North American Journal of Fisheries Management 18:847–853, 1998

Gill-Net Saturation by Lake Trout in Michigan Waters of Lake Superior

MICHAEL J. HANSEN*

University of Wisconsin–Stevens Point, College of Natural Resources
1900 Franklin Street, Stevens Point, Wisconsin 54481, USA

RICHARD G. SCHORFHAAR

Michigan Department of Natural Resources, Charlevoix Fisheries Station
96 Grant Street, Charlevoix, Michigan 49720, USA

JAMES H. SELGEBY[1]

U.S. Geological Survey, Biological Resources Division
Great Lakes Science Center, Lake Superior Biological Station
2800 East Lake Shore Drive, Ashland, Wisconsin 54806, USA

Abstract.—We conducted experimental fishing for lake trout *Salvelinus namaycush* in Michigan waters of Lake Superior to determine the importance of soak time on catch per effort (CPE) in numbers per kilometer of standard gill net. We modeled CPE as a nonlinear function of the number of nights between setting and lifting (soak time), in which the nets fill at a certain rate toward some maximum after which the nets cannot hold more fish. We found that lake trout CPE increased with soak time at a rate that varied with lake trout density toward a saturation level that was independent of lake trout density. The CPE values of nets soaked 2–5 nights divided by the CPE of nets soaked 1 night were significantly lower than would be expected had CPE increased as a linear function of the number of nights soaked. We derived a means for correcting gill-net CPE values for differing soak times to a common base of 1 night soaked. We concluded that it is inappropriate to assume lake trout catches in gill nets will increase in direct proportion to the number of nights soaked and recommend that CPE of lake trout in gill nets be corrected for soak time.

The efficiency of any fishing gear will decrease as fish accumulate in the gear until it becomes saturated and no more fish are caught (Hamley 1975). If the presence of fish already captured does not deter new fish from being captured, then the rate of capture is proportional to the vacant amount of gear and the number of fish present in the area fished (Beverton and Holt 1954). The maximum level at which fishing gear becomes saturated is related to fish density and to the vacant area of the net (Beverton and Holt 1954). Therefore, average size of fish caught can influence the saturation level because large fish leave less vacant space in the gear than do small fish.

The type of gear ultimately determines the degree to which saturation affects its fishing power (Beverton and Holt 1954). For example, Beverton and Holt (1954) argued that longlines and gill nets were prone to saturation because the number of hooks or meshes in a gang could easily be exceeded by the number of fish available for capture. In contrast, they argued that trawls rarely captured enough fish for the cod end to become completely filled. Such saturation of the fishing gear renders the catch per effort (CPE) meaningless as an index of density or abundance of the fish caught (Beverton and Holt 1954).

In Great Lakes commercial fisheries for lake trout *Salvelinus namaycush,* catch in weight per length of gill net increased with the time between setting and lifting (soak time) but not in direct proportion to soak time (R. Hile, U.S. Bureau of Commercial Fisheries, unpublished report, cited in Hile 1962). However, Hile (1962) concluded that soak time varied too little among years to cause a detectable difference in lake trout CPE, whether adjusted for soak time or not. He argued that it was therefore not necessary to account for soak time in computing CPE for the commercial fishery.

Kennedy (1951) found that gill nets fished in Great Slave Lake, Canada, caught increased weight of fish, but at a decreasing rate, as the number of nights soaked increased. The gill nets filled toward the same maximum weight of fish, but at

---

* Corresponding author: mhansen@uwsp.edu

[1] Retired. Present address: Route 1, Box 24, Iron River, Wisconsin 54847, USA.

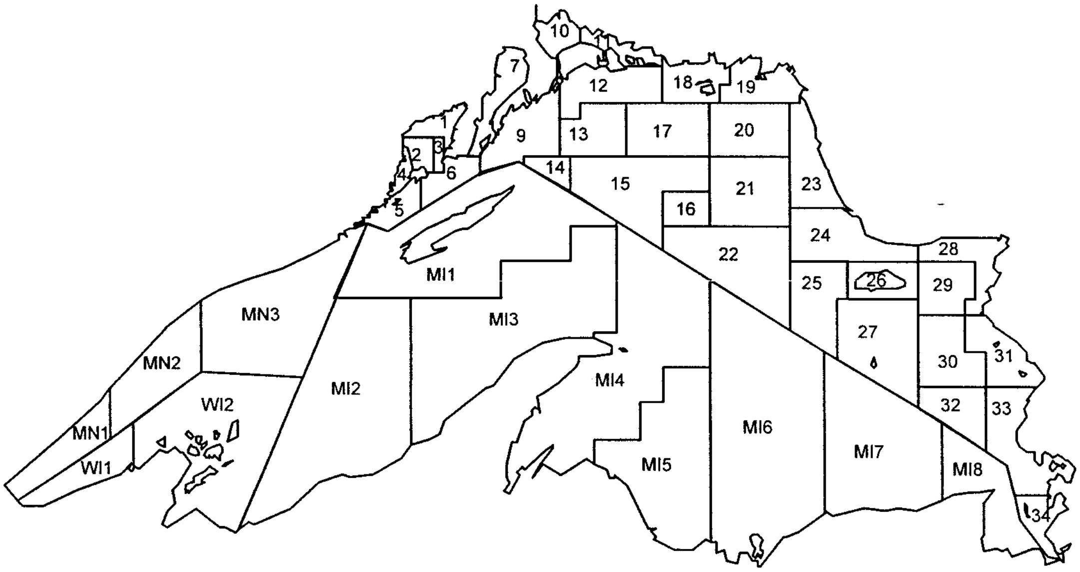

FIGURE 1.—Lake trout management areas of Lake Superior. Areas of U.S. waters are denoted by state abbreviations: MI = Michigan, MN = Minnesota, and WI = Wisconsin. Canadian areas are marked by numbers only.

different rates that were related to the density of fish in the area (termed ''availability''). He developed correction factors, based on fish availability and the number of days between lifts, which could be used to compare the CPE among gill-net lifts with varied numbers of nights soaked. Kennedy's saturation curves are often cited as examples of such curves (Hamley 1975).

No one has yet determined the rates at which numbers of lake trout are caught in gill nets or the maximum number of lake trout that can be caught (as contrasted with the biomass caught). In each of the Great Lakes, gill nets are used to index lake trout stock density, as part of binational interagency restoration programs (Cornelius et al. 1995; Elrod et al. 1995; Eshenroder et al. 1995; Hansen et al. 1995; Holey et al. 1995). We conducted experimental gill-net fishing in Michigan waters of Lake Superior to determine the importance of soak time on the CPE of lake trout numbers caught in the assessment fisheries.

We addressed three questions. First, does increased soak time of gill nets cause lake trout CPE to increase linearly or nonlinearly? Second, does the rate at which gill nets fill vary with lake trout density? Third, does the maximum number of lake trout caught vary with fish density? To address these questions, we fished experimental gill nets in two periods of greatly different lake trout density and in several areas that also differed in lake trout density. We then fit the data to a saturation model to see if parameters of the model varied with lake trout density.

Methods

Experimental gill nets were fished in Michigan waters of Lake Superior in four areas in 1970, when lake trout density was at its peak, and six areas in 1995, when lake trout density was less than half as great (Hansen et al. 1995). In 1970, fishing was conducted in two areas of Keweenaw Bay (Figure 1; MI4), one area near Marquette (MI5), and one area near Munising (MI6). In 1995, fishing was conducted in three areas off the western shore of the Keweenaw Peninsula (MI3) and in three areas of Keweenaw Bay (MI4). Fishing was conducted by contract fishermen in 1970 and by the Michigan Department of Natural Resources in 1995, and all fishing was in May.

Nets were constructed of 114-mm-stretched mesh, 210/2 multifilament nylon twine, 18 meshes deep, and 1/2 hanging basis. Nets ranged in length from 549 to 1,829 m in 1970, but were all 457 m in 1995. Three identical net gangs were set in 1970 and five identical net gangs were set in 1995 on the first day of each event in the same area and at the same depth. Individual net gangs were then lifted about every 24 h for the next three consecutive days in 1970 and on the next five consecutive days in 1995. The net gangs were set close enough together to be considered replicate sets for the same lake trout stock but were far enough apart to prevent interference with each other and, therefore, were independent of each other.

Fishing events were replicated in each area three to six times in 1970 and two times in 1995. In 1970, fishing events were repeated four times in one area and six times in another area of MI4, three times in one area of MI5, and three times in one area of MI6. In 1995, fishing events were repeated twice in each of three areas of MI3 and twice in each of three areas of MI4. Each fishing event was considered to be a replicate sample of the lake trout stock density in the area fished. Therefore, 108 total net gangs were fished, 48 in 1970 and 60 in 1995.

Because soak times were short in our study, we modeled lake trout CPE, in number of fish caught per kilometer of gill net, as an asymptotic function of the number of nights between setting and lifting, as provided in model 3.0 by Zhou and Shirley (1997):

$$\mathrm{CPE} = \alpha(1 - e^{-\beta\times\mathrm{NIGHTS}}), \qquad (1)$$

where α is the maximum CPE that would be attained after an infinitely long soak time and β is the rate at which CPE approaches α. Lake trout density, which varied among years and areas, might have determined α and β. Therefore, we used nonlinear methods to fit a sequence of successively more complex models. The simplest, model A (2 parameters), was fit with a single α and a single β. Models B and C, of intermediate complexity (11 parameters), were fit by coding the densities with dummy variables (0 or 1) either for one α and multiple βs (model B) or for multiple αs and one β (model C). The most complex, model D (20 parameters), was fit by coding densities with dummy variables (0 or 1) for multiple αs and βs.

Residual errors were heteroscedastic, so we used ordinary least squares to fit the four models after transformation of both sides of equation (1) into natural logarithms. Ratios of residual mean sums of squares of nested models (likelihood ratio tests) were used to determine whether a more complex model significantly improved the overall fit compared with a less complex model ($P < 0.05$; Bates and Watts 1988). Parameter estimates and asymptotic standard errors were obtained numerically by using a Gauss–Newton method that relied on exact derivatives (SPSS 1997). Residual errors were examined for conformity with assumptions of homogeneity, normality, independence, and linearity (Kirby 1993).

TABLE 1.—Sums of squares explained by four models of lake trout catch per effort (CPE) in gill nets versus soak time in Michigan waters of Lake Superior, 1970 and 1995 (α is the maximum attainable CPE and β is the rate at which CPE approaches α).

Source	Sum of squares	df	Mean-square	*F*-ratio	*P*
Model A (one α and β)					
Regression	1,583.36	2	791.68	727.66	0.000
Residual	115.33	106	1.09		
Model B (one α and multiple βs)					
Regression	1,663.27	11	151.21	414.09	0.000
Residual	35.42	97	0.37		
Model C (multiple αs and one β)					
Regression	1,659.40	11	150.85	372.39	0.000
Residual	39.29	97	0.41		
Model D (multiple αs and βs)					
Regression	1,666.15	20	83.31	225.26	0.000
Residual	32.54	88	0.37		
Added sums-of-squares tests					
Model D/A	82.78	18	4.60	12.44	0.000
Model C/A	76.03	9	8.45	20.85	0.000
Model B/A	79.91	9	8.88	24.31	0.000
Model D/B	2.88	9	0.32	0.86	0.560
Model D/C	6.75	9	0.75	2.03	0.045

Final model estimates were used to derive ratios of the CPE after 2–5 nights soaked to the CPE after 1 night soaked. The average ratio across all 10 areas fished, along with their 95% confidence intervals, was used to determine if the ratios were significantly lower than would be expected if catches increased as a linear function of nights soaked. Therefore, the CPE ratio of 5 nights to 1 night soaked would be expected to be 5 if catches had increased linearly with soak time.

Results

Gill-net saturation was best described by a model with one α for all densities and a different β for each density (model B; Table 1). Models B, C, and D each improved on model A in describing the increase in CPE with soak time among different densities. Model D improved on model C but not on model B. Model B therefore accounted for significantly greater sums of squares than model C even though models B and C could not be statistically compared (because they are not nested).

Lake trout CPE increased with soak time toward one maximum level ($\alpha = 211.443$ lake trout) for all densities (Figure 2; Table 2). Rates of increase in lake trout CPE (β) toward this maximum level were greater for all four areas fished in 1970 than

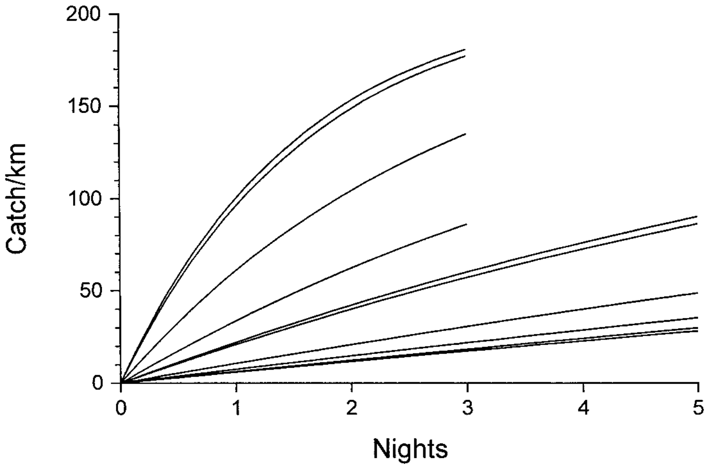

FIGURE 2.—Lake trout catch/km of gill net (i.e., CPE) soaked for 1–5 nights in Michigan waters of Lake Superior in 1970 (four areas, 1–3 nights soaked) and 1995 (six areas, 1–5 nights soaked).

for the six areas fished in 1995. The maximum obtainable CPE of lake trout in gill nets of the type used in this study was not reached after 3 nights soaked in 1970 or 5 nights soaked in 1995. This suggests that CPE provided a reasonable index of lake trout abundance at all soak times examined.

Ratios of estimated CPE values at successively greater soak times were significantly lower than expected if CPE had increased as a linear function of nights soaked (Figure 3). These ratios could not, however, be used to correct CPE values for gill-net catches of different soak times because the rate of increase in CPE toward the maximum level varied with lake trout density. Corrections for different soak times should be determined from equation (1), rearranged to derive β from CPE, nights soaked, and $\alpha = 211.443$:

$$\beta = \frac{-\log_e\left(1 - \frac{\text{CPE}}{211.443}\right)}{\text{NIGHTS}}. \qquad (2)$$

The estimate of β should then be inserted into equation (1), with NIGHTS $=1$ and $\alpha = 211.443$ to standardize CPE to a 1-night set. This correction of CPE is, of course, appropriate only for gill nets of the type used in this study.

Discussion

Our results suggest that lake trout CPE (numbers) in gill nets increased at a rate that depended on fish density but that the maximum number of fish that could be held in each gill net did not vary with fish density. Similarly, Kennedy (1951) found

TABLE 2.—Parameter estimates (PE), asymptotic standard errors (ASE), and Wald 95% confidence limits for a model of lake trout catch per effort (CPE) in gill nets versus soak time in Michigan waters of Lake Superior, 1970 and 1995 (α is the maximum attainable CPE and β is the rate at which CPE approaches α).

				Confidence limit	
Parameter[a]	PE	ASE	PE/ASE	Lower	Upper
α	211.443	87.121	2.427	38.532	384.355
$\beta_{70\text{-}1}$	0.602	0.470	1.282	−0.330	1.535
$\beta_{70\text{-}2}$	0.173	0.090	1.933	−0.005	0.351
$\beta_{70\text{-}3}$	0.639	0.527	1.212	−0.407	1.685
$\beta_{70\text{-}4}$	0.338	0.216	1.570	−0.089	0.766
$\beta_{95\text{-}1}$	0.111	0.059	1.872	−0.007	0.228
$\beta_{95\text{-}2}$	0.028	0.013	2.110	0.002	0.055
$\beta_{95\text{-}3}$	0.052	0.025	2.038	0.001	0.102
$\beta_{95\text{-}4}$	0.030	0.014	2.104	0.002	0.059
$\beta_{95\text{-}5}$	0.036	0.017	2.086	0.002	0.071
$\beta_{95\text{-}6}$	0.104	0.055	1.889	−0.005	0.214

[a] Parameter β is given for each of four areas sampled in 1970 (β_{70}) and each of six areas sampled in 1995 (β_{95}).

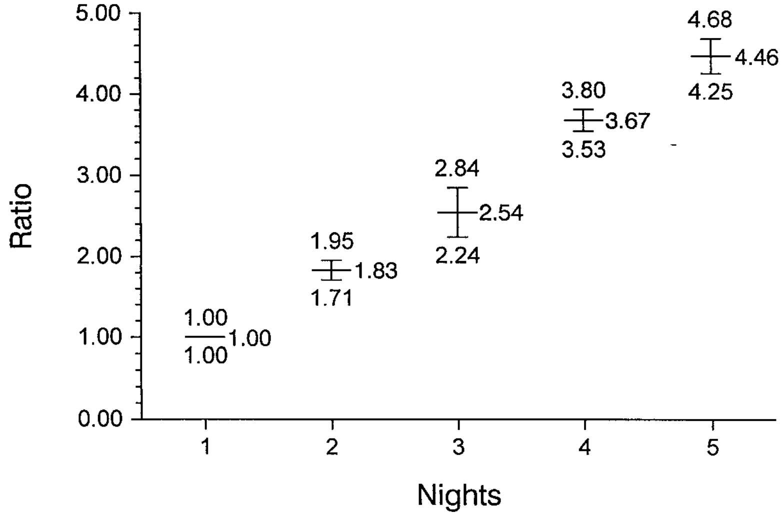

FIGURE 3.—The average ratio (values offset to right) of lake trout CPE for gill nets soaked for 1–5 nights to CPE for nets soaked 1 night (±95% confidence intervals; limit values given above and below mean) in Michigan waters of Lake Superior in 1970 (four areas, 1–3 nights soaked) and 1995 (six areas, 1–5 nights soaked).

that lake trout CPE (weight) in gill nets in Great Slave Lake increased at rates that depended on density, toward a maximum saturation level that did not depend on density. We expected the saturation level of our gill nets (α) to be lower in 1970, when the average size of lake trout was slightly larger, than in 1995 (Figure 4; Hansen et al. 1995). However, because asymptotic CPE was similar in 1970 and 1995, lake trout size did not seem to influence the maximum number that could be held in gill nets of the type used in our study.

Commercial fishery CPE may not accurately reflect fish density if soak time is not taken into account because fishermen adjust their effort in response to density-dependent changes in gear efficiency. Austin (1977) found that the catch per trap of Caribbean spiny lobster *Panulirus argus* decreased at a declining rate with respect to soak time. The profit-maximizing soak time declined along with abundance because the number of possible lifts in a day was usually fixed for any fisherman. Numbers of traps fished by each vessel declined as lobster stocks declined, which increased the catch per trap day compared with lev-

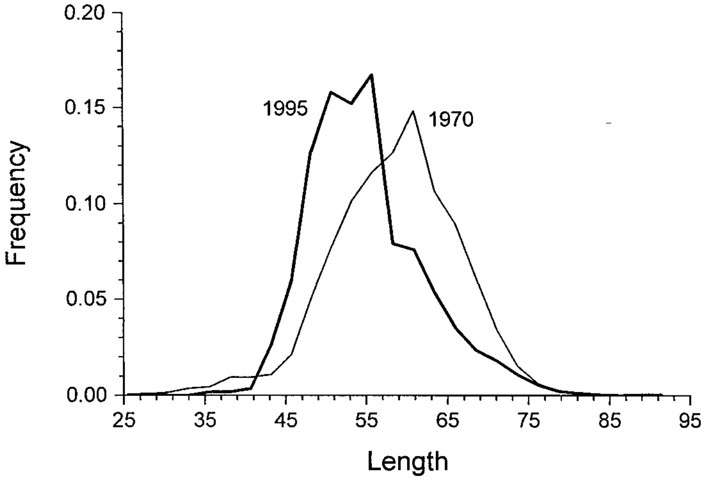

FIGURE 4.—Length-frequency (cm) of lake trout caught in gill nets in Michigan waters of Lake Superior, 1970 and 1995.

els taken at the previously longer soak times. This behavior may explain why Hile (1962) was unable to detect any differences in lake trout CPE at different soak times.

Net saturation for a particular species may depend on the mix of species present and on the relative abundances of those species. Minns and Hurley (1988) found that as soak time increased, the CPE in gill nets increased for some fish species but decreased for others. Differences were attributed to specific activity patterns and relative abundances, which caused crepuscular species such as yellow perch *Perca flavescens* to be caught earlier during the net set than nocturnal species such as walleye *Stizostedion vitreum*. Catches of the species that were caught first affected catches of species that were caught later. This effect was unlikely to have influenced our study or the earlier analyses by Hile (1962) because the number of species present in Lake Superior is so few compared with Lake Erie (Minns and Hurley 1988).

Our results differ from those of G. L. Curtis and others (Great Lakes Science Center, unpublished), who developed correction factors for gill-net CPE to standardize 2- and 3-night sets to a uniform base of 1 night. Their correction factors for 2-night (1.52) and 3-night (1.80) sets were based on an assumed common rate (β) at which catches approached the maximum attainable catch (α). However, our results suggest that lake trout density determines the rate at which catch approaches the maximum (but not the maximum attainable catch). Therefore, standardizing CPE values of different soak times to a 1-night set cannot be accomplished with a single set of correction factors. Rather, standardization of CPE values must be based on the observed CPE in the area fished, the maximum obtainable catch for the gear, and the number of nights soaked (equations 1, 2).

Our results permit standardization of lake trout CPE in gill nets of the type used in this study. Previous summaries of lake trout CPE with this gear in Lake Superior (e.g., Hansen et al. 1995), which were based on correction factors derived by Curtis and others (unpublished), should be updated by using the procedure we described. In addition, if lake trout density in Lake Superior increases to levels substantially higher than in 1970, it may be necessary to recalibrate the gill-net saturation model. Finally, lake trout assessment fisheries in other Great Lakes may rely on gill nets with mesh sizes or constructions different from those used in our study. Those programs will require development of saturation models specific to their gill nets.

Acknowledgments

We thank the Lake Superior Technical Committee, an advisory committee of the Great Lakes Fishery Commission, who contributed to discussions about this study. Charles Anderson, Mark Ebener, Mark Holey, Charles Madenjian, James Peck, and an anonymous reviewer contributed valuable suggestions as reviewers of the manuscript. Asa Wright initiated the 1970 field sampling. Wayne MacCallum provided the map of Lake Superior lake trout management areas. This work was supported by funds from the U.S. Federal Aid in Sport Fish Restoration Act and by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and from the State of Wisconsin (Federal grant R/LR-77). This paper is contribution 1027 of the U.S. Geological Survey, Biological Resources Division, Great Lakes Science Center.

References

Austin, C. B. 1977. Incorporating soak time into measurement of fishing effort in trap fisheries. Fishery Bulletin 75:213–218.

Bates, D. M., and D. G. Watts. 1988. Nonlinear regression analysis and its applications. Wiley, New York.

Beverton, R. J. H., and S. J. Holt. 1954. On the dynamics of exploited fish populations. Chapman and Hall, New York.

Cornelius, F. C., K. M. Muth, and R. Kenyon. 1995. Lake trout rehabilitation in Lake Erie: a case history. Journal of Great Lakes Research 21(Supplement 1):65–82.

Elrod, J. H., and six coauthors. 1995. Lake trout rehabilitation in Lake Ontario. Journal of Great Lakes Research 21(Supplement 1):83–107.

Eshenroder, R. L., N. R. Payne, J. E. Johnson, C. H. Bowen II, and M. P. Ebener. 1995. Lake trout rehabilitation in Lake Huron. Journal of Great Lakes Research 21(Supplement 1):108–127.

Hamley, J. M. 1975. Review of gillnet selectivity. Journal of the Fisheries Research Board of Canada 32: 1943–1969.

Hansen, M. J., and eleven coauthors. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. Journal of Great Lakes Research 21(Supplement 1):152–175.

Hile, R. 1962. Collection and analysis of commercial fishery statistics in the Great Lakes. Great Lakes Fishery Commission Technical Report 5.

Holey, M. E., and eight coauthors. 1995. Progress toward lake trout restoration in Lake Michigan. Journal of Great Lakes Research 21(Supplement 1):128–151.

Kennedy, W. A. 1951. The relationship of fishing effort by gill nets to the interval between lifts. Journal of the Fisheries Research Board of Canada 8:264–274.

Kirby, K. N. 1993. Advanced data analysis with SYSTAT. Van Nostrand Reinhold, New York.

Minns, C. K., and D. A. Hurley. 1988. Effects of net length and set time on fish catches in gill nets. North American Journal of Fisheries Management 8:216–223.

SPSS. 1997. SYSTAT 7.0: statistics. SPSS, Chicago.

Zhou, S., and T. C. Shirley. 1997. A model expressing the relationship between catch and soak time for trap fisheries. North American Journal of Fisheries Management 17:482–487.

Received September 19, 1997
Accepted April 4, 1998