Partitioning total size selectivity of gill nets for walleye (*Stizostedion vitreum*) into encounter, contact, and retention components

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Abstract: Contact and retention components were estimated by indirect methods for walleye (*Stizostedion vitreum*) in Lake Erie, Dexter Lake (Ontario), and nine Minnesota lakes. In all 11 lakes, the retention function was well described by a unimodal function of fish size/mesh perimeter, and the addition of a contact component significantly improved model fit. A plausible range of models was identified for Lake Erie by considering the contact component to be constant or proportional to mesh size. Total catchabilities were estimated for two lakes by direct methods and encounter probabilities estimated by comparison of direct and indirect selectivities. Encounter probabilities estimated for Dexter Lake increased proportionately to fish length. Encounter probabilities estimated for Mille Lacs had a more complex form and were not well described by allometric power functions such as those sometimes used to describe swimming speed and encounter rates.

Résumé : Les composantes contact et rétention ont été estimées de façon indirecte pour le doré jaune (*Stizostedion vitreum*) des lacs Érié et Dexter (Ontario) et neuf lacs du Minnesota. Dans les 11 lacs, la fonction de rétention était bien décrite par une fonction unimodale taille du poisson/périmètre de la maille, et l'ajout d'une composante contact a permis d'améliorer de façon appréciable l'ajustement du modèle. Une gamme plausible de modèles a été déterminée pour le lac Érié en supposant la composante contact constante ou proportionnelle à la taille de maille. Le pouvoir de capture total a été estimé pour deux lacs en appliquant des méthodes directes et la probabilité de rencontre a été estimée en comparant les sélectivités directes et indirectes. Cette probabilité augmentait en proportion de la longueur des poissons dans le lac Dexter. Celle obtenue pour les lacs Mille était plus complexe et n'était pas bien décrite par des fonctions de puissance allométriques semblables à celles utilisées pour décrire la vitesse de nage et le taux de rencontre.

[Traduit par la Rédaction]

Introduction

This paper describes the size selectivity of multifilament gill nets for walleye (*Stizostedion vitreum*) in Lake Erie, Dexter Lake (Ontario), and nine Minnesota lakes. The number of fish expected to be captured in a net is dependent on the number in the population and the probabilities of encountering the net (approaching the net), contacting the net after encounter, and being retained after contact. Direct methods (fishing known populations) have been used to estimate total selectivity (Hamley and Regier 1973), and indirect methods (comparing catch distribution over several mesh sizes) have been used to estimate length, mesh, and retention components (Millar and Holst 1997). However, the relationship of these components to total selectivity and to the events leading to capture remains obscure.

The relationship between statistical models and physical processes is clarified by adding to the conceptual model of Rudstam et al. (1984) and the statistical model of Millar and Holst (1997). Encounter is defined here as approaching into a proximity where the net may be detected and the fish may alter behavior to approach or avoid the net. The expected total catch is

$$(1)\qquad C_{lm} = N_l P(\mathrm{E}) P(\mathrm{C}) P(\mathrm{R}) f_m$$

where C_{lm} is the expected total catch of fish of length l in a net of mesh m, N_l is the population of fish of length l, $P(\mathrm{E})$ is the probability of encounter, $P(\mathrm{C})$ is the probability of contact, $P(\mathrm{R})$ is the probability of retention, and f_m is the fishing effort with mesh m. If one assumes that encounter is dependent on fish size, contact is dependent on mesh size, and retention is dependent on fish size and mesh size, then the equation for expected total catch can be written as

$$(2)\qquad C_{lm} = N_l \alpha_l \beta_m \gamma_{lm} f_m$$

with the probabilities in the same order as above.

Equation 2 suggests a simpler statistical model including a length component, a mesh component, and a retention component. If the number of fish is unknown, as in indirect analysis, the number of fish and encounter probability are combined in a single length component $\omega_l = N_l \alpha_l$ that estimates abundance on encounter. The mesh component β_m estimates the probabilities of contacting meshes. If fishing effort is unknown, effort becomes confounded in this mesh component. For indirect analysis, the total number of fish C_{lm} of length l caught in mesh m is assumed to be an observation of a Poisson random distribution:

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Table 1. Features of the lakes and data sets for which mesh factors and retention components were estimated by indirect methods.

Lake	Area (ha)	Sampling years	Walleye captured
Dexter	409	68–70	1 659
Erie	2 566 734	78–89	10 761
Cass	12 050	83–94	2 509
Kabetogama	10 425	83–95	2 768
Lake of the Woods	128 288[a]	91–95	4 077
Leech	44 280	83–95	3 495
Mille Lacs	53 628	86–95	5 102
Rainy	89 357	83–95	1 131
Upper Red	43 626	84, 87–95	1 153
Vermilion	19 875	84–92	2 240
Winnibigoshish	23 692	88–91, 93–95	640

Note: Dexter Lake and Lake Erie catch data from Hamley and Regier (1973) and Henderson and Wong (1991), respectively.

[a] Minnesota waters.

$$(3) \qquad C_{lm} \sim \mathrm{Po}(\omega_l \beta_m \gamma_{lm} f_m)$$

where the mean catch value $\omega_l \beta_m \gamma_{lm} f_m$ is the product of relative abundance on encountering a net, a mesh or contact component, a retention component, and fishing effort. Indirect methods allow estimation of β_m and γ_{lm} selectivity components and estimation of ω_l as a nuisance parameter; however, indirect methods alone cannot separate N_l and α_l. When the number in the population is known, the total catch is assumed to be an observation of a Poisson random distribution:

$$(4) \qquad C_{lm} \sim \mathrm{Po}(N_l \alpha_l \beta_m \gamma_{lm} f_m)$$

and the encounter factor can be estimated too.

These statistical models partition encounter, contact, and retention processes only under the restrictive assumptions that (*i*) length and not mesh or fish size/mesh perimeter ratio x influences encounter rate, (*ii*) mesh and not length or size/perimeter ratio influences contact rate, (*iii*) and retention depends on fish size/mesh perimeter ratio and not otherwise on length or mesh. The conceptual model of Rudstam et al. (1984) is the same as eq. 1 when contact probabilities are assumed constant. Rudstam et al. (1984) used the word “encounter” to mean contact with the net. The statistical model of Millar and Holst (1997) is the same as eq. 3. Millar and Holst (1997) described the assumptions or inferences that may be made about the forms of ω_l, β_m, and γ_{lm}. They noted that maximum likelihood may be applied for estimation and that for many choices, the model may be expressed in log-linear form.

Millar and Holst (1997) made an important point that the partitioning of expected catch into length, mesh, and retention components $\omega_l \beta_m \gamma(x)$ is indeterminate. That is, identical expected catches are obtained by multiplying $\gamma(x)$ by $(l/m)^c$, β_m by m^c, and ω_l by l^{-c} for any choice of c. I refer to multiplication in this way as a rotation because plots of the component functions appear to rotate when values of c are small. Under some assumptions about the forms of the three components, a statistically unique model may be estimated; however, even for such a model, the researcher should consider whether rotation with $c \neq 0$ would yield a more realistic description of the events leading to capture.

This paper describes the size selectivity of multifilament gill nets for walleye. Contact and retention components are estimated by indirect methods for walleye captured in 11 lakes. The indeterminancy problem is examined and two Lake Erie models are chosen from a family with equally good fit to illustrate a plausible range of indirect models. The encounter component and total selectivity are estimated by combining direct and indirect methods for Dexter Lake and for Mille Lacs, Minnesota. Experiments that might resolve the choice of models are discussed.

Methods

Data sources

Data on 11 lakes were obtained from three sources (Table 1): data on Lake Erie calculated and estimated from tables and figures in Henderson and Wong (1991), data on Dexter Lake published in Hamley and Regier (1973), and original data on nine Minnesota lakes collected by the Minnesota Department of Natural Resources (DNR).

Henderson and Wong (1991) described the size frequency distributions of Lake Erie walleye caught by mesh size. The smoothed frequency distributions are selectivity functions only under the assumptions that all girth groups are equally abundant on encountering nets and that contact probabilities are equal for all meshes. From Henderson and Wong’s (1991) figures, I reconstructed a smoothed estimate of catch by girth group and mesh. The data were on 10 761 walleyes captured in 11 meshes (25, 29, 32, 35, 38, 41, 44, 48, 51, 54, and 57 mm bar) fished with equal effort in gangs. The nets were multifilament clear nylon (210/2 thread) hung with a web/line ratio of 1.83–2.16. Panels were 33 m long, hung in the sequence 57, 29, 48, 25, 44, 54, 32, 38, 35, 51, and 41 mm.

Hamley and Regier (1973) published the data on recaptures of marked walleye from which they made direct estimates of total gillnet selectivity. In addition, data on total captures of 1659 walleyes (marked or unmarked) caught in gill nets were tabulated. I used the latter data on total captures in gill nets to estimate the mesh size and retention components of selectivity and then used the data on marked fish to estimate total selectivities and (by the difference) the length component. Seven mesh sizes were used: 19, 25, 32, 38, 44, 51, and 57 mm bar measure. Panels were 30.5 m long by 1.5 m deep. Two panels of the same mesh were tied loosely end-to-end for each set; however, meshes were fished separately, not otherwise in a gang. On each day, four mesh sizes were set. Net material was multifilament No. 210/3 nylon left untreated or white in color. Nets were hung with a web/line ratio of 2.0 (H. Regier, 21 Hollybrook Cres., Willowdale, ON M2J 2H5, personal communication).

Data on total length of 5102 walleyes and the mesh size of experimental gill nets in which they were captured in Mille Lacs, Minnesota, in the years 1986–1995 were compiled. All walleye sampled in 1991–1994 were sexed and were aged from spines or scales; subsamples were sexed and aged in other years. Panels of five mesh sizes (19, 25, 32, 38, and 51 mm bar measure) were woven end-to-end in that sequence in a gang, and gangs were fished with equal effort each year (32 sets) in a standardized way (Scidmore 1970). Each panel was 15.24 m long by 1.82 m deep. The meshes were multifilament No. 104 twisted nylon. All meshes were hung with a web/line ratio of 2.0 and were left untreated or white in color.

Data on total length and mesh of capture were compiled for walleye captured by similar standardized nets and sampling de-

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signs in eight other large Minnesota lakes over varied time periods (Table 1).

Population estimates by age and year were provided for Mille Lacs walleye by P.J. Radomski (Minnesota DNR, 1601 Minnesota Dr., Brainerd, MN 55744, personal communication). His estimates were produced by virtual population analysis (VPA) (Pope 1972) of angler harvest by age data and tuned with gillnet and trawl age-specific catch per effort data. The analysis assumed natural mortality rate $M = 0.60$ for age 1 and $M = 0.29$ for older ages. The latter mortality rate was estimated by Pauly's (1980) equation. Analyses by various other VPA and catch at age algorithms (ADAPT VPA, LOWESTOFT VPA, CAGEAN) yielded results consistent with Radomski's. Angler harvest was also estimated by length group and year from annual nonuniform probability access based angler surveys. These harvest estimates were provided by R.E. Brusewitz (Minnesota DNR, 1200 S. Minnesota Ave., Aitkin, MN 56431, personal communication). Brusewitz also provided data on a 1981–1985 experiment in which 1735 walleye were tagged and 158 tags were returned by anglers in the year following tagging. These data allow a direct estimate of the form of angler selectivity to be compared with an estimate derived from the final gillnet selectivity function in order to corroborate the gillnet model.

Analytical methods

Catches were tallied by length or girth groups. The published groupings were used for Dexter Lake and Lake Erie. For Mille Lacs, length groups were 12 mm wide. For other Minnesota lakes, groups were 25 mm wide. The midpoint of each length group range l was used as the characteristic length for that group, and the length to perimeter ratio x was calculated for each combination of length l in mesh m. When retention was to be estimated as a factor γ_x, x values were grouped and assigned the value of the group midpoint.

Indirect methods

The statistical model of eq. 3 was estimated by maximum likelihood methods for each of the 11 lakes. No assumptions were made about length distributions on encounter ω_i; they were estimated as factors. Models were fitted with contact coefficients β_m constant or estimated as factors. Likelihood ratios were examined to test whether estimating contact coefficients significantly improved the fit. Models with polynomial or rational polynomial retention functions $\gamma(x)$ were fit to all lakes. Specifically, relative retention was

$$(5) \qquad \gamma(x) = \exp(k + b_1 x^{-1} + b_2 x^{-2} + \ldots)$$

or

$$(6) \qquad \gamma(x) = \frac{1}{k} \cdot \exp\frac{(b_0 + b_2 x + \ldots)}{(1 + b_1 x + b_3 x^2 \ldots)}$$

where x is a fish size/perimeter ratio. The constant k normalizes relative retention on a 0 to 1 scale. It was confounded with other normalizing constants in the initial output, but was easily calculated at the maximum of the rest of the retention function. Each of these classes of retention functions provided better fits than similar order exponential polynomials of x or $\log(x)$, and eq. 5 simplifies to log-linear forms. In preliminary analyses, models with polynomials of x or $\log(x)$ often failed to converge on a solution. Models were fitted for polynomials of increasing order until likelihood ratio tests showed that the additional term did not significantly improve the fit. Patterns of deviance residuals were examined. Because unimodal and bimodal selectivity curves have been proposed for walleye, indirect models were fit for Lake Erie and Mille Lacs with retention as a factor γ_x, making no assumption about the parametric form. Log-linear models were fitted using SAS Proc GENMOD as described in Millar and Holst (1997). Other models were fitted by SELECT methods (Millar 1995) using SYSTAT (Wilkinson et al. 1992).

On Dexter Lake, meshes were not fished with equal effort and not all meshes were fished each year. The length distributions on encountering nets and fishing efforts therefore differed by mesh and year y; thus, the statistical model for indirect analysis was modified to be

$$(7) \qquad C_{lmy} \sim \mathrm{Po}(\omega_{ly} \beta_m \gamma_{lm} f_{my})$$

where C_{lmy} is catch of walleye (whether marked or not) and f_{my} is number of net-nights. The indirect analyses were done with data on total catch of walleye because the sample size was larger than for marked walleye.

In the family of indirect models obtained by rotating with an exponent c, some choices of c give more realistic descriptions of the individual components. For Lake Erie, I chose a value of c such that the adjusted β_m estimates showed no trend when regressed on mesh size and another value of c, increased by 1.0, for which the adjusted β_m estimates were roughly proportional to mesh size. Contact coefficients should be constant or increase with mesh size because visibility is greater for small meshes.

Direct and combined methods

Hamley and Regier (1973) presented data on the number of recaptures ρ_{lmy} of marked fish in gill nets by length, mesh, and year and on the number of exposures η_{lmy} of marked fish to nets by length, mesh, and year. One marked fish at large on the night one net was set constituted one exposure to that mesh. The statistical model for direct analysis was thus

$$(8) \qquad \rho_{lmy} \sim \mathrm{Po}(\eta_{lmy} \alpha_l \beta_m \gamma(x))$$

where β_m and $\gamma(x)$ are the estimates obtained previously by indirect analysis of all walleye captures in gill nets. This model is log-linear and α_l was estimated by maximum likelihood. Capture probabilities (= catchabilities) were then calculated as $\hat{q}_{lm} = \hat{\alpha}_l \hat{\beta}_m \hat{\gamma}(x)$.

A length selectivity function $\alpha(l)$ for Dexter Lake was estimated by fitting a linear regression to the $(l, \hat{\alpha}_l)$ points. The function was fitted by weighted least squares, where the weight was the relative number of exposures of the length-class.

For Mille Lacs, VPA population estimates by age and year were distributed over lengths to obtain estimates by length group and year. In distributing fish over lengths, I initially assumed that the proportion of males in the population remained 0.5 at all ages. The mean length at age at the time of net sampling was calculated separately for males and females from von Bertalanffy growth equations (R.E. Brusewitz, personal communication). The equations described length at annulus formation; however, mean length at sampling was estimated by calculating length at age +1, as nearly a full year's growth had occurred before netting. Fish were further distributed over length groups, assuming normal length distributions about the means with variances as estimated by age and sex from 1991–1994 samples (when all fish were aged and sexed). The age 10+ population estimates were distributed over ages 10–20 in a stable age distribution calculated with a survival rate of 0.544. The 0.544 value was obtained by summing population estimates of age 9 for 1984–1995 and dividing by the sum of population estimates for age 8 for 1983–1994. After thus distributing all age groups over all length groups, the numbers were summed to obtain population estimates by length groups $\hat{N}_l$. Net catches in 1986–1995 were also summed by length group to obtain C_l. Capture probabilities per experimental gang were estimated by $\hat{q}_l = C_l / (32\hat{N}_l)$.

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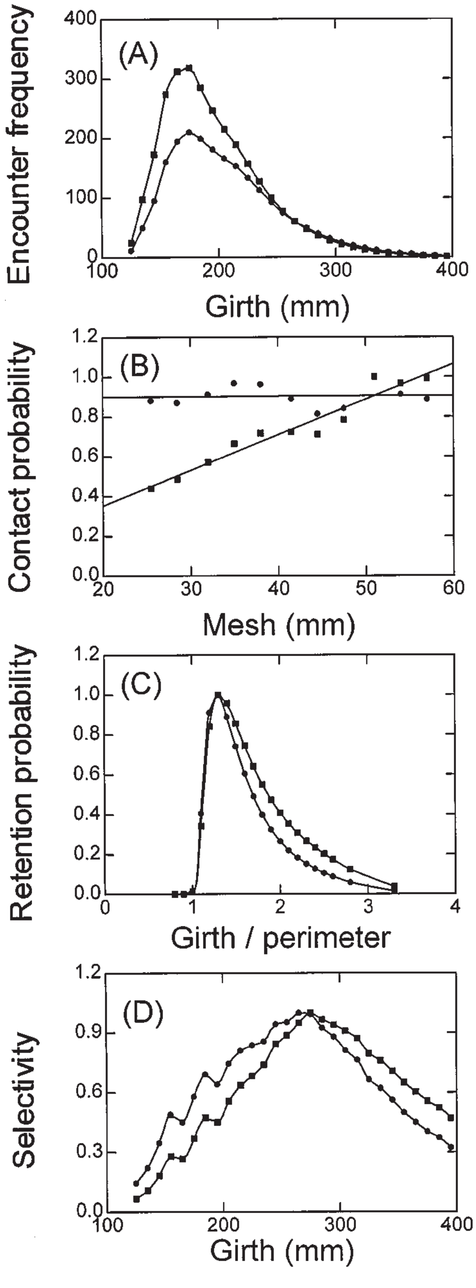
Fig. 1. Two solutions from a family of models with girth, mesh, and x factors fitted to Lake Erie walleye data. These solutions cover a plausible range of values for contact probabilities and were calculated with rotation constants $c = -300.15$ (circles) and $c = -299.15$ (squares). Indirect methods estimated (A) the frequency with which fish encountered each mesh over the period of sampling, (B) the relative probability of contact, and (C) the relative probability of retention. (D) The selectivity of a gang of 11 meshes estimated by indirect methods is actually an estimate of relative capture probability after encountering a gang.



The remaining encounter factor was estimated by $\hat{\alpha}_l = \hat{q}_l / \sum_m \hat{\beta}_m \hat{\gamma}(x)$, where $\sum_m \hat{\beta}_m \hat{\gamma}(x)$ was calculated at the length group midpoints from the coefficients estimated by indirect methods. The $\hat{\alpha}_l$ values are estimates of the probability that a fish of length l will encounter a panel in the experimental gang. An encounter probability function was fitted to the $(l, \hat{\alpha}_l)$ points by least-squares regression. From the three components, a function to estimate catchability for a single mesh could be calculated by $\hat{q}_m(l) = \hat{\alpha}(l)\hat{\beta}_m\hat{\gamma}(x)$. The corresponding estimate for catchability in the experimental gang is $\hat{q}(l) = \hat{\alpha}(l)\sum_m \hat{\beta}_m \hat{\gamma}(x)$. The process of distributing fish over length groups and then calculating $\hat{q}_l$, $\hat{\alpha}_l$, $\hat{\alpha}(l)$, and $\hat{q}(l)$ was done twice, first assuming that the proportion of males in the population was 0.5 at all ages and then assuming that the proportion changed (increasing linearly with age from 0.5 at age 1 to 0.6 at age 4 and then decreasing linearly from 0.6 at age 5 to 0.5 at age 20).

As a test, each model was applied to calculate an expected proportion of males by age in the net catch for comparison with observed values. After population estimates were distributed over lengths, retaining sex and age identifiers, numbers were multiplied by $\hat{q}(l)$ to generate an expected catch by age and sex. The expected proportion of males in the catch was graphically compared with the observed proportion in the 1991–1994 catch. This comparison was made iteratively; it led to rejection of the first $\hat{q}(l)$ model and then to alteration of the second model at large fish lengths before a satisfactory final model was obtained.

Each Mille Lacs $\hat{q}(l)$ model was also tested by comparison of harvest estimates from creel surveys with population estimates made by applying each model. Models were rejected if harvest estimates by length and year $\hat{H}_{ly}$ regularly exceeded population estimates derived from the model $\hat{N}_{ly} = C_{ly} / \hat{q}(l)$. For the final model, exploitation was estimated for 1986–1995 ($\hat{U}_{ly} = \hat{H}_{ly} / \hat{N}_{ly}$). The mean exploitation for each length was calculated as a measure of angler selectivity θ_l and compared with angler selectivity estimated from 1981–1985 tag return data. Exploitation rates were estimated from tag return data by smoothing splines, and confidence intervals were constructed by bootstrapping 1000 times (Anderson 1995).

Results

Lake Erie

Indirect analysis of a model containing girth, mesh, and retention factors identified a family of solutions (deviance 407.7, 247 df) in which the contact probability changed regularly with mesh size. The retention factor estimates had a skewed unimodal form; therefore, models with parametric retention functions in the form of eq. 5 were estimated. A model with fitted mesh factors and a retention function with terms up to b_5x^{-5} had a good fit (deviance = 189.8, 228 df), although deviance values were considered approximate because the data were previously smoothed and truncated. This model had a significantly better fit than those with contact probabilities held constant (likelihood ratio 30.4, 10 df) or proportional to mesh to a power (likelihood ratio 28.5, 9 df). Deviance residuals exhibited runs of positive and negative values, a result of working from smoothed frequency distributions, and the largest negative residuals occurred about $x = 1.05$, near where the distributions had been truncated. Two solutions from the family with equal fit illustrate the indeterminate aspect of indirect analysis. Rotation of the initial mesh factors by m^c with $c = -300.15$ produced a solution in which relative contact coefficients did not show any systematic change when regressed on mesh size. Rotation with $c = -299.15$ produced a solution in which the relative contact coefficients increased with mesh size, falling about the line $\beta = -0.004 + 0.018m$ ($r^2 = 0.94$). Much larger values for c appeared implausible because they would produce very low contact probabilities for the 25-mm mesh, and smaller (19-mm) meshes caught walleye in appreciable numbers in

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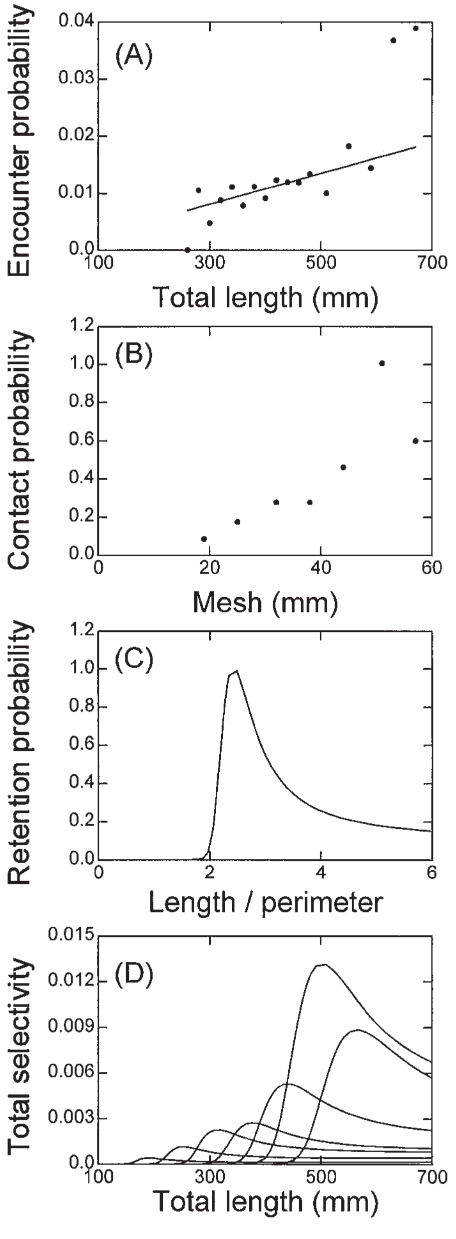
Fig. 2. Encounter, contact, and retention components of total selectivity estimated for Dexter Lake walleye. (A) Encounter probabilities were estimated by a combination of indirect and direct methods. Indirect methods estimated (B) the relative probability of contact and (C) the relative probability of retention. (D) The total selectivity or catchability of each mesh was calculated as the product of encounter, contact, and retention components.



Minnesota lakes. Although the two illustrated solutions yield equal values for expected catch by girth and mesh, they imply different numbers of fish approaching the nets, different contact and retention components, and different overall "selectivity" for the gang of 11 meshes (Fig. 1). The solution with $c = -300.15$ estimated that 2119.8 walleye approached each mesh over the entire sampling period (the sum of ω_l estimates). Of the 23 317 total fish thus encountering nets, 10 761 or 46% were captured. Solutions with smaller or larger c produced increasing estimates of number of fish approaching nets and decreasing estimates of proportion captured. The solution with $c = -299.15$ estimated that 2857.9 fish approached each mesh, or 31 437 encountering nets with 34% being captured. Indirect estimates of selectivity are incomplete descriptions of capture probability because they do not include the probability of encounter. Nevertheless, within the range of plausible c values (–300.15 to –299.15), it appears that walleye with girths about 170 mm most frequently approached nets, that the retention function was a strongly skewed bell shape with a peak at $x = 1.28 - 1.31$, and that selectivity of the mesh gang reached maximum at girths about 265–275 mm. After rotation with the specified c and incorporation of a normalizing constant, the retention function for $c = -300.15$ was $\gamma(x) = \exp(-300.15 \log(x) + 840.5122 - 2561.6547x^{-1} + 4415.0283x^{-2} - 5054.0536x^{-3} + 3245.0131x^{-4} - 889.0413x^{-5})$. The function for $c = -299.15$ was the same except that the first two constants were –299.15 and +840.2549.

Dexter Lake

Indirect models based on eq. 6 were fitted to the Dexter Lake data; however, models based on eq. 5 or other polynomials did not consistently converge to a solution. Models with estimated mesh factors provided a better fit than models with constrained mesh factors (likelihood ratio test, $p < 0.05$), and addition of a b_4 parameter to the retention function did not improve the fit ($p > 0.05$). The best model had a deviance of 313.1 with 192 df. The deviance residuals of the model were reasonably distributed. The resulting indirect selectivity model (Tables 2 and 3; Figs. 2B and 2C) had mesh component estimates that increased regularly with mesh size, except that the estimate was unusually large (1.677) for 51-mm bar mesh. This estimate had a large SE (0.555) and appeared to be an aberration. An unusual value relative to the largest mesh may have occurred because the same meshes were not fished each year and meshes were not tied in a gang. The mesh factor estimates were renormalized to a maximum value of 1.0 before calculating selectivities to ensure that the final model would not imply a net capable of catching more than 100% of fish encountering it. The retention function showed a strongly skewed unimodal shape, with a maximum value at a total length/perimeter ratio of 2.57. The shape of the indirect model incorporating mesh and retention components differed markedly from the bimodal functions shown by Hamley and Regier (1973) for the larger mesh sizes. When the Hamley and Regier (1973) selectivities were calculated and used to generate the expected proportion of each length group in each mesh (each year), the fit had a deviance of 462.2 (versus 313.1 for the indirect model). Thus, the indirect model with a unimodal retention function provided a better description of the distribution of total walleye catch among meshes.

Encounter probabilities were estimated from the mark–recapture data after incorporating the contact and retention estimates from the indirect analysis. The encounter probability estimates for the length groups $\hat{\alpha}_l$ increased with total length (TL); however, because there were few exposures to nets for walleye outside the 320–530 mm total length range, the form of the relationship there remained uncertain (Fig. 2A). Encounter probability was proportional to TL ($\hat{\alpha}(l) = 0.2658 \times 10^{-3} \times l$). This encounter function falls

Table 2. Estimates (SE in parentheses) of the mesh size components β_m of gillnet selectivity for walleye in 10 lakes.

	Mesh (mm bar measure)						
Lake	19	25	32	38	44	51	57
Dexter	0.143 (0.057)	0.291 (0.105)	0.464 (0.155)	0.465 (0.151)	0.770 (0.224)	1.677[a] (0.555)	1.00
Cass	0.162 (0.060)	0.303 (0.084)	0.559 (0.113)	0.694 (0.101)		1.00	
Kabetogama	0.289 (0.078)	0.418 (0.084)	0.648 (0.096)	0.770 (0.083)		1.00	
Lake of the Woods	0.311 (0.072)	0.703 (0.122)	0.855 (0.112)	0.921 (0.089)		1.00	
Leech	0.110 (0.027)	0.209 (0.039)	0.330 (0.045)	0.433 (0.043)		1.00	
Mille Lacs	0.185 (0.039)	0.392 (0.061)	0.734 (0.083)	0.898 (0.067)		1.00	
Rainy	0.396 (0.293)	0.580 (0.310)	0.601 (0.223)	0.656 (0.160)		1.00	
Upper Red	0.107 (0.070)	0.477 (0.247)	0.734 (0.279)	0.681 (0.181)		1.00	
Vermilion	0.167 (0.061)	0.288 (0.079)	0.430 (0.087)	0.534 (0.080)		1.00	
Winnibigoshish	0.059 (0.067)	0.130 (0.107)	0.255 (0.146)	0.472 (0.171)		1.00	

Note: Estimates are relative to a value of 1.0 for the largest mesh. Under some restrictive assumptions, the mesh factors are estimates of relative probability of a fish contacting the mesh after encountering it.

[a] Dexter lake values were normalized to a maximum value of 1.0 before plotting or use in other calculations.

Table 3. Coefficients (SE in parentheses) of the retention component of gillnet selectivity for walleye $\hat{\gamma}(x)$ estimates for 10 lakes.

	Coefficients				k	x at
Lake	b_0	b_1	b_2	b_3	(= maximum)	maximum
Dexter	–1.463 (0.142)	–1.013 (0.015)	0.728 (0.074)	0.268 (0.007)	12.565	2.427
Cass	–1.837 (0.141)	–0.929 0.012	0.898 (0.076)	0.229 (0.005)	43.395	2.548
Kabetogama	–1.905 (0.149)	–1.013 (0.015)	1.001 (0.084)	0.276 (0.007)	23.056	2.413
Lake of the Woods	–1.880 (0.134)	–0.976 (0.013)	1.008 (0.075)	0.261 (0.006)	28.807	2.444
Leech	–1.945 (0.142)	–0.951 (0.012)	0.988 (0.075)	0.245 (0.005)	30.560	2.530
Mille Lacs	–2.053 (0.154)	–1.013 (0.015)	1.058 (0.086)	0.280 (0.007)	15.209	2.503
Rainy	–2.119 (0.411)	–0.897 (0.037)	1.214 (0.260)	0.235 (0.015)	57.813	2.545
Upper Red	–1.299 (0.217)	–0.917 (0.024)	0.700 (0.131)	0.229 (0.010)	25.913	2.471
Vermilion	–1.776 (0.159)	–0.956 (0.014)	0.925 (0.088)	0.246 (0.007)	38.389	2.458
Winnibigoshish	–3.467 (1.081)	–0.988 (0.066)	1.804 (0.591)	0.289 (0.037)	24.450	2.686

Note: Under some restrictive assumptions, the retention function estimates the relative probability of a fish being retained after contacting a net.

within the range of power functions that have been used to correct for encounter rates (Rudstam et al. 1984; Henderson and Wong 1991; Spangler and Collins 1992). Total selectivity curves estimated as the product of encounter, contact, and retention components differ among mesh sizes (Fig. 2D). All curves differ from the bimodal ones illustrated by Hamley and Regier (1973), although the curves for the two smallest meshes had small positive slopes at the largest fish lengths. The comparison of direct and indirect models shows that indirect models are biased because they cannot estimate the encounter component of total selectivity. The total selectivity model had a deviance of 194.5 when applied to the data on captures of marked fish from a known population. When the Hamley and Regier (1973) selectivity curves were similarly applied (after fitting the constant necessary to convert relative selectivities to capture probabilities), the deviance was 190.3. The Hamley and Regier (1973) curves thus give a slightly better fit to the mark–recapture data set from which they were derived, but a poorer fit to the data on distribution of total walleye catch among nets.

Mille Lacs

Indirect analysis of a model containing length, mesh, and retention factors identified a family of solutions (deviance = 339.4, 189 df) that suggested that contact probabilities changed with mesh size and that retention had a unimodal form. A model based on eq. 6 with estimated mesh size factors provided a better fit than one with a constant contact probability ($p < 0.05$), and the addition of a b_4 parameter to the retention function did not improve the fit. The final indirect model had a deviance of 475.1 with 191 df, and deviance residuals appeared reasonably distributed. This fitted model showed that the probability of contact increased regularly with mesh size for Mille Lacs walleye (Table 2; Fig. 3B). The retention function described a strongly skewed bell shape (Table 3; Fig. 3C). Combining the indirect estimates of contact and retention components for the five meshes suggested that the aggregate selectivity of the gang had two peaks, with a local minimum between lengths most vulnerable to 38- and 51-mm meshes.

The direct estimates of total capture probabilities q_l of Mille Lacs walleye in experimental nets increased sharply over lengths from 350 to 500 mm (Fig. 4). Estimates of encounter probabilities α_l were nearly constant at the smallest lengths and then increased sharply over lengths from 355 to 575 mm (Fig. 3A). Encounter probabilities $\alpha(l)$ were fitted by a piecewise linear function when six outliers at the largest length groups were omitted; however, a quadratic piece was added at the largest lengths to obtain a final model that was consistent with data on sex ratios of captured walleye and with harvest estimates. The quadratic piece was obtained by multiplying the second linear part by a linear forc-

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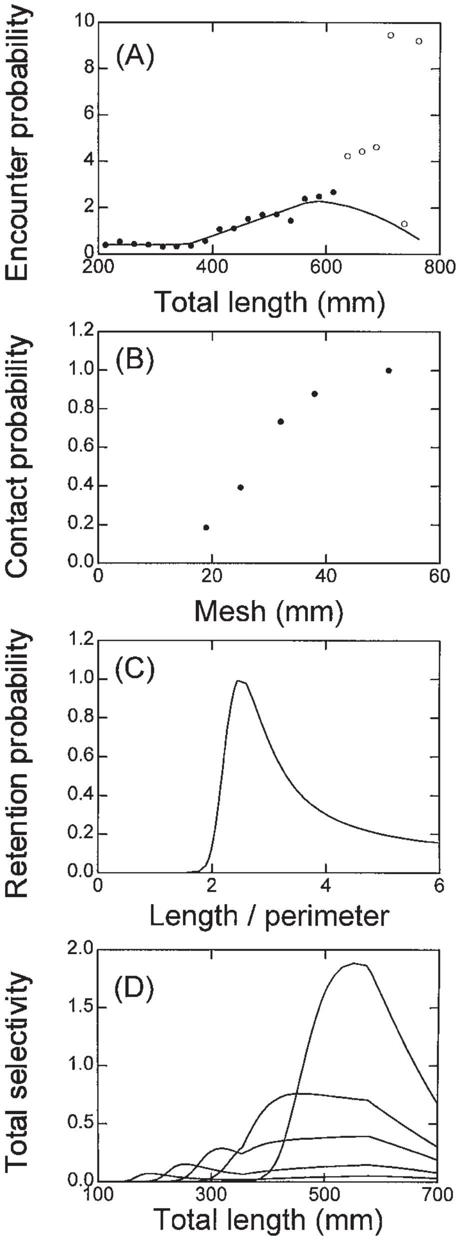
Fig. 3. Encounter, contact, and retention components of total selectivity estimated for Mille Lacs walleye. (A) Encounter probabilities were estimated by a combination of indirect and direct methods and were multiplied by 10^5 before plotting. Indirect methods estimated (B) the relative probability of contact and (C) the relative probability of retention. (D) The total selectivity or catchability of each mesh was calculated as the product of encounter, contact, and retention components and multiplied by 10^5 before plotting.



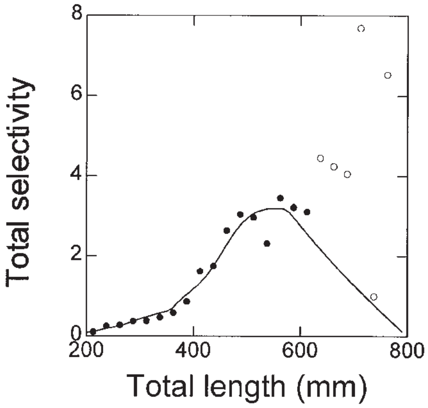
ing function that decreased from 1.0 at l = 575 mm to 0.0 at l = 800 mm. The three pieces were

$$\hat{\alpha}(l) = 0.395 \times 10^{-5} \text{ for } l \le 355.6$$

$$\hat{\alpha}(l) = (-2.706 + 0.00872l) \times 10^{-5} \text{ for } 355.6 < l \le 575.0$$

$$\hat{\alpha}(l) = (-9.621 + 0.043l - 0.0000388l^2) \times 10^{-5} \text{ for } 575.0 < l.$$

Fig. 4. Direct estimates of total selectivity of experimental gangs of five meshes for walleye in Mille Lacs and the selectivity function calculated as the product of encounter, contact, and retention components. All values were multiplied by 10^5 before plotting.



This relationship bore little resemblance to the power functions with exponents of 0.5–1.0 that have been used thus far to correct for encounter rates (Rudstam et al. 1984; Henderson and Wong 1991; Spangler and Collins 1992).

Total selectivities (or catchabilities) are proportional to the product of the encounter, contact, and retention components. Because the encounter component increases sharply at lengths from 355 to 575 mm, the total selectivity curves of the meshes (Fig. 3D) and of the experimental gang (Fig. 4) differ markedly from curves that correct only for mesh and retention components. Total selectivities of the smallest three meshes are bimodal and resemble Hamley and Regier's (1973) curves, while the selectivities of the largest two meshes are unimodal and do not.

A preliminary model based on an assumption that the proportion of males in the population was 0.5 at all ages was estimated and rejected. When net catches were divided by the preliminary catchability estimates to produce population estimates by length group and year, the population estimates for walleye >450 mm TL were less than the corresponding creel survey harvest estimates in many years. In addition, the preliminary model implied that the proportion of males in the net catches should be <0.5 for walleye less than age 8, and the data did not show this (Fig. 5, line A).

The encounter component and total selectivity were reestimated after assuming that the proportion of males in the population increased from 0.5 at age 1 to 0.6 at age 4 and then decreased from 0.6 at age 5 to 0.5 at age 20. Observations about angling selectivity suggested that the discrepancy between observed and expected proportion of males in the net catch was best resolved by assuming that the proportion of males in the population changed in this way. Angler exploitation increases at lengths about 275 mm, and walleye recruit to the fishery before they fully recruit to the experimental nets (Fig. 6). Tag return data for Mille Lacs from 1982 to 1986 and Jacobson's (1994) analysis of Big Sand Lake suggest that vulnerability of walleye to angling may decrease at the larger sizes. In addition, release rates estimated in the 1990s in the Mille Lacs creel survey increase from 3% to more than 50% at lengths from 430 to 710 mm (R.E. Brusewitz, personal communication). Under the

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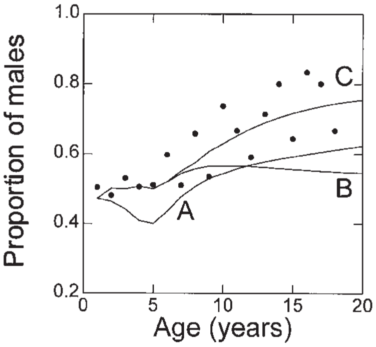
Fig. 5. Proportion of male walleyes observed in the Mille Lacs net catch (circles) and the proportion expected in the catch for successive total selectivity models (lines). Line A: the proportion expected in the catch when the proportion in the population was assumed to be 0.5 at all ages and a nonlinear encounter function was fitted. Line B: the proportion expected in the catch when the proportion in the population was assumed to increase from 0.5 at age 1 to 0.6 at age 4 and then decrease from 0.6 at age 5 to 0.5 at age 20. The encounter function had the linear pieces shown in Fig. 6A. Line C: the proportion expected when the encounter function was altered downward at total lengths from 575 to 800 mm as shown in Fig. 3A.



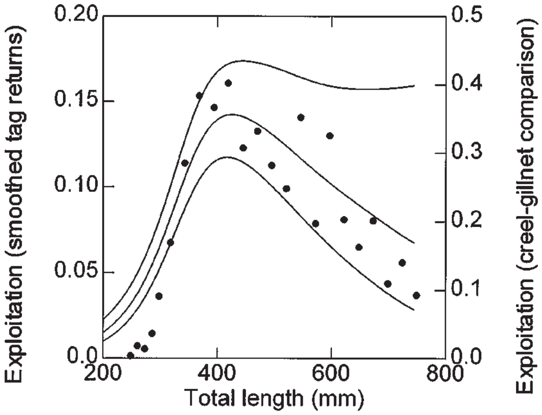
assumption that the proportion of males in the population changed with age, the proportion expected in the catch matched observed values well up to age 7 (Fig. 5, line B). To obtain a satisfactory match at older ages, it was necessary to alter the piecewise linear encounter function at lengths >575 mm. The linear piece was multiplied by a linear adjustment function that decreased from 1.0 at TL = 575 mm to 0.0 at TL = 800 mm, producing a third quadratic piece. With this final encounter function (Fig. 3A), the proportion of males expected in the catch matched observed proportions well (Fig. 5, line C). The mean exploitation rates had a similar form to the estimates from the earlier tag return data (Fig. 6), and few harvest estimates by length and year exceeded corresponding population estimates.

The final model was consistent with harvest estimates by length and year, with the observed proportion of males in the catch by age, and with the form of angler selectivity estimated by tag returns.

Other Minnesota lakes

Indirect selectivity models based on eq. 6 were estimated for eight other Minnesota lakes. The estimated models were similar to that for Mille Lacs (Tables 2 and 3) and are not illustrated. Models with fitted mesh factors provided a better fit than models with equal factors (the improvement was not significant in Winnibigoshish), and the addition of b_4 parameters did not improve the fit. Mesh component estimates increased with mesh size, and retention functions reached maximum values at TL/perimeter values near 2.5.

Fig. 6. Angler selectivity estimated from 1981–1985 tag returns (smoothed, 95% confidence intervals) and the mean exploitation for 1986–1995 estimated by dividing angler harvest estimates by gillnet model population estimates (circles).



Discussion

The incorporation of contact probability into the conceptual model of Rudstam et al. (1984) provides a link between the physical processes leading to capture and formal statistical models of Kirkwood and Walker (1986) and Millar and Holst (1997). In indirect analyses, the fish length, mesh size, and retention components may be considered relative estimates of abundance on encountering nets, probability of contact, and probability of retention, respectively. To interpret the components in this way, one must assume that (*i*) encounter probability is a function solely of fish size, (*ii*) contact probability is a function solely of mesh size, and (*iii*) retention probability is a function of fish size and mesh size, usually a function solely of the fish size/mesh perimeter ratio. These assumptions have not been tested but could be by observation and experimentation in large tanks, such as used by Fujimori et al. (1994). The length component is a biased estimate of population size distribution because it does not correct for encounter probability; thus, separate estimates of encounter probability are needed.

The length component will be a biased estimate of abundance on encountering nets if the form of contact and retention components is inappropriate. Indirect analyses are severely limited in their ability to resolve the form of the contact and retention components, and some additional assumptions are often necessary to obtain a statistically unique model. Even then, a fitted model can be rotated to identify an infinite family of models that generate equal expected catch values but have different length, contact, and retention components. Possible ways to identify the most realistic model from the set of models with equally good fit include direct observation of retention probabilities of fish of various sizes after contact with nets, acoustic or photographic monitoring of the size distribution of fish swimming past a specified point, comparison of catches in encircling nets with those of conventional sets, observation of detection and avoidance behavior in the vicinity of nets, and experiments with competing gear in various spatial configurations. New observations are required, for there is no compelling biological evidence for any of the usual assumptions about the form of encounter, contact, or retention components.

Published descriptions of selectivity of gill nets for walleye have not been based on statistical models (Regier et al. 1969; Hamley and Regier 1973; Willis et al. 1985; Henderson and Wong 1991) and do not agree on the form of contact or retention components. The increases of amplitude

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of selectivity curves with increasing mesh size that are evident in the figures of Regier et al. (1969) and Hamley and Regier (1973) are similar in magnitude to the increases of mesh components estimated for Dexter Lake and nine Minnesota lakes; however, Willis et al. (1985) and Henderson and Wong (1991) chose not to adjust amplitude. Indirect analyses cannot identify the most realistic form of the contact component, and the components presented here can be rotated to fall anywhere in the general range of published values, as illustrated for Lake Erie. The contact estimates for the Minnesota lakes fell along a straight line with a negative intercept. Rotating the models for Minnesota lakes to remove the linear trend would produce equally good fits with contact probability estimates that would be greatest for the panels in the middle of the net gang. Because the panels were woven together in order of mesh size, the rotated contact estimates would suggest that fish are led along the gang and that position of the panel influences contact probability.

In developing indirect selectivity models, it is common to assume that the retention function scales with mesh size and sometimes to examine this assumption by comparisons among a set of candidate models (Millar 1995). The retention functions presented here for 11 lakes scale with mesh size and are all strongly skewed and unimodal. They resemble the indirect models illustrated by Regier et al. (1969) and Hamley and Regier (1973, see their fig. 10) and resemble the tabulated values in Willis et al. (1985, the reciprocals of their correction factors are selectivities) and Henderson and Wong (1991). When the unimodal retention functions were multiplied by the appropriate encounter probability function, the total selectivity curves for the smaller meshes became bimodal. This analysis confirms Hamley and Regier's (1973) conclusion that the shapes of the total selectivity curves change with mesh size, although the details of the selectivity curves differ, particularly for large meshes. The length distributions of wedged and tangled walleye overlap in both Dexter Lake and Mille Lacs data sets; therefore, separating the modes of capture appears unnecessary. Retention probabilities appeared to have a unimodal form even when estimated as factors for Lake Erie or Mille Lacs walleye. I agree with Henderson and Wong (1991) that the modes of capture are often difficult to distinguish in the field and that the two processes are dependent.

The encounter functions estimated for Dexter Lake and Mille Lacs were conditioned on specific indirect estimates of contact and retention probabilities. For these lakes, total catchabilities estimated as the product of three selectivity components should be realistic even if each component is a somewhat distorted representation of the events leading to capture. The encounter functions differed most for small and large fish outside the size range of the Dexter Lake data. The form of the functions may also show differences in swimming behavior between the two lakes.

Rudstam et al. (1984) assumed that encounter rates were directly proportional to swimming speeds. This "direct proportionality" assumption would be appropriate when swimming is strongly directional and individuals change directions infrequently because individuals spend little time in areas previously traversed and because there would be little local depletion of the stock in the vicinity of the net (or learned avoidance). The direct proportionality assumption may be appropriate for species that are pelagic or migratory and for nets set for short intervals. It may not be appropriate if individuals change direction frequently or have a limited home range. In this situation, a random walk or diffusion model may more appropriately describe encounter rates as a function of swimming speed and turning frequency.

Given the uncertainties about the appropriate form for the encounter probability component, what precautions should a biologist take in developing and applying models of gillnet selectivities? It is reasonable to correct for contact and retention components estimated by indirect methods based on clearly stated statistical models (Kirkwood and Walker 1986; Millar 1995; Millar and Holst 1997), recognizing that indirect methods neatly partition abundance on encounter, contact probability, and retention probability only under restrictive assumptions that have not been tested. One should understand that indirect methods that accurately describe contact and retention processes will produce biased estimates of population size structure because the estimated length factors confound abundance and encounter probability. Indirect methods that estimate relative frequencies of length groups encountering nets (Kirkwood and Walker 1986; Millar 1995; Millar and Holst 1997) are superior to methods that assume that all groups are equally abundant on encounter (Helser et al. 1991; Henderson and Wong 1991; Hansen et al. 1997). It is a strength of indirect methods that they may be based on relatively large data sets accumulated in routine monitoring. Although several studies have contrasted selectivity functions or relative abundances estimated by direct and indirect methods, none have identified the missing encounter component in indirect models as a reason for differences (Borgstrøm 1989; Winters and Wheeler 1990; Borgstrøm and Plahte 1992; Mattson 1994; Pierce et al. 1994; Hansson and Rudstam 1995). Where possible, direct and indirect methods of estimating gillnet selectivity should be compared to quantify the encounter component. Other studies that measure the form of the retention function, the size distribution encountering nets, or contact probabilities are necessary to identify the most realistic model from a set of indirect models with equal expected catch values.

The relative efficiency of two meshes is the relative number of fish that the meshes would be expected to capture if all size groups were equally abundant (Regier and Robson 1966). The efficiencies are proportional to the area under the total selectivity curves of Figs. 2 and 3. They increase with mesh size because the range of fish lengths likely to be retained scales with mesh size, because contact probabilities generally increase with mesh size, and because encounter probabilities increase with fish length over much of the size range.

The primary assumption of the statistical model underlying the indirect methods is that the catches C_{lm} were independent observations from a Poisson distribution with expected mean catch rates as given in eq. 3. Catch rates may vary during the period nets are set, as is likely for species showing diel activity cycles; however, the mean rates should be the same for all nets. This means that nets should be set for a fixed period. Nets were fished overnight, throughout the period that walleye are most active and vulnerable in the samples analyzed in this study. Catch rates of walleye (and other species) are known to decrease as the set time increases (Minns and Hurley 1988), perhaps because there is progressive local depletion of the stock; however, mean encounter rates may still be the same for all nets fished overnight, as the statistical model assumes.

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