are shown for both the gill net (q_G) and trawl (q_T). Loge instantaneous mortality estimates (linear approximations of the standard deviations in parentheses) associated with fishing (F) and double-crested cormorants (C) are as follows: \( F = -1.12 (0.03) \); \( C = -1.06 (0.18) \).
their total length (effective instantaneous cormorant mortality averaged 0.330, 0.205, and 0.058 for ages 2, 3, and 4, respectively). Very few age-5 or older walleye were expected to be vulnerable to cormorant mortality in our model. Both instantaneous fishing and instantaneous cormorant mortality were additive to the fixed instantaneous natural mortality rate (0.101). Annual survival estimates for walleye were quite different for the two time periods (before and after 1990; Fig. 2) because of both the additional cormorant mortality and implementation of an 18-in size limit in recent years. No single age class of walleye was considered fully vulnerable to both fishing and cormorant mortality.

The model estimated an initialization value for walleye density (9 walleye·ha⁻¹). Annual recruitment (at age-1) deviations were applied to this density estimate to initiate new year classes in the model. A lower number of age-1 walleye (associated with higher mortality between ages 0 and 1) likely contributed to the overall decline seen in our catches. The highest annual adult density occurred during the first year included in the model (1958) because of the presence of a large number of age-4 walleye; however, later cohorts did produce higher densities at younger ages (Fig. 3). Since 1990, the average densities of both subadult (ages 1–3) and adult (age-4 and older) are barely half of earlier average densities (Fig. 4).

Relative selectivity of gillnet mesh sizes

We calculated relative selectivity for the individual gillnet mesh sizes based on walleye length distributions external to the estimation model (see Materials and methods). Because gillnet catchability values from the estimation model were age-specific, we assigned length-at-age values based on estimated growth rates and back-calculated length-at-age estimates using all available data (1958–2002) so that the model estimates could be visually compared with size-based relative selectivity patterns (Fig. 5). The gillnet catchability estimates from the estimation model increased slightly faster with walleye length from ages 1 to 6 than the selectivity derived from catches in the different mesh sizes.

Discussion

We combined multiple sources of information and used a minimal number of limiting assumptions to estimate mortality and age-specific density of age-1 and older walleye in Oneida Lake as well as age-specific catchability values for both the standard gill net and trawl. This approach simultaneously used weighted contributions from three data sets (gill net, trawls, and adult mark–recapture), which were collected over a 46-year period, to construct an internally consistent picture of the development of the walleye population over time in the absence of annual fishery effort and harvest data.

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Mortality
During the earlier years, mortality of subadult walleye was primarily natural mortality, although these young fish occasionally were large enough to be affected by fishing mortality. As a result, estimated average annual survival of age-1 walleye during the initial time period (1958–1989) was high (90.4%) but fell to the lowest observed average annual survival estimate (63.9%) during the second time period (1990–2002) when this age was also affected by the additional mortality parameter. As such, the average annual survival of age-1 walleye showed the greatest change of all the represented age classes between the two mortality time periods. The average annual survival of age-2 walleye showed the greatest change of all the represented age classes between the two mortality time periods. The average annual survival of age-2 walleye in the first time period (86.0%) was slightly lower than that for age-1 fish because length-at-age values suggested a small proportion of age-2 walleye would have been vulnerable to angler harvest during the first time period, when some years had no length-based harvest restrictions (we assumed a 12-in minimum harvest size for these years). Similar to age-1 fish, the average survival of age-2 walleye was lower during the second time period, as these fish were influenced by the double-crested cormorant mortality parameter. Previously, Rudstam et al. (2004) observed that mortality of subadult walleye in Oneida Lake had increased and suggested that this was a result of increased predation by double-crested cormorants. Results of our estimation exercise support this hypothesis. Rudstam et al. (2004) used only the trawl data as an index of age-1 abundance and
only mark–recapture data combined with trap-net catches to estimate age-4 abundance. Here, we simultaneously used three long-term, fishery-independent data series that contain separate, age-specific information and confirmed high mortality of subadult walleye after 1990. Although this does not directly identify the causative source of this additional mortality, we also suggest that cormorants were the most likely source of increased mortality for subadult walleye (see Rudstam et al. 2004).

The overall changes in average survival of ages 3 and 4 walleye between time periods were much less than that for the youngest two age classes. This was due in part to these ages typically being less vulnerable to predation from double-crested cormorants and to increased length limits, offering protection of fish between 15 and 18 inches, during the second time period when double-crested cormorants increased in abundance. Overall, the two estimated mortality parameters included in the model suggested mortality additional to the fixed natural mortality level, although the actual influence of these two additional parameters varied among ages. To facilitate calculation of natural mortality, we used data from a few years that included measures of angler harvest. We believe our estimate of a relatively low natural mortality for all age groups is reasonable because mortality of age-1 walleye in Oneida Lake is expected to be primarily due to predation, and most of this mortality likely occurred prior to our sampling; however, we did explore model sensitivity to this fixed value by modifying the natural mortality rate by factors of 0.5 and 2. During our sampling period, age-1 walleye would have outgrown some gape-limited predators, and age-0 fishes typically dominate the diets of adult walleye (Chevalier 1973; Forney 1974). Double-crested cormorants are the only predator in the lake known to select for age-1 walleye.

For age-5 and older walleye, the applied instantaneous fishing mortality \( (F) \) ranged from 0.03 to 0.3 depending on observed fish size and the size limits imposed during a given year. This range of mortality is similar to previous calculations from Oneida Lake (VanDeValk et al. 2002, 2005b) but is not a particularly high fishing mortality — for a single season, annual mortality from fishing can approach 50\% \( (F = 0.78; \text{Forney 1967}) \). However, our model did not allow fishing mortality in individual years to be higher than the estimated value of full vulnerability to the fishery. Angler harvest can be highly variable, as evidenced by a comment by the Editor of Conservationist in 1961: “Oneida Lake fishermen—and they are legion—have long tried to guess why walleyed pike fishing, for which the lake is famous, could be so good one year, almost a waste of time the next” (see Forney and Eipper 1961). For a given year, angler catch rates in Oneida Lake is primarily determined by the availability of forage fish to walleye and largely unrelated to walleye abundance (Forney and Eipper 1961; Forney 1965; VanDeValk et al. 2005a). Even so, adult walleye survival during recent years should have benefited from more restrictive harvest regulations, which were in place during years when double-crested cormorant mortality was affecting subadults. For Oneida Lake, exploitation by anglers has been measured for only a few years, and because of this lack of long-term information, we did not attempt to directly include variable angler harvest in this estimation exercise. However, if harvest is known, then this information could be included in a similar estimation model.

**Age-specific gear catchability**

Fish populations are often sampled using both passive and active gears, but catch rates of these gear types are not directly comparable unless the catchabilities are known. The problems associated with comparing or combining data from the two sampling approaches generally arises from the difficulty in quantifying the sampling area of the passive gear; however, both gear types provide information on the size of the population. Here, the choice of weighting coefficients used to regulate the influence of each input data set on the estimates had relatively little influence on the catchability estimates. The mark–recapture procedures offered the most direct measure of absolute abundance for Oneida Lake walleye. Although we have confidence in these mark–recapture estimates of adult walleye abundance (confidence intervals are typically ±20\%), this input data set contained no direct estimates for subadults and had no estimates for many of the years that the population was sampled with both the trawl and gill net. The two walleye collection gears likely have different age biases; trawl data are likely better than gill nets to serve as an indicator of subadult abundance, while gill nets are likely better than trawls as an indicator of adult abundance. We had no basis for initially weighting one data set more than the other and felt that giving equal weight to all three long-term input data series was the most appropriate assumption.

Our model estimates did include the assumption that age-specific gear catchability has not changed in Oneida Lake over the study period. This assumption is reasonable because the sampling protocols and gears have been standardized on Oneida Lake for nearly half a century. This is in contrast with many organized commercial fisheries where technological advancements can lead to increased catchability over time. However, caution is necessary when applying the assumption of constant catchability over time, even for standardized sampling (Gordoa and Hightower 1991). Catchability may also respond to fluctuations in abundance (Peterman and Steer 1981) and to changes in environmental conditions, such as temperature, oxygen levels, or water clarity (Nielsen 1983). Additionally, ecological changes may indirectly affect catchability by influencing encounter probabilities of various gears if the growth rates, foraging behaviors, or preferred habitats of the target species are altered (Henderson and Wong 1991). Although it has been shown elsewhere that neither abundance nor environmental conditions have had strong effects on the gillnet catchability of adult walleye in Oneida Lake (J.R. Jackson, unpublished data), this may not be the case for trawl catches, as water clarity has increased in the lake since the arrival of zebra mussels (Idrisi et al. 2001).

The relative size selectivity of gill nets can also be estimated from the length distributions of fish caught in different mesh sizes (Hamley 1975). For Oneida Lake, we used the length distribution of Oneida Lake walleye captured in different mesh sizes to construct relative selectivity curves where the modal length and standard deviation of the selectivity curve were each a linear function of mesh size and the relative selectivity at the modal length of each
mesh size were assumed to be equal. The combined selectivity of this set of gill nets generally increased to 440 mm because the larger walleye may be caught in more than one mesh size. The catchability of larger fish may actually be higher than predicted from this curve because large mesh may be less visible than small mesh (Hamley 1975) or because larger fish may have a higher encounter rate (Rudstam et al. 1984) or become more easily entangled (Grant et al. 2004). Hamley and Regier (1973) found substantially higher catchability for larger walleye in a study where a known population was fished with experimental gill nets. Our model results generally support the shape of the relative selectivity curve. Although our estimates of catchability increased slightly faster than was predicted by this curve, the increase was less than predicted by the Hamley and Regier (1973) selectivity curves. Rudstam et al. (1984) suggested that encounter probability should increase with fish length to approximately the 0.5 power based on an argument of length dependence of routine swimming speed for several fishes. For Oneida Lake walleye, an increase in encounter probability with fish length to the 0.3 power was sufficient to account for the difference in slope between the estimation model results and the relative selectivity of the nets. This suggests that accounting for increased catchability of larger walleye is less important than suggested by Hamley and Regier (1973; see also Henderson and Wong 1991 and Grant et al. 2004).

Compared with studies using gill nets, less attention has been given to assessing freshwater trawl selectivity. Consideration of indirect selectivity of towed gears may involve use of covered cod ends, trouser trawls, twin-gear, or alternate hauls using nonselective gear variants (Millar and Fryer 1999). Generally, larger individuals may possess greater physical ability to escape the path of the gear. Olin and Malinen (2003) found that large (>19.9 cm) European perch (Perca fluviatilis) and zander (Sander lucioperca) were under-represented in trawl catches relative to gill nets. Our estimated values for trawl catchability also suggest walleye are captured with reduced efficiency at larger sizes. Because we were interested in temporal changes in mortality, we could not assess the concurrent changes in water clarity or light penetration on trawl catchability, although vision also likely plays an important role in gear avoidance (Glass and Wardle 1989). Note, however, that a decrease in catchability due to increased water clarity in the 1990s would increase the additional mortality required between ages 1 and 4 to explain the current decrease in cohort strength at age-4. Our observations of increased subadult mortality discussed above are therefore conservative against potentially unaccounted for decreased catchability in the trawl (or gill nets).

In summary, our estimation model simultaneously used three long-term data sets to estimate walleye density, mortality, and catchability associated with the standard trawl and gillnet surveys. Although fishery catch data are commonly incorporated into stock assessments, we performed this estimation exercise without annual information of angler harvest. Even under the restrictive constraints placed on the mortality parameters, the model produced age-specific catchability estimates of the anticipated form for both gill net and trawl. Our final estimate of walleye population structure is generally congruent with earlier estimates for adult walleye, which were based mostly on mark–recapture and a trap-net index (e.g., Mills and Forney 1988; Rudstam et al. 2004). The current model uses all three available long-term data series and, in contrast with earlier calculations, consistently produces realistic declines in walleye abundance with age. Likewise, the model followed the high variation in walleye year-class strength, with the maximum estimated density of age-1 fish more than 50 times larger than the lowest density estimated for this age class. Here, the highest estimated density for an adult age class occurred during 1958 for age-4 walleye, and this is consistent with previous measures of the strong 1954 year class moving into the adult population (Forney 1967). The model estimates suggest a strong reduction in average annual survival of subadult walleye in Oneida Lake after 1990 in accordance with hypothesized predation effects of double-crested cormorants (e.g., Rudstam et al. 2004). However, data limitations and imposed constraints on mortality do not allow this model to directly identify year-to-year changes in mortality caused by variable harvest rates. Overall, the use of multiple long-term data sets allowed for the estimation of several population parameters of interest and improved our understanding of the development of the walleye population over time and our sampling of it, even though a time series of more traditionally used fishery catch data was not available for this study.

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