Gillnet selectivity for lake trout (*Salvelinus namaycush*) in Lake Superior

Michael J. Hansen, Charles P. Madenjian, James H. Selgeby, and Thomas E. Helser

Abstract: Gillnet selectivity for lake trout (*Salvelinus namaycush*) was estimated indirectly from catches in nets of 102-, 114-, 127-, 140-, and 152-mm stretch measure. Mesh selectivity was modeled as a nonlinear response surface that describes changes in the mean, standard deviation, and skewness of fish lengths across mesh sizes. Gillnet selectivity for lake trout was described by five parameters that explained 88% of the variation in wedged and entangled catches, 81% of the variation in wedged catches, and 82% of the variation in entangled catches. Combined catches of wedged and entangled lake trout were therefore described more parsimoniously than separate catches of wedged and entangled lake trout. Peak selectivity of wedged and entangled fish increased from 588 to 663 mm total length as mesh size increased from 102 to 152 mm, and relative selectivity peaked at a total length of 638 mm. The estimated lake trout population size–frequency indicated that gillnet catches were negatively biased toward both small and large lake trout. As a consequence of this bias, survival of Lake Superior lake trout across ages 9–11 was underestimated by about 20% when the catch curve was not adjusted for gillnet selectivity.

Résumé : Nous avons estimé indirectement la sélectivité des filets maillants pour le touladi (*Salvelinus namaycush*) à partir des captures faites au moyen de filets de 102, 114, 127, 140 et 152 mm (maille étirée). Nous avons modélisé la sélectivité du maillage sous forme de surface de réponse non linéaire qui décrit les changements dans la moyenne, l'écart-type et l'asymétrie des longueurs de poissons en fonction de la taille des mailles. Nous avons décrit la sélectivité des filets maillants pour le touladi à partir de cinq paramètres qui expliquent 88 % de la variation pour les captures maillées et emmêlées, 82 % de la variation pour les captures maillées et 85 % de celle des captures emmêlées. Nous avons donc décrit les captures combinées de poissons maillés et de poissons emmêlés de façon moins détaillée que les captures de maillés et emmêlés séparément. La sélectivité maximale pour les poissons maillés et emmêlés s'est accrue de 588 à 663 mm (longueur totale) pour une augmentation correspondante de la taille du maillage de 102 à 152 mm; la sélectivité relative a atteint un sommet à 638 mm de longueur totale. D'après l'estimation du rapport taille–fréquence de la population de touladi, il semblerait que les captures au filet maillant avaient un biais négatif pour les touladis de petite et de grande taille. En raison de ce biais, la survie du touladi de 9 à 11 ans dans le lac Supérieur était sous-estimée d'environ 20 % dans les cas où la courbe des captures ne tenait pas compte de la sélectivité des filets maillants.
[Traduit par la Rédaction]

Introduction

Gill nets are widely used for the commercial harvest and for the assessment of many fish populations, but are highly selective for certain sizes of fish. The size selectivity of a particular mesh size therefore needs to be known to effectively regulate its commercial use (Regier and Robson 1966). Gear selectivity, for example, can greatly affect the estimated allowable harvest for gillnet fisheries, which is crucial for managing these fisheries (Madenjian and Ryan 1995). The selectivity of a gillnet mesh size for a target species is normally determined from a series of different-sized gill nets that are simultaneously fished (Hamley 1975). The estimated selectivity of the various mesh sizes are then used to estimate the size composition of the target fish population, which is used to regulate the commercial fishery.

Various indirect methods have been proposed for estimating selectivity of gill nets to overcome the need for independent estimates of the size–frequency of the target population (Regier and Robson 1966; Hamley 1975). Central to such indirect methods of gillnet selectivity estimation is the assumption that the selectivity curves for all mesh sizes have the same shape and size (Baranov's geometrical similarity assumption; Hamley 1975). This assumption allows the computation of the underlying, but unknown, population size–frequency by scaling the selectivity of different mesh sizes to one size-class of fish (Type B curves) to the same height and then calculating the selectivity of a single mesh size (Type A curves).

Gillnet selectivity has not been estimated for lake trout

Received May 1, 1996. Accepted April 9, 1997.
J13454

M.J. Hansen.[1] University of Wisconsin–Stevens Point, College of Natural Resources, Stevens Point, WI 54481, U.S.A.
C.P. Madenjian. U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, U.S.A.
J.H. Selgeby.[2] U.S. Geological Survey, Great Lakes Science Center, Lake Superior Biological Station, 2800 East Lake Shore Drive, Ashland, WI 54806, U.S.A.
T.E. Helser.[3] National Marine Fisheries Service, Northeast Fisheries Science Center, James J. Howard Marine Sciences Laboratory, Highlands, NJ 07732, U.S.A.

[1] Author to whom correspondence should be addressed. e-mail: mhansen@uwsp.edu

[2] Present address: Route 1, Box 24, Iron River, WI 54847, U.S.A.

[3] Present address: West Virginia University, Wildlife and Fisheries, P.O. Box 6125, Morgantown, WV 26505, U.S.A.

(*Salvelinus namaycush*) in the Great Lakes, although Pycha (1962) estimated the relative efficiency of cotton and multifilament nylon gill nets for lake trout in Lake Superior. Previous estimates of gillnet selectivity for other species have usually been based on fish that were wedged in the meshes, but not for fish that were entangled in the meshes (Hamley 1975). Gillnet selectivity for wedged and entangled fish would be useful for managing a gillnet fishery, particularly when a substantial proportion of the fish caught in the gill net are entangled rather than wedged. Such gillnet fisheries for lake trout are still important in Lake Superior (Hansen et al. 1995), and gillnet selectivity estimates would therefore have practical value in managing these fisheries.

Total annual survival of a fish population can be estimated using the catch-curve method, but survival will be underestimated if catches used to construct the catch curve are not adjusted for gillnet selectivity (Regier and Robson 1966; Ricker 1975). The catch-curve method is used to estimate total annual mortality of lake trout caught in gillnet assessment fisheries in Lake Superior, but these estimates are acknowledged to overestimate mortality (underestimate survival) because of selectivity of the gill nets (Hansen et al. 1994).

In this study, we propose to model the selectivity of gill nets for lake trout to (1) determine if the shape and size of the selectivity curves are similar, as expected from the geometrical similarity assumption, (2) compare the selectivity curves for fish that were either wedged or entangled with the selectivity curves for fish that were wedged only and entangled only, and (3) compare survival estimates from catch curves derived from gillnet catches unadjusted for gillnet selectivity with survival estimates adjusted for gillnet selectivity.

Methods

We estimated the selectivity of five gillnet mesh sizes (102-, 114-, 127-, 140-, and 152-mm stretch measure) for lake trout using the nonlinear iterative least-squares method described by Helser et al. (1991, 1994). The residual least-squares errors of the estimated selectivity for the various mesh sizes were then used in a bootstrap procedure to estimate confidence intervals around estimates of relative selectivity and of the various size-classes of fish in the lake trout population in a refuge in western Lake Superior. We compared the relative selectivity of gill nets and population size–frequencies for fish that were wedged or entangled and for fish that were wedged only and entangled only. We also compared survival estimates from catch curves derived from gillnet catches unadjusted for gillnet selectivity with survival estimates adjusted for gillnet selectivity.

Gillnet catches

Nylon multifilament gill nets were set in Gull Island Refuge, near the Apostle Islands, Lake Superior, from 23 April through 9 May 1973. This location was chosen because a population of large, mostly native lake trout inhabited the area (Swanson and Swedberg 1980; Schram et al. 1995). Gill nets 3657.6 m in length were made up of eight 457.2-m sections, each of which was composed of five 91-m panels, 0.9144 m apart, with one panel each of 102-, 114-, 127-, 140-, and 152-mm stretch measure multifilament nylon twine. The net was 1.8288 m in height with a 1:2 hanging ratio. Net twine was 210/2 for the 102- to 140-mm meshes and 210/3 for the 152-mm mesh.

The net was lifted after 1 day on seven dates, but was lifted after 4 days on one date due to a storm. Lake trout were examined for mode of capture (wedged or entangled), measured (millimetres total length), and enumerated by mesh size. Fish were most often entangled by the mouthparts or teeth if they penetrated the mesh forward from the eyes, but were most often wedged if they penetrated the mesh past the eyes. Fish that penetrated a mesh so that the mesh encircled them between the eye and the dorsal fin were therefore considered wedged whereas others that were caught were considered entangled.

Girth measurements at the eye and at the dorsal fin were taken from a random sample of 170 fish to estimate the linear relationships between total length and girths at the eye and at the dorsal fin (Hamley 1975). We then plotted lengths of entangled fish against the perimeter of the mesh in which they were caught and compared these lengths with the maximum girth and eye girth linear relationships to determine which of the entangled lake trout could have been wedged in the same mesh. Any entangled lake trout that was caught in a mesh with a perimeter less than the upper 95% confidence interval of the maximum girth relationship or greater than the lower 95% confidence interval of the eye girth relationship was judged to have been capable of being wedged in that mesh. The 95% confidence intervals that we used for these comparisons were for individual observations, rather than for mean values, since we were comparing individual fish with the relationships (Draper and Smith 1981).

Model for estimating selectivity

We estimated gillnet selectivity indirectly because direct estimation requires knowledge of the true size structure of the fish population (Hamley 1975), and such data were unavailable. Helser et al. (1991, 1994) developed a method for indirectly fitting Type A and Type B selectivity curves simultaneously using a nonlinear iterative least-squares approach to estimate the response surface of gillnet selectivity as a function of both mesh size and fish size. The method improves on other approaches by simultaneously fitting Type A and Type B curves, by allowing assessment of overall model fit to the data, and by allowing evaluation of the reliability of parameter estimates (Helser et al. 1991; Millar 1992, 1995). The method can also be extended to estimate confidence intervals for the population size–frequency distribution (Helser et al. 1994). The method is based on an assumed skew-normal probability density function

$$s_{ij} = \frac{1}{\sigma_i\,(2\pi)^{1/2}}\,\exp^{-(l_j-\mu_i)^2/2\sigma_i^2}\left(1 - \frac{1}{2q_i\sigma_i^{3/2}}\left(\frac{(l_j-\mu_i)}{\sigma_i} - \frac{(l_j-\mu_i)^3}{3\sigma_i^3}\right)\right)$$

where s_{ij} = selectivity of mesh *i* for fish of size *j*, μ_i = mean size of fish caught (millimetres total length) in mesh size *i*, σ_i = standard deviation of the size of fish in mesh *i*, q_i = skewness coefficient of the size of fish in mesh *i*, and l_j = mean size of fish in size-class *j*. The moments of the probability density function, μ_i, σ_i, and q_i, are estimated as linear (or quadratic) functions of mesh size, m_i (millimetres stretch measure of mesh *i*). In our analysis, μ_i and σ_i were linearly related to m_i, and q_i was a constant:

$$\mu_i = \mu_0 + \mu_1 m_i$$

$$\sigma_i = \sigma_0 + \sigma_1 m_i$$

$$q_i = q_0$$

The estimating function

$$E(\pi_{ij}) = n_{ij}/n_i$$

uses observed proportions of fish size-classes in each mesh size as expected values for mesh selectivity s_{ij}, where π_{ij} = proportion of fish size *j* in mesh size *i*, n_{ij}/n_i, n_{ij} = catches of fish of size-class *j* in mesh *i*, and n_i = total catch of fish in mesh *i*, $\Sigma_j n_{ij}$. The population size–frequency, N_j, can be estimated by dividing the composite catch for each size interval, n_j, by the relative selectivity of that interval, S_{ij}, where

$$n_j = \Sigma_i n_{ij}$$

$$S_{ij} = \Sigma_i s_{ij}/\max_j(\Sigma_i s_{ij})$$

Estimation of selectivity

We estimated selectivity of each mesh size for fish size-classes from

Table 1. Numbers of wedged and entangled lake trout by size interval in five mesh sizes of gill nets set during spring 1973 in Gull Island Refuge, Lake Superior.

Total length	Mesh size (mm)					
(mm)	102	114	127	140	152	Total
438	6	1	0	0	0	7
463	6	3	0	0	1	10
488	18	5	3	0	0	26
513	10	16	7	1	0	34
538	17	18	9	5	1	50
563	8	14	24	10	4	60
588	11	20	30	22	10	93
613	20	15	16	23	9	83
638	11	20	20	29	17	97
663	15	19	25	26	23	108
688	7	22	21	14	25	89
713	10	19	11	15	21	76
738	5	16	13	10	11	55
763	1	6	11	2	4	24
788	0	1	3	5	0	9
813	1	1	3	1	3	9
838	0	1	1	1	2	5
863	0	0	0	1	3	4
Total	146	197	197	165	134	839

Table 2. Numbers of wedged lake trout by size interval in five mesh sizes of gillnets set during spring 1973 in Gull Island Refuge, Lake Superior.

Total length	Mesh size (mm)					
(mm)	102	114	127	140	152	Total
438	6	0	0	0	0	6
463	5	3	0	0	0	8
488	16	4	1	0	0	21
513	9	14	6	1	0	30
538	9	17	6	5	0	37
563	6	10	20	7	4	47
588	6	14	23	20	9	72
613	6	6	11	20	8	51
638	7	10	13	23	14	67
663	5	7	13	15	21	61
688	0	7	11	8	23	49
713	1	7	2	8	16	34
738	1	5	4	4	9	23
763	0	1	1	1	1	4
788	0	0	0	1	0	1
813	1	0	0	0	2	3
838	0	0	0	1	0	1
863	0	0	0	0	3	3
Total	78	105	111	114	110	518

438 through 863 mm (25-mm intervals) by (1) computing the mean, standard deviation, and skewness of the sizes of fish caught in each mesh, (2) fitting linear relationships across mesh sizes for each moment of the fish size distribution, and (3) using the linear parameter estimates as seeds for the iterative least-squares search for parameters of the nonlinear model. We fit the model using SAS (SAS Institute Inc. 1989) and Systat (Systat Inc. 1992) procedures for nonlinear estimation, using the results from both derivative-dependent (Gauss–Newton and quasi-Newton, respectively) and derivative-free (DUD and SIMPLEX, respectively) algorithms as seeds for further searches (Seber and Wild 1989). We assumed that a global minimum sum of squares had been reached when all search methods converged on the same set of parameters for the nonlinear model.

Estimation of population size–frequencies

We estimated the relative abundances of the size-classes in the population by, first, estimating the total selectivity of the gear by summing the selectivity of the five mesh sizes for each fish size-class. Next, we estimated the relative selectivity of the gear for each fish size-class by dividing the total selectivity of the gear by the maximum total selectivity observed for any fish size-class. Last, we estimated the size–frequency of the population by dividing the observed catches by the relative selectivity of the gear for each fish size-class.

We used a bootstrap procedure to estimate 95% confidence intervals for the relative selectivity of the gear and for the estimated relative abundances of the various size-classes in the population (Efron 1979). We used the parameters, estimates, and residuals from the nonlinear iterative least-squares procedure outlined above as inputs for 1000 iterations of a bootstrap. In each iteration of the bootstrap, each predicted selectivity value was assigned a randomly selected residual (with replacement) from the set of residuals obtained in the nominal nonlinear iterative least-squares solution. The mean, 5% quantile, and 95% quantile from 1000 trials of the bootstrap procedure were used as estimates of the mean and its 95% confidence interval.

Bias in estimates of total annual survival

We constructed age-class distributions for estimating the bias in total annual mortality of lake trout caused by gillnet selectivity. The age–length key for lake trout caught in Wisconsin waters of Lake Superior in 1973 (Appendix) was used to construct age-class distributions from three size-class distributions of lake trout (Ricker 1975): (1) fish caught in 114-mm stretch measure nets, the standard assessment gear for indexing lake trout abundance and mortality in Lake Superior (Hansen et al. 1995), (2) fish caught in the five-mesh graded series from 102 through 152-mm stretch measure, and (3) the estimated population size–frequency for lake trout from the nonlinear least-squares estimation described above.

Age-class distributions were used to estimate rates of total instantaneous mortality (*Z*) from the descending limb of the catch curves (Ricker 1975). We used fish 9–11 years of age for estimating total instantaneous mortality because these three age-classes were represented in all three age-class distributions and were therefore fully vulnerable to the gear used to construct the age-class distributions. Estimates of total instantaneous mortality were then used to estimate annual survival rates (*S*), which were used to determine bias of the survival rates derived from catches in 114- and in 102- to 152-mm-mesh nets.

Results

Gillnet catches

Of the 839 lake trout caught in the five meshes, 62% (518 fish) were wedged and 38% (321 fish) were entangled (Tables 1 and 2). Both girth at the eye and girth at the dorsal fin were linearly related to lake trout total length (Fig. 1, top panel). Most entangled lake trout (98%; 316 of 321 fish) were larger than the upper 95% confidence interval of the maximum girth relationship and smaller than the lower 95% confidence interval of the eye girth relationship and could therefore have been wedged in the same mesh (Fig. 1, bottom panel). In contrast, only 2% (five fish) of the fish caught could not have been wedged in

Fig. 1. Maximum girth (MG, upper line) and girth at the eye (EG, lower line) versus total length of lake trout caught in gill nets (top panel) and mesh opening perimeter versus total length of lake trout entangled in gill nets (bottom panel). All fish were caught in spring 1973 at Gull Island Refuge, Lake Superior. Parallel lines display means and 95% confidence intervals of individual observations and are plotted for comparison on the lower panel.

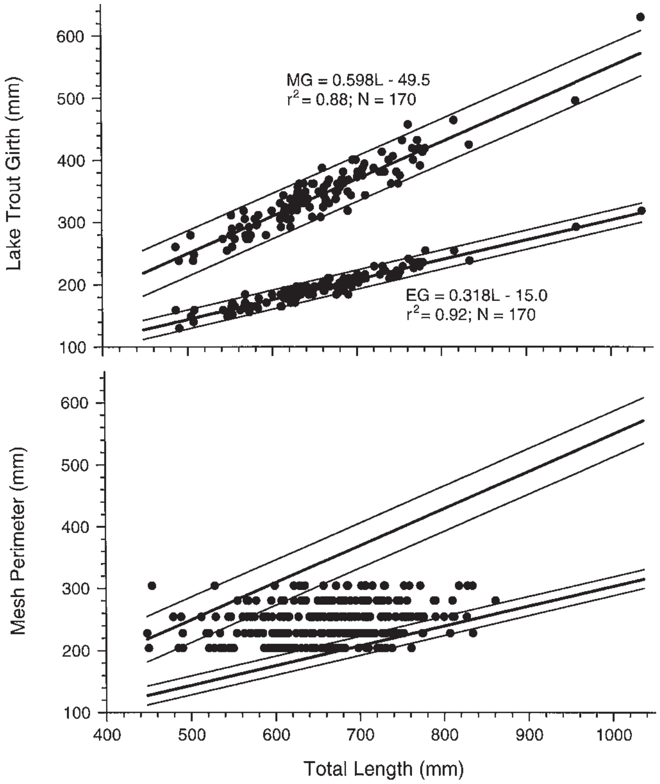
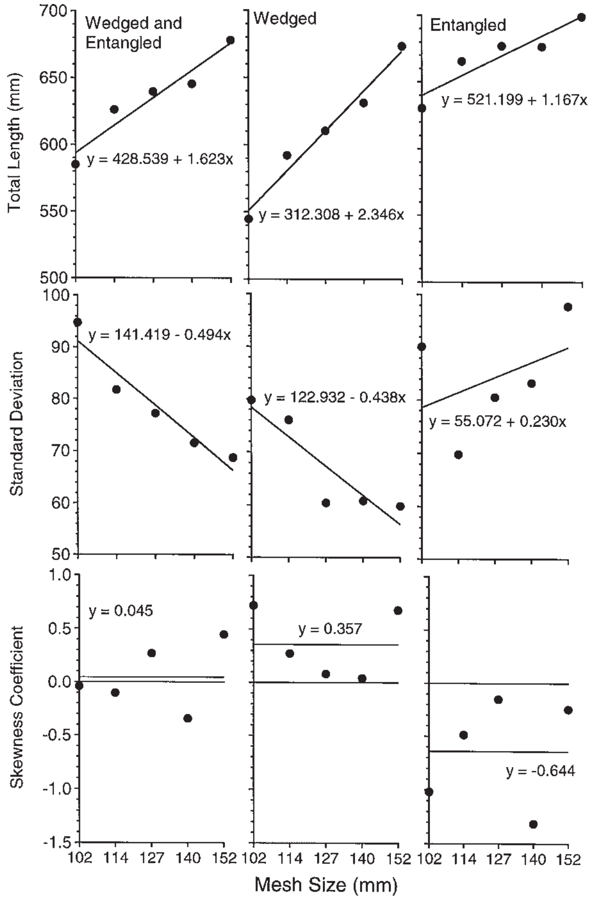


Fig. 2. Changes in the mean, standard deviation, and skewness of lake trout total length caught in gillnet mesh sizes of 102- to 152-mm stretch measure.



that mesh because they were either too small (two fish) or too large (three fish).

Mesh selectivity

Mean lengths of lake trout wedged or entangled in gill nets increased with mesh size, standard deviations decreased, and skewness varied without trend (Fig. 2, left panels). We fit a five-parameter model to the data on relative catches of lake trout wedged or entangled in the five meshes. The model had terms for a linear increase in mean length across meshes (slope, μ_1, and intercept, μ_0), a linear decrease in standard deviation of length across meshes (slope, σ_1, and intercept, σ_0), and no change in skewness of length across meshes (mean, q_0). The model explained 88% of variation in the proportions of fish of various sizes caught in the five mesh sizes (Table 3).

Mean lengths of lake trout wedged in gill nets increased with mesh size, standard deviations decreased, and skewness varied without trend (Fig. 2, center panels). We fit a five-parameter gillnet selection model to the data on relative catches of lake trout wedged in the five meshes. This model also had terms for a linear increase in mean length across meshes (slope, μ_1, and intercept, μ_0), a linear decrease in standard deviation of length across meshes (slope, σ_1, and intercept, σ_0), and no change in skewness of length across meshes (mean, q_0). The model explained 81% of variation in the proportions of fish of various sizes caught in the five mesh sizes (Table 3).

Mean lengths of lake trout entangled in gill nets increased with mesh size, standard deviations increased, and skewness varied without trend (Fig. 2, right panels). We again fit a five-parameter gillnet selection model to the data on relative catches of lake trout entangled in the five meshes. This model also had terms for a linear increase in mean length across meshes (slope, μ_1, and intercept, μ_0), a linear decrease in standard deviation of length across meshes (slope, σ_1, and intercept, σ_0), and no change in skewness of length across meshes (mean, q_0). The model explained 82% of variation in the proportions of fish of various sizes caught in the five mesh sizes (Table 3).

Selectivity of the five meshes for length-classes of wedged and entangled lake trout was skewed toward larger fish (Fig. 3). Peak selectivity increased from 588 to 663 mm for wedged and entangled lake trout as mesh size increased from 102 to 152 mm. Peak selectivity matched peak observed catches for each of the five meshes, although the shape of the selectivity curves for the three small meshes better matched dispersion of the observed catches than for the two large meshes. The five mesh selectivity curves appeared to have similar sizes and shapes, and therefore satisfied Baranov's geometrical similarity assumption for such analyses (as cited in Hamley 1975).

Table 3. Parameter estimates, asymptotic confidence intervals, and model r^2 for wedged and entangled lake trout in five mesh sizes of gill nets set during spring 1973 in Gull Island Refuge, Lake Superior.

	Coefficient		Asymptotic 95% confidence interval	
Parameter	Initial	Final	Lower	Upper
Wedged and entangled				
μ_0	428.539	242.376	149.233	335.519
μ_1	1.623	1.780	1.052	2.508
σ_0	141.419	232.689	137.662	327.716
σ_1	–0.494	–0.173	–0.915	0.569
q_0	0.045	–0.086	–0.096	–0.076
Model r^2	0.884			
Wedged only				
μ_0	312.308	544.869	392.774	696.964
μ_1	2.346	1.894	0.714	3.074
σ_0	122.932	306.753	101.430	512.077
σ_1	–0.438	–0.591	–2.143	0.960
q_0	0.357	0.085	0.068	0.101
Model r^2	0.812			
Entangled only				
μ_0	521.199	413.100	275.510	550.690
μ_1	1.167	0.594	–0.529	1.717
σ_0	55.072	156.988	–16.215	330.191
σ_1	0.230	0.632	–0.758	2.022
q_0	–0.644	–0.078	–0.091	–0.065
Model r^2	0.825			

Selectivity of the five meshes for wedged lake trout was skewed toward smaller fish whereas that for entangled lake trout was skewed toward larger fish (Fig. 4). As mesh size increased from 102 to 152 mm, peak selectivity for wedged lake trout increased from 563 to 663 mm, but for entangled lake trout increased from 613 to 688 mm. Peak selectivities of the five meshes rarely matched the peak observed catches for either wedged or entangled lake trout. The lack of overall model fit, both for wedged and for entangled lake trout, appeared to be caused by a change in the shape and size of the underlying selectivity of the gill nets, a violation of the geometrical similarity assumption.

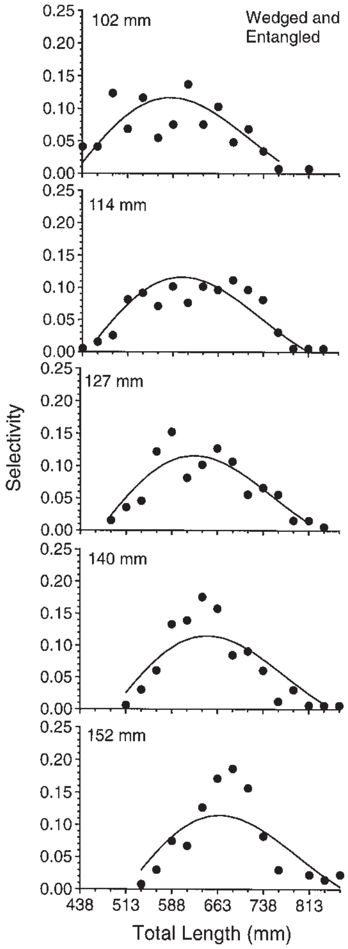
Relative selectivity

Relative selectivity peaked for lake trout 638 mm long that were wedged and entangled in the five gillnet meshes (Fig. 5). We did not estimate relative selectivity for separate catches of wedged and entangled lake trout because their mesh selectivity was poorly estimated. Relative selectivity was estimated with similar precision for all lengths of wedged and entangled lake trout, as evident by the relatively similar confidence intervals for the estimates at each length-class. Relative selectivity for wedged and entangled lake trout increased relatively smoothly from lake trout 438 mm long to the peak and decreased relatively smoothly from the peak to fish 863 mm long.

Population size–frequency

The size–frequency of the lake trout population that was estimated to have been caught in five gillnet mesh sizes was relatively broad and flat, compared with the size–frequency of the sample that was observed to have been wedged or entangled in the nets (Fig. 6). Relative numbers of lake trout 488–788 mm total length were estimated with greater precision than either smaller or larger size-classes, as seen from the relative widths of the confidence intervals around the estimates. Numbers of lake trout estimated in each length-class were greater than the observed catches for most length-classes, which shows how highly selective gill nets are for lake trout.

Fig. 3. Observed (points) and estimated (lines) mesh selectivity of lake trout wedged and entangled, combined, in gill nets in spring 1973, Gull Island Refuge, Lake Superior.



Bias in estimated annual survival

Age-class distributions of lake trout wedged and entangled in 114-mm single-mesh gill nets and in 102- to 152-mm graded-mesh gill nets were not greatly different from one another, but were each different from that of the estimated population (Fig. 7). Instantaneous total annual mortality (*Z*) of lake trout aged 9–11 years was 1.06 for catches in 114-mm nets and 1.03 for catches in 102- to 152-mm nets, but was only 0.57 for the estimated population. Accordingly, annual survival (*S*) of lake trout aged 9–11 years was 35% for catches in 114-mm nets and 36% for catches in 102- to 152-mm nets, but was 57% for the estimated population that accounted for gillnet selectivity.

Discussion

Indirect estimation of gillnet selectivity requires that the

Fig. 4. Observed (points) and estimated (lines) mesh selectivity of lake trout wedged and entangled, separate, in gillnets in spring 1973, Gull Island Refuge, Lake Superior.

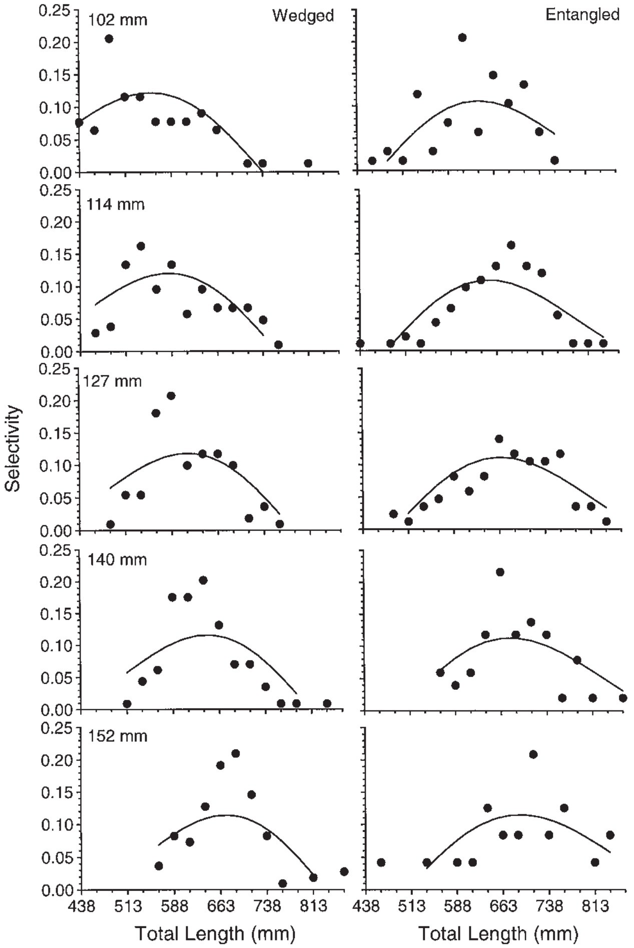


Fig. 5. Estimated mesh selectivity (from Fig. 3) and relative selectivity (mean ± 95% confidence intervals) of lake trout in five gillnet mesh sizes in spring 1973, Gull Island Refuge, Lake Superior.

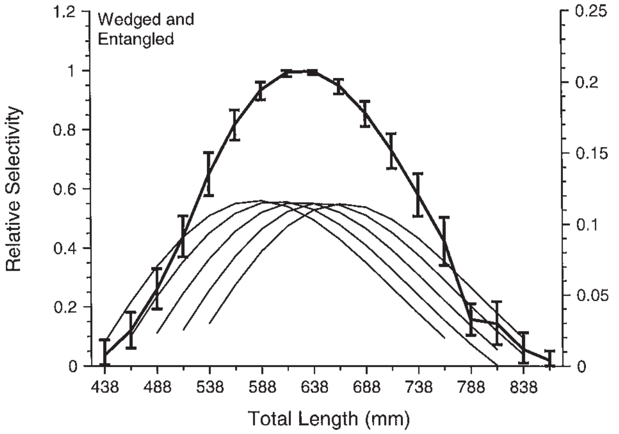


Fig. 6. Observed catches (bars) and estimated population size–frequencies (mean ± 95% confidence intervals) of lake trout in five gillnet mesh sizes in spring 1973, Gull Island Refuge, Lake Superior.

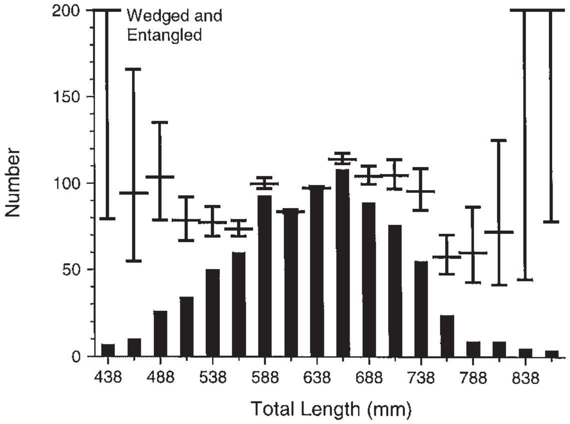
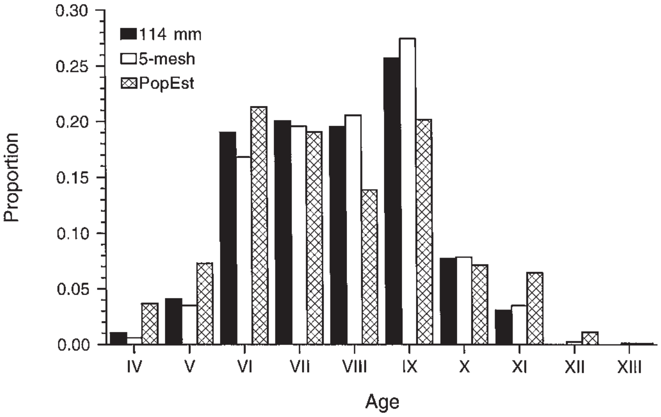


Fig. 7. Age–frequency distributions for lake trout caught in Wisconsin waters of Lake Superior in 114-mm single-mesh gill nets and 102- to 152-mm graded-mesh gill nets and from the estimated population.



selectivity curves for all meshes have the same size and shape (Baranov's geometrical similarity hypothesis; Hamley 1975). We found that the selectivity curves for wedged and entangled lake trout in five meshes of gill nets were similar in size and shape, but not when wedged and entangled fish were modeled separately. Our conclusion is based on the observation that peak values and overall distributions of mesh selectivity matched observed catch frequencies for wedged and entangled lake trout, but not for separate catches of either wedged or entangled lake trout. The relatively poorer fit of the estimated selectivity of our largest two meshes to observed catches was likely caused by the rarity of lake trout larger than 800 mm total length in Gull Island Refuge in 1973. Only 5% of spawning-aged lake trout in Gull Island Refuge were older than age 10 in 1973 (Swanson and Swedberg 1980), the age at which most fish would have been larger than 800 mm total length. Because of the rarity of large lake trout in the Gull Island Refuge population, gillnet selectivity could not be accurately estimated from pairs of different meshes (e.g., Holt's method; Hamley 1975), rather than from the set of five meshes (Helser et al. 1991, 1994; Millar 1992, 1995). For example, selectivity estimated from our two largest meshes would imply a different shape of the selection curve (more peaked) than from all five meshes (more broadly domed). Contemporary catches in the two largest meshes are likely closer to our estimated population size–frequency because the proportion of large fish in the population in Gull Island Refuge has increased since 1973 (Schram et al. 1995).

A second assumption of indirect estimation of gillnet selectivity is that probabilities of fish encountering the net are equal for all sizes of fish (Helser et al. 1994). This assumption may be violated if fish of certain sizes are more likely to encounter the net than fish of other sizes (Hamley 1975). Rudstam et al. (1984) argued that this assumption is not true for fish that spend all or most of their time swimming, such as coregonines, scombrids, and carangids, and corrected their estimates of gillnet selectivity for cisco (*Coregonus artedi*) by assuming that encounter probability increased with fish length. However, Borgstrøm and Plahte (1992) contended that this approach is inappropriate for salmonines like brown trout (*Salmo trutta*) that make short excursions to catch prey fish. Tagging studies of lake trout in the Apostle Island region of Lake Superior have shown that few fish stray more than 80 km from their point of capture (Eschmeyer et al. 1953; Buettner 1961; Rahrer 1968). Of the few lake trout that strayed greater distances, Eschmeyer et al. (1953) showed that the incidence of moving more than 80 km was greater as fish increased from 225 to 500 mm total length, but there was no apparent increase in distance moved for fish larger than 500 mm total length. Since 95% of the lake trout caught in our nets exceeded 500 mm total length, we assumed that corrections of gillnet selectivity to account for size-based encounter probability were unwarranted.

A third assumption for indirect estimation of gillnet selectivity is that probabilities of fish being retained in the net are affected only by mesh size (Helser et al. 1994). This assumption may be violated if fish of a certain size tend to move along a portion of the net of certain mesh size into another portion of the net of another mesh size (Regier and Robson 1966). We minimized the likelihood of this bias by leaving gaps between the panels of different mesh sizes and by lifting the net after one night of fishing whenever possible (Regier and Robson 1966). Our one net that soaked four nights before it was lifted did not appear to be affected by saturation, as the total catch was similar to that obtained from summing one night's catch at the previous four nights' catch rate and three nights' catches at the succeeding two nights' catch rate.

The model we used to estimate gillnet selectivity was based on an assumed skew-normal distribution because lake trout may become tangled by their teeth and maxillaries, which generally causes selectivity curves to be broadly domed and skewed to the right (Hamley 1975), as we found in this study. In comparison, the selection curve for lake whitefish (*Coregonus clupeaformis*) (Regier and Robson 1966), a salmonid species without a large mouth, is relatively normal whereas the selection curves for other salmonids with larger mouths, such as rainbow trout (*Oncorhynchus mykiss*) (Fujimori et al. 1992), sockeye salmon (*Oncorhynchus nerka*), chum salmon (*Oncorhynchus keta*), pink salmon (*Oncorhynchus gorbuscha*) (reviewed by Hamley 1975), Arctic char (*Salvelinus alpinus*), and brown trout (reviewed by Jensen 1986), are more skewed.

Our estimates of gillnet selectivity should prove valuable in managing gillnet fisheries for lake trout in Lake Superior. Selectivity can be incorporated into Ricker equilibrium models in the same manner as was done by Madenjian and Ryan (1995) to arrive at recommended allowable harvests for gillnet fisheries for lake trout in Lake Superior. Estimated gillnet selectivity can also be used to understand and adjust for bias in estimates of lake trout mortality from lake trout catches in single-mesh and graded-mesh assessment nets. We found that estimated annual survival was biased low by more than 20%, whether estimated from catches in 114-mm single-mesh nets or from catches in 102- to 152-mm graded-mesh nets. Bias of this magnitude in estimated annual survival should be taken into account in setting limits for total allowable harvest of lake trout in Lake Superior.

Acknowledgments

P.M. Haack and C.R. Bronte assisted with data analysis. C.R. Bronte, P.H. Eschmeyer, L.D. Jacobson, and J.F. Savino reviewed the manuscript. This article is contribution 973 of the U.S. Geological Survey, Great Lakes Science Center, Ann Arbor, Mich.

References

Borgstrøm, R., and Plahte, E. 1992. Gillnet selectivity and a model for capture probabilities for a stunted brown trout (*Salmo trutta*) population. Can. J. Fish. Aquat. Sci. **49**: 1546–1554.

Buettner, H.J. 1961. Recoveries of tagged, hatchery-reared lake trout from Lake Superior. Trans. Am. Fish. Soc. **90**: 404–412.

Draper, N.R., and Smith, H. 1981. Applied regression analysis. 2nd ed. John Wiley & Sons, Inc., New York.

Efron, B. 1979. Bootstrap methods: another look at the jackknife. Ann. Stat. **7**: 1–26.

Eschmeyer, P.H., Daly, R., and Erkkila, L.F. 1953. The movement of tagged lake trout in Lake Superior, 1950–1952. Trans. Am. Fish. Soc. **82**: 68–77.

Fujimori, Y., Matuda, K., and Losanes, L.P. 1992. Method of estimating gillnet selectivity curve in a water tank experiment by Monte Carlo simulation. Nihon Suisan Gakkai-shi, **58**: 193–198.

Hamley, J.H. 1975. Review of gillnet selectivity. J. Fish. Res. Board Can. **32**: 1943–1969.

Hansen, M.J., Ebener, M.P., Shively, J.D., and Swanson, B.L. 1994. Lake trout. *In* The state of Lake Superior in 1992. *Edited by* M.J. Hansen. Great Lakes Fish. Comm. Spec. Publ. 94-1. pp. 13–34.

Hansen, M.J., Peck, J.W., Schorfhaar, R.G., Selgeby, J.H., Schreiner, D.R., Schram, S.T., Swanson, B.L., MacCallum, W.R., Burnham-Curtis, M.K., Curtis, G.L., Heinrich, J.W., and Young, R.J. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. J. Great Lakes Res. **21**(Suppl. 1): 152–175.

Helser, T.E., Condrey, R.E., and Geaghan, J.P. 1991. A new method of estimating gillnet selectivity, with an example for spotted seatrout, *Cynocion nebulosus*. Can. J. Fish. Aquat. Sci. **48**: 487–492.

Helser, T.E., Geaghan, J.P., and Condrey, R.E. 1994. Estimating size composition and associated variances of a fish population from gillnet selectivity, with an example for spotted seatrout (*Cynocion nebulosus*). Fish. Res. **19**: 65–86.

Jensen, J.W. 1986. Gillnet selectivity and the efficiency of alternative combinations of mesh sizes for some freshwater fish. J. Fish Biol. **28**: 637–646.

Madenjian, C.P., and Ryan, P.A. 1995. Effect of gear selectivity on recommended allowable harvest with application to the Lake Erie yellow perch fishery. N. Am. J. Fish. Manage. **15**: 79–83.

Millar, R.B. 1992. Estimating the size-selectivity of fishing gear by conditioning on the total catch. J. Am. Stat. Assoc. **87**: 962–968.

Millar, R.B. 1995. The functional form of hook and gillnet selection curves cannot be determined from comparative catch data alone. Can. J. Fish. Aquat. Sci. **52**: 883–891.

Pycha, R.L. 1962. The relative efficiency of nylon and cotton gill nets for taking lake trout in Lake Superior. J. Fish. Res. Board Can. **19**: 1085–1094.

Rahrer, J.F. 1968. Movements of adult lake trout in Lake Superior. Trans. Am. Fish. Soc. **97**: 481–484.

Regier, H.A., and Robson, D.S. 1966. Selectivity of gill nets, especially to lake whitefish. J. Fish. Res. Board Can. **23**: 423–454.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Rudstam, L.G., Magnuson, J.J., and Tonn, W.M. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Can. J. Fish. Aquat. Sci. **41**: 1252–1255.

SAS Institute, Inc. 1989. SAS/STAT user's guide, version 6, 4th ed. Vol. 2. SAS Institute, Inc., Cary, N.C.

Schram, S.T., Selgeby, J.H., Bronte, C.R., and Swanson, B.L. 1995. Population recovery and natural recruitment of lake trout at Gull Island Shoal, Lake Superior, 1964–1992. J. Great Lakes Res. **21**(Suppl. 1): 225–232.

Seber, G.A.F., and Wild, C.J. 1989. Nonlinear regression. John Wiley & Sons, Inc., New York.

Swanson, B.L., and Swedberg, D.V. 1980. Decline and recovery of the Lake Superior Gull Island Reef lake trout (*Salvelinus namaycush*) population and the role of sea lamprey (*Petromyzon marinus*) predation. Can. J. Fish. Aquat. Sci. **37**: 2074–2080.

Systat, Inc. 1992. Systat for Windows: statistics, version 5 edition. Systat, Inc., Evanston, Ill.

Appendix. Proportion of lake trout per age-class within various length-classes caught in spring gillnet assessment fisheries in Wisconsin waters of Lake Superior in 1973.

Total length	Age (years)									
(mm)	4	5	6	7	8	9	10	11	12	13
438	0.18	0.22	0.37	0.18	0.04	0.00	0.00	0.00	0.00	0.00
463	0.06	0.22	0.45	0.14	0.03	0.10	0.00	0.00	0.00	0.00
488	0.02	0.06	0.34	0.56	0.01	0.00	0.00	0.00	0.00	0.00
513	0.04	0.12	0.52	0.29	0.04	0.00	0.00	0.00	0.00	0.00
538	0.03	0.15	0.35	0.40	0.07	0.00	0.00	0.00	0.00	0.00
563	0.00	0.02	0.60	0.30	0.08	0.01	0.00	0.00	0.00	0.00
588	0.00	0.12	0.22	0.35	0.22	0.09	0.00	0.00	0.00	0.00
613	0.00	0.00	0.21	0.29	0.36	0.14	0.00	0.00	0.00	0.00
638	0.00	0.00	0.09	0.23	0.37	0.24	0.08	0.00	0.00	0.00
663	0.00	0.00	0.01	0.11	0.14	0.61	0.12	0.00	0.00	0.00
688	0.00	0.00	0.01	0.04	0.29	0.51	0.15	0.00	0.00	0.00
713	0.00	0.00	0.05	0.01	0.23	0.50	0.12	0.09	0.00	0.00
738	0.00	0.00	0.00	0.02	0.24	0.37	0.21	0.15	0.00	0.02
763	0.00	0.00	0.00	0.04	0.07	0.39	0.29	0.21	0.00	0.00
788	0.00	0.00	0.00	0.00	0.00	0.38	0.13	0.50	0.00	0.00
813	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.25	0.00