

Factors Affecting Survival Rates of a Recovering Lake Trout Population Estimated by Mark–Recapture in Lake Superior, 1969–1996

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Abstract.—We used data from a long-term Wisconsin Department of Natural Resources mark–recapture study to examine the dynamics of survival in a recovering population of lake trout *Salvelinus namaycush* in western Lake Superior from 1969 to 1996. Survival rates were estimated using the Cormack–Jolly–Seber method, and a series of models were constructed to examine the effect of year, size, sex, and origin (hatchery versus wild) on the survival rates of lake trout captured within the Gull Island Shoal refuge established in 1976. To select among the models, we used Akaike’s information criterion corrected for small sample size and overdispersion. Our estimates of survival rates were adjusted using previously published tag loss rates for the three types of tags used since 1969. Survival estimates for wild fish varied widely among years; the lowest survival rates were observed in 1973 and 1974 and again in 1985 and 1986. Survival rates of wild fish were dependent on sex and size: survival rates for male lake trout were 7% lower on average than those for female fish (means, 0.76 and 0.83), and large-sized fish tended to have higher survival rates. Survival rates of hatchery-reared fish could not be estimated for the entire time period owing to sample-size issues; however, between 1983 and 1996 we found that hatchery fish survival rates were on average about 3% lower than those for wild fish. Survival estimates within the refuge were higher than estimates reported by others for fish outside the refuge and slightly higher than estimates from other Great Lakes studies.

Survival is one of the fundamental factors governing the persistence of populations. In fish populations, estimation of survival rates typically involves either removal methods or tagging methods. Because tagging studies do not require sacrificing animals they are a viable approach to studying survival in populations undergoing recovery. When applied to numerically depressed or protected populations, tag returns from sport or commercial fishers may be few or nonexistent, and recaptures are instead monitored directly by investigators. In the Great Lakes, such an approach has been used to study the recovery of populations of native lake trout *Salvelinus namaycush* that had been severely depressed as a result of overfishing and predation by sea lampreys *Petromyzon marinus* (Cornelius et al. 1995; Elrod et al. 1995; Eshenroder et al. 1995; Hansen et al. 1995; Holey et al. 1995).

The Gull Island Shoal population in southwestern

Lake Superior is one of the few lake trout populations that persisted under the intense mortality imposed by fishing and sea lamprey predation. In the early 1960s, the Gull Island Shoal population was at a record low level of abundance (Swanson and Swedberg 1980). Aggressive fishery management measures were implemented to increase stock size and reduce mortality rates. Mortality rates were reduced as sea lamprey predation rates decreased and as harvest and effort restrictions were placed on commercial and recreational fisheries (Hansen et al. 1995). In addition, the state of Wisconsin established the Gull Island Shoal refuge in early 1976 (Hansen et al. 1995; Schram et al. 1995). This refuge, which is closed to fishing, encompasses a 70,000-ha area along the eastern edge of the Apostle Islands and is used by lake trout as a spawning area (Schram et al. 1995; Figure 1). Because 93% of mature lake trout stay within 40 km of the spawning shoal and return to the same area to spawn (Rahrer 1968), it was believed that the refuge would be effective in decreasing fishing mortality rates on the Gull Island Shoal population. With regulations in place and

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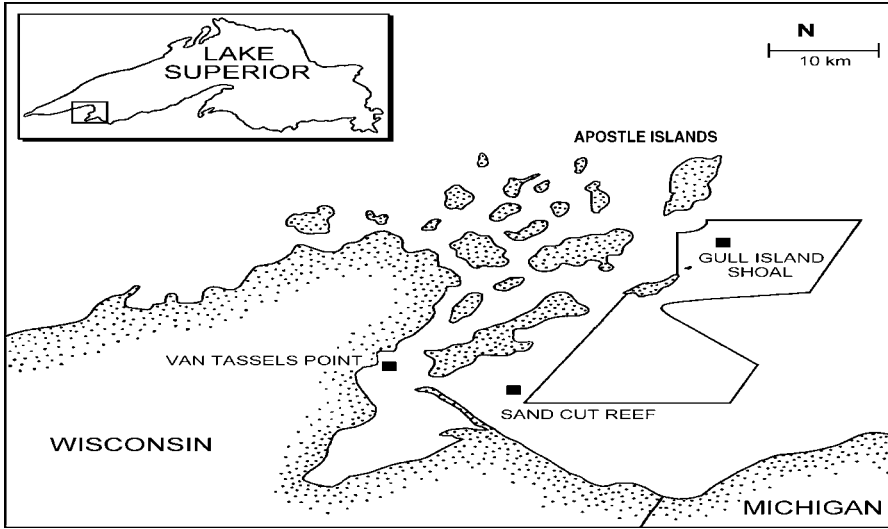


FIGURE 1.—The study area in Lake Superior where adult lake trout were captured from 1969 to 1996. Gill-net sampling sites are indicated by squares; the solid line demarcates the Gull Island Shoal refuge, in which commercial and sportfishing have been prohibited since 1976.

continued stocking of hatchery-raised fish that helped to buffer sea lamprey predation within the Apostle Islands area, the Gull Island Shoal population began to gradually recover (Schram et al. 1995).

Survival rates of adult lake trout at Gull Island Shoal increased during the recovery period, but the dynamics of survival remain unexplored. In addition, factors such as sex, origin of fish (hatchery or wild), and size may have contributed to the variation in survival rates but the effects of these factors are unknown. Male and female fish may experience different survival rates because of possible differences in their availability to the fishery associated with behavioral differences. During the recovery period, the ratio of wild to hatchery fish in the Apostle Islands area changed markedly, such that hatchery lake trout dominated assessment gill-net catches from the late 1960s to the mid-1980s (Hansen et al. 1995). Understanding the role of adult hatchery fish in the recovery process requires knowledge of their survival rates relative to those of wild fish. Survival rates may also vary with size or age of fish and whereas regulations that protect large, mature fish may increase survival rates of the large fish, survival rates of small fish may also be improved if these fish strongly associate with the refuge or with large fish. Thus, a better understanding of the role of sex, origin, and size of fish and how these factors may change through time may lead to insights on the recovery process in long-lived, slow growing fish such as lake trout. Lake trout from this population have been shown to be much older than previously thought (Schram and Fabrizio 1998).

Although age-specific survival rates can be readily estimated with current survival models, we lack sufficient age data from these fish. Instead, we examine size as a proxy. Fabrizio et al. (2001) demonstrated that mature lake trout from Gull Island Shoal continue to grow as they age.

In this paper, we use data from a long-term mark-recapture study to examine the dynamics of survival in a recovering population of lake trout from Lake Superior. We estimate survival rates of adult lake trout captured within the refuge at Gull Island Shoal and investigate the effect of various factors (sex, origin, and size) on survival rates. We use the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965, Seber 1965, 1982) and apply it to mark-recapture data collected annually by the Wisconsin Department of Natural Resources (DNR) between 1969 and 1996. Our estimates are compared with other survival rate estimates available for this population and other lake trout populations in the Great Lakes.

Methods

Field sampling.—Wisconsin DNR biologists captured live adult lake trout from spawning reefs in the Gull Island Shoal area of Lake Superior during the October–November spawning season from 1969 to 1996 (Figure 1). Fish were captured using graded-mesh nylon or monofilament gill nets comprised of six 91-m panels of 114-, 127-, 140-, 152-, 165-, and 178-mm stretch-mesh netting. Beginning in 1986, additional gill nets consisting of 91-m panels of 140- and 152-mm

stretched mesh were used. Nets were set for 24 h and most fish were captured in the vicinity of Gull Island Shoal; the remaining fish were captured at Sand Cut Reef or Van Tassels Point (Figure 1). Fish ranged between 35.6 and 118.1 cm total length (TL). The average size of our tagged fish was around 70 cm and varied little during the study period.

Lake trout not severely injured or killed by the gillnetting process were measured for TL and tagged with individually numbered Floy FD-67, FD-67C, or FD-68BC anchor tags. The FD-67 tag consisted of an anchor and a vinyl tube bearing an identification number and return address. The FD-67C tag was similar but had a shorter tube. The third type of tag, FD-68BC, had a plastic bead on the distal end of the tube to prevent separation of the tube from the nylon anchor. The FD-67 tag was applied to all fish captured between 1969 and 1977; the FD-67C tag was used between 1978 and 1982; all other lake trout received the FD-68BC tag. We determined sex by expression of milt or eggs. If the fish carried a tag we recorded the identification number and usually applied a second anchor tag near the middle and base of the dorsal fin before rerelease.

In fisheries applications tagging trauma may cause lower survival for newly tagged fish. The effects of anchor tags on the survival of mature lake trout have not been studied directly, but we believe that such effects are minor and possibly nonexistent in our study. Anchor tags are routinely used by fishery investigators and fish have been at liberty for many years after tagging.

Mark-recapture data.—Only tag returns from the DNR gill-net sampling were considered in survival analyses. There were totals of 37,319 wild fish and 8,996 hatchery fish used in our analyses. Recaptured fish were rereleased alive except for 493 fish that died on recapture. Some fish were captured multiple times and bore several tags, some as many as six.

Some fish were part of a series of double-tagging experiments and as such received two tags at the time of initial capture (see Fabrizio et al. 1999). The double-tagging experiments were used to estimate tag-shedding rates for each of the three tag types. For FD-67 tags, the tag retention rate estimate for wild fish was 0.8047 (SE = 0.0303) and for hatchery fish it was 0.9355 (SE = 0.0304). For FD-67C tags, the tag retention estimate for wild and hatchery fish was the same 0.7331 (SE = 0.0166), a very low value. For FD-68BC tags, the tag retention estimate for wild and hatchery fish was 0.9259 (SE = 0.0356). Fish that were double tagged in 1973, 1974, 1978, 1979, 1980, 1982, 1984, and 1985 and recaptured subsequently were removed from the data sets used in the survival analyses. This meant that the survival estimates and the tag loss estimates were independent of each other.

Statistical methods.—We used the Cormack–Jolly–Seber (CJS) suite of models and fitted the models using one of the procedures in the software program MARK (White and Burnham 1999). The CJS model (Cormack 1964; Jolly 1965; Seber 1965; Pollock et al. 1990; Williams et al. 2002) considers recaptures of tagged fish only and allows estimation of the apparent survival rate (ϕ_i) and capture probability (p_i). Apparent survival is the complement of the sum of mortality and emigration. For apparent survival rate to be equal to true survival rate (S) there must be no permanent emigration (Pollock et al. 1990). Another assumption is that there is no temporary emigration when fish leave the population and then return. We explore the effect of permanent and temporary emigration on the bias of our survival estimates in the Discussion section. Additional assumptions of the CJS model are as follows:

- (1) Every animal present in the population at sampling time i has an equal probability of capture.
- (2) Survival is equal for every marked animal that is present from one sampling period to the next.
- (3) Tags or marks are not overlooked or lost.
- (4) All animals are released immediately after the sampling period and all sample periods have a short duration (i.e., are instantaneous; Pollock et al. 1990).
- (5) All animals behave independently with respect to survival and capture processes.

Pollock et al. (1990) showed that violation of the equal-catchability assumption owing to inherent heterogeneity in capture probabilities among animals has little effect on survival estimates. Similarly, heterogeneity of survival rates in combination with heterogeneous capture rates can cause small positive or negative biases in survival rates (Pollock et al. 1990). Because all recaptures were processed by Wisconsin DNR personnel, no tags were overlooked upon recapture; however, tag loss can lead to serious underestimation of survival rates by decreasing the effective number of recaptures in the population. Estimation of tag loss rates from double-tagging experiments analyzed in Fabrizio et al. (1999) were used in this study to eliminate bias associated with tag loss. The most recently used FD-68BC tag had the best tag retention rate (93%), but ideally tag loss rates should be even lower than this. Overall, the first four assumptions are reasonable for this study in which fish were sampled during a short sampling period and released in good condition. The fifth assumption may be violated if two or more fish share capture or survival probabilities; this may arise among schooling fish, for example, which would cause overdispersion. In this case, a variance

inflation factor may be estimated to correct for the lack of independence (Burnham and Anderson 2002) and we did this as discussed in the methods.

For wild fish, we analyzed data from all tag types from 1969 to 1995 (FD-67, FD-67C, and FD-68BC) combined. We fitted a suite of models in MARK that allowed for possible year and sex effects on the survival and capture probability parameters. The most general model is a model that has a survival and a capture probability parameter for each year and each sex, and corresponds to the original CJS formulation. In the interests of parsimony (Burnham and Anderson 2002) it is useful to consider models with fewer parameters. One way to do this is simply to make parameters constant over sexes, years or both. The most restrictive model is a model with one survival parameter and one capture probability parameter, which means that survival and capture probability do not vary either by sex or by year. For a particular model parameters are estimated by iterative maximum likelihood methods. As this is a generalized linear model we used a link function and chose the logistic link function, which is recommended for parameters like survival and capture probability that are bounded between 0 and 1. With a logistic link the model is linear on the logit scale.

Additive models are another way to achieve models with fewer parameters. For example, an additive model of sex and year for survival rates defines the logit of the survival probability as a linear additive function of a sex effect and a year effect. Furthermore, a consistent sex difference in survival on the logit scale is assumed across all years. It is also possible to include an additive model for capture probability in a similar way. Detailed model building strategies are provided in the complete online book for MARK software (<http://www.phidot.org/software/mark/docs/book/>) as well as in the help notes (<http://www.warnercnr.colostate.edu/~gwhite/mark/mark.htm>).

We found that an analysis of the hatchery fish alone over all tag types provided extremely imprecise survival estimates owing to small sample sizes and low capture probabilities. Therefore, to potentially improve survival estimates for hatchery fish, we analyzed the joint wild and hatchery fish data set for the FD-68BC tag recapture information (1983–1995). Only the FD-68BC tag data were used because the tag retention rates of the FD-67C tag were low and those for the FD-67 tag differed for wild and hatchery fish (Fabrizio et al. 1999). We hypothesized that an additive model for wild and hatchery-reared fish would allow us to borrow strength from the large wild fish data set to improve the estimates of survival for the hatchery-reared fish. In this case, the logit of survival consists of

a linear component reflecting origin (wild or hatchery) and year. A survival parameter is estimated for each year, but only a single parameter is necessary to distinguish between survival rates for wild and hatchery fish.

We also investigated the influence of size effects on survival and capture probabilities separately by treating size as a continuous linear covariate on the logit scale in our CJS analyses for the data set comprising the wild FD-68BC tagged fish. We used this subset of the data because it had the largest sample sizes and lowest tag loss rates. If we had analyzed the complete data, the estimated regression coefficient of the size covariate would have been biased by different tag loss rates in the different periods.

Because of the large suite of models considered, we used the now-standard model selection approach based on Akaike's information criterion corrected for small sample size (AIC_c) and adjusted for overdispersion (QAIC_c) (Akaike 1973; Burnham and Anderson 2002). The purpose of using AIC was to select one model from a range of alternatives that most adequately described the data with as few parameters as possible so that precision of the resulting estimates would be maintained. Goodness of fit (GOF) tests are not currently possible for the covariate models in MARK; however, we fitted our most general models without covariates and then assessed GOF using the program RELEASE (Burnham et al. 1987), which is accessed from MARK. We obtained a χ^2 test statistic with degrees of freedom (df), and we calculated the variance inflation factor (\hat{c}) using the equation

$$\hat{c} = \chi^2/\text{df}.$$

This is one approach suggested by White and Burnham (1999) and Burnham and Anderson (2002). We suspected overdispersion might be present in our data sets because schooling behavior in lake trout could violate the independence assumption. We found that \hat{c} was about 1.5 for all our different wild fish data sets and for consistency, used that value for all QAIC_c calculations including those involving the hatchery fish.

We obtained adjusted estimates of survival rates ($\hat{\phi}_i^*$) using the standard equation (Pollock et al. 1990:52) with $\hat{\phi}_i^* = \hat{\phi}_i/\hat{\theta}$, where $\hat{\theta}$ is the appropriate estimate of tag retention on a yearly basis, and $\hat{\phi}_i$ is the estimate of survival rate from the CJS model.

Based on the delta method (Seber 1982:7), the variance of the estimate is given by

$$\text{Var}(\hat{\phi}_i^*) \cong (\hat{\phi}_i^*)^2 \left[\frac{\text{Var}(\hat{\phi}_i^*)}{\hat{\phi}_i^2} + \frac{\text{Var}(\hat{\theta})}{\hat{\theta}^2} \right],$$

provided that the tag retention rate and the survival rate

TABLE 1.—Values of the Akaike information criterion adjusted for small sample size and overdispersion (QAIC_c; the overdispersion parameter = 1.5) used to selection the best of 18 candidate models of wild lake trout survival in Lake Superior, 1969–1996 (see text for details). A period indicates that the parameters are constant over that attribute; multiplication symbols denote full models, plus signs additive models. The best model (lowest QAIC_c value) is presented first; the values in the third column are the differences between QAIC_c values of the individual models and that of the best model.

Model	QAIC _c	ΔQAIC _c	Model weight	Number of parameters
φ(sex + year), p(sex + year)	22,924.854	0.00	0.992	56
φ(year), p(sex + year)	22,934.394	9.54	0.008	55
φ(year), p(sex × year)	22,953.324	28.47	0.000	81
φ(sex × year), p(sex × year)	22,977.829	52.98	0.000	108
φ(sex), p(sex × year)	23,049.731	124.88	0.000	56
φ(.), p(sex × year)	23,064.013	139.16	0.000	55
φ(year), p(sex)	23,107.040	182.19	0.000	29
φ(sex × year), p(year)	23,126.358	201.50	0.000	81
φ(sex × year), p(sex)	23,126.607	201.75	0.000	56
φ(sex), p(year)	23,209.043	284.19	0.000	29
φ(year), p(year)	23,216.195	291.34	0.000	54
φ(sex × year), p(.)	23,299.578	374.72	0.000	55
φ(.), p(year)	23,315.503	390.65	0.000	28
φ(sex), p(sex)	23,352.242	427.39	0.000	4
φ(.), p(sex)	23,363.860	439.01	0.000	3
φ(year), p(.)	23,390.225	465.37	0.000	28
φ(sex), p(.)	23,523.318	598.46	0.000	3
φ(.), p(.)	23,628.707	703.85	0.000	2

estimates are independent. Here independence of the estimates is guaranteed because we used separate data sets to calculate them.

Results

Wild Fish Survival Analyses

For wild fish, we present results for the full data set containing information for all tag types (1969–1996). According to the QAIC_c values, the additive model of sex and year effects (φ[sex + year], p[sex + year]) was the best model (Table 1). The adjusted survival estimates from this model (Table 2) varied from year to year (male from 0.44 to 1.00, female from 0.54 to 1.00). However, the estimates tend to be higher for later years, and female survival rates were higher than those of male fish in general (mean male survival = 0.76, SE = 0.0322; mean female survival = 0.83, SE = 0.0271). Smoothed annual survival estimates depict the decrease in survival rates in the period before the refuge was established (1969–75) and the increase that occurred thereafter (Figure 2). Survival rates of lake trout during the postrefuge period tended to be higher, but fluctuated with a notable decrease in the mid-1980s (1985–1986; Table 2).

Hatchery-Reared Fish Survival Analyses

Survival rates of hatchery-reared lake trout were estimated from the combined wild and hatchery fish data set for tag type FD-68BC. The model selection results are summarized in Table 3; according to the QAIC_c criterion, the additive model of origin (wild or

hatchery) and year for survival probability φ(origin + year) and recapture probability p(origin + year) was the best model. Survival estimates based on this model varied annually with wild fish having 3% higher survival rates than hatchery fish (Table 4). Models where wild and hatchery fish had equal survival and equal capture probabilities had fewer parameters but much poorer fits to the data based on the AIC and, therefore, should not be used.

Modeling the Influence of Individual Fish Size on Survival

We used the FD-68BC tag recapture information for wild fish to examine the effect of size on survival because tag loss rates are low for this tag type and using one tag type eliminated confounding caused by different tag loss rates. We constructed several models with a linear logistic size effect and, as before, the AIC_c values of these models were also adjusted using $\hat{c} = 1.5$. According to the QAIC_c criterion, the best model has an additive effect of sex, year, and size (φ[sex + year + size], p[sex + year + size]). These results suggest a positive relationship between survival and size and no sex differences in this relationship; that is, for both male and female fish, survival increases as size increases and female survival rates are higher than those of males (Table 5). However, an additive model with an interaction term for sex and size was the second best model (φ[sex + year + sex × size], p[sex + year + sex × size]). This model with the interaction term indicated the effect of size on male survival rate was

TABLE 2.—Yearly estimates of survival rates and SEs for wild male and female lake trout from a version of the Cormack—Jolly—Seber model ($\hat{\phi}$) and that model adjusted for tag retention ($\hat{\phi}^*$). Here survival and capture probability have an additive sex and year effect structure.

Year	Male				Female			
	$\hat{\phi}$	SE	$\hat{\phi}^*$	SE	$\hat{\phi}$	SE	$\hat{\phi}^*$	SE
1969	1.0000	0.0000	1.0000	0.0377	1.0000	0.0000	1.0000	0.0377
1970	0.6988	0.1829	0.8684	0.2296	0.7625	0.1577	0.9474	0.1992
1971	0.3819	0.1009	0.4745	0.1266	0.4608	0.1086	0.5726	0.1367
1972	0.5798	0.1428	0.7205	0.1795	0.6562	0.1333	0.8155	0.1685
1973	0.3541	0.0778	0.4400	0.0981	0.4313	0.0854	0.5360	0.1080
1974	0.4096	0.0689	0.5090	0.0877	0.4898	0.0752	0.6086	0.0963
1975	0.6250	0.1030	0.7766	0.1313	0.6974	0.0943	0.8667	0.1216
1976	0.6561	0.0929	0.8153	0.1195	0.7252	0.0828	0.9012	0.1084
1977	0.5504	0.0890	0.6839	0.1135	0.6287	0.0867	0.7813	0.1117
1978	0.6038	0.1054	0.8237	0.1450	0.6783	0.0978	0.9253	0.1350
1979	0.9879	0.1553	1.0000	0.1588	0.9912	0.1130	1.0000	0.1163
1980	0.5278	0.0733	0.7199	0.1013	0.6072	0.0734	0.8284	0.1019
1981	1.0000	0.0008	1.0000	0.0227	1.0000	0.0006	1.0000	0.0227
1982	0.5478	0.0529	0.7473	0.0741	0.6263	0.0545	0.8543	0.0768
1983	0.8426	0.1034	0.9100	0.1171	0.8810	0.0819	0.9515	0.0957
1984	0.9218	0.1271	0.9955	0.1425	0.9422	0.0958	1.0000	0.1087
1985	0.5281	0.0686	0.5703	0.0773	0.6075	0.0694	0.6561	0.0791
1986	0.5211	0.0674	0.5628	0.0760	0.6009	0.0683	0.6489	0.0778
1987	0.6885	0.0804	0.7436	0.0914	0.7535	0.0712	0.8138	0.0830
1988	0.6850	0.0652	0.7398	0.0760	0.7505	0.0599	0.8106	0.0718
1989	0.9000	0.0957	0.9720	0.1099	0.9257	0.0731	0.9997	0.0879
1990	0.7806	0.0993	0.8431	0.1121	0.8312	0.0827	0.8977	0.0958
1991	0.5788	0.0750	0.6251	0.0845	0.6553	0.0730	0.7077	0.0834
1992	0.7295	0.1075	0.7878	0.1200	0.7886	0.0907	0.8517	0.1033
1993	0.7336	0.1576	0.7923	0.1729	0.7921	0.1349	0.8555	0.1494
1994	0.6738	0.2112	0.7277	0.2298	0.7407	0.1857	0.8000	0.2029
Mean	0.6733	0.0362	0.7634	0.0322	0.7317	0.0314	0.8319	0.0271

positive; however, the size effect on female survival rate was negative suggesting a decrease in female survival rate as size increases. We note that because we observed small numbers of female fish, model selection was equivocal in this case. Additional survival studies with a large-size range of female fish may clarify this relationship.

Discussion

Emigration

We believe that only a small percentage of fish emigrate permanently (S.T.S., unpublished data), which translates into only a negligible negative bias in the survival estimates. Natural movement patterns of tagged animals can lead to temporary emigration when an animal enters and leaves the study site repeatedly. Temporary emigration may occur in some fisheries studies (Potak-Zehfuss et al. 1999), including ours, because some fish may not spawn every year or at the same site every year. Unfortunately, we were unable to determine what proportion of the spawning population failed to return to the spawning area every year. In laboratory experiments Henderson and Wong (1998) found the proportion of lake trout spawning varied from about one third to one depending on food rations. In field studies, others have demonstrated strong

spawning site fidelity for wild lake trout at Gull Island Shoal (Rahrer 1968; Swanson 1973; Krueger et al. 1986) and in other areas of Lake Superior (Eschmeyer 1955; Ebener 1990). Also, the mean distance moved by tagged lake trout during the spawning season in the Apostle Islands was greater for non-spawning-season recaptures (44.28 km) than for spawning-season recaptures (9.46 km) (Kapusinski et al. 2005). For hatchery fish, the evidence is mixed; Rybicki (1990) estimated that only 12–15% of lake trout planted in a

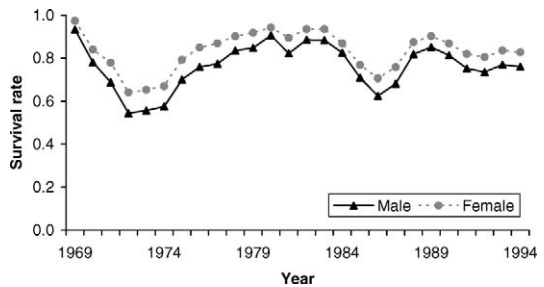


FIGURE 2.—Plots of smoothed estimates (3-year moving averages) of the survival rates for male and female wild lake trout based on the additive model with sex and year (see Table 2 for annual estimates).

TABLE 3.—Values of the Akaike information criterion adjusted for small sample size and overdispersion (QAIC_c) used to select the best of 18 models of lake trout survival based on the FD-68BC tag–recapture information (1983–1995). Origin is wild or hatchery. (See Table 1 for more details.)

Model	QAIC _c	ΔQAIC _c	Model weight	Number of parameters
φ(origin + year), p(origin + year)	15,785.665	0.00	0.976	28
φ(year), p(origin)	15,793.112	7.45	0.024	15
φ(year), p(origin × year)	15,801.385	15.72	0.000	39
φ(origin × year), p(year)	15,805.301	19.64	0.000	39
φ(origin + year), p(origin × year)	15,809.724	24.06	0.000	40
φ(origin × year), p(origin)	15,809.851	24.19	0.000	28
φ(year), p(year)	15,810.291	24.63	0.000	26
φ(origin × year), p(.)	15,812.458	26.79	0.000	27
φ(origin), p(year)	15,814.348	28.68	0.000	15
φ(origin × year), p(origin × year)	15,816.473	30.81	0.000	52
φ(year), p(.)	15,817.903	32.24	0.000	14
φ(origin), p(origin × year)	15,827.021	41.36	0.000	28
φ(.), p(origin × year)	15,827.960	42.29	0.000	27
φ(.), p(year)	15,839.437	53.77	0.000	14
φ(origin), p(origin)	15,923.209	137.54	0.000	4
φ(.), p(origin)	15,923.339	137.67	0.000	3
φ(origin), p(.)	15,924.693	139.03	0.000	3
φ(.), p(.)	15,946.952	161.29	0.000	2

refuge in northern Lake Michigan strayed to sites outside the refuge, but Swanson (1973) stated that hatchery-reared lake trout released in Wisconsin waters did not exhibit homing to known spawning reefs.

We suspect that temporary emigration is not important for the Gull Island Shoal population of lake trout. Random temporary emigration causes no bias in survival rate estimates (Kendall et al. 1997). However, if temporary emigration is modeled as a Markovian process (i.e., the probability of being a temporary emigrant at the *i*th occasion depends on whether the fish was a temporary emigrant on the [*i* – 1]th occasion), such emigration may contribute small biases in survival rate estimates. Numerical calculations with simulated mark–recapture data have shown that the

positive bias in survival rate estimates is only about 4% when 30% of the spawning population fails to spawn at Gull Island Shoal in consecutive years (J.Y. and K.H.P., unpublished data).

Dynamics of Survival at Gull Island Shoal

Our wild fish survival rate estimates varied widely among years and between the sexes, males having on average about a 7-percentage-point lower survival rate than females (0.76 versus 0.83). Our rates are perhaps more variable than those reported for lake trout populations in small Canadian lakes observed for 9–24 years (Mills et al. 2002), but our study encompassed a population from a large lake that had been subject to overfishing and sea lamprey predation. Some of the

TABLE 4.—Estimates of survival rates and SEs for wild and hatchery lake trout from a version of the Cormack—Jolly—Seber model ($\hat{\phi}$) and that model adjusted for tag retention ($\hat{\phi}^*$). Here survival and capture probability have an additive origin and year effect structure.

Year	Wild				Hatchery			
	$\hat{\phi}$	SE	$\hat{\phi}^*$	SE	$\hat{\phi}$	SE	$\hat{\phi}^*$	SE
1983	0.7870	0.0783	0.8500	0.0907	0.7548	0.0905	0.8152	0.1027
1984	1.0000	0.0001	1.0000	0.0385	1.0000	0.0001	1.0000	0.0385
1985	0.5259	0.0602	0.5680	0.0686	0.4803	0.0661	0.5187	0.0741
1986	0.5387	0.0655	0.5818	0.0742	0.4931	0.0723	0.5326	0.0807
1987	0.6771	0.0744	0.7312	0.0852	0.6359	0.0827	0.6868	0.0931
1988	0.6152	0.0559	0.6645	0.0655	0.5712	0.0648	0.6169	0.0739
1989	0.9394	0.0938	1.0000	0.1070	0.9281	0.1106	1.0000	0.1253
1990	0.7695	0.0923	0.8311	0.1047	0.7355	0.1024	0.7944	0.1147
1991	0.5341	0.0650	0.5769	0.0736	0.4885	0.0736	0.5276	0.0821
1992	0.8347	0.1179	0.9015	0.1319	0.8079	0.1337	0.8726	0.1483
1993	0.7151	0.1448	0.7724	0.1591	0.6765	0.1575	0.7306	0.1724
1994	0.7168	0.2204	0.7741	0.2399	0.6783	0.2344	0.7326	0.2548
Mean	0.7211	0.0448	0.7709	0.0443	0.6875	0.0487	0.7357	0.0490

TABLE 5.—Survival estimates as a function of size for male and female wild lake trout from 1983 to 1996 using a model in which survival and capture probability have an additive sex, year, and size effect structure.

Size (cm)	Male	Female
50	0.6922	0.7814
60	0.7482	0.8292
70	0.7994	0.8714
80	0.8452	0.9079
90	0.8853	0.9391
100	0.9199	0.9654

variation among years is probably explained by high sea lamprey mortality during the mid-1980s (Linton 2002). Schram (unpublished data) estimated survival based on a catch-curve approach of 0.87 for males and 0.79 for females from 1993 to 1996; these rates are similar to our estimates based on the capture–recapture approach.

Survival estimates for hatchery lake trout were, on average, about 3 percentage points lower than those for wild fish during the period 1983–1996; in addition, the selection of an additive model to account for these differences indicated that survival rates were consistently lower from year to year in hatchery fish. These results imply that survival of both hatchery and wild fish responds in the same manner to yearly variations in abiotic or biotic factors. Alternatively, these results may have been obtained if permanent emigration is more likely to occur for hatchery fish than for wild fish. However, such a difference in permanent emigration rates would need to be maintained annually. Krueger et al. (1986) found that hatchery-reared lake trout released along the shoreline and at offshore locations did not return in sufficient numbers to reestablish spawning populations. Also, Swanson (1973) found 38% of hatchery-reared lake trout leaving Wisconsin waters and moving eastward into Michigan waters. Additional hypotheses include possible behavioral differences between hatchery and wild fish leading to an increased tendency for hatchery fish to be more susceptible to fishing or sea lamprey mortality. Hansen et al. (1994) concluded that declining abundance of stocked lake trout in U.S. waters of Lake Superior resulted from increased mortality, which may have been caused by competition, predation, or by a combination of these and other factors.

Our estimates of mean survival rates for wild and hatchery fish (wild, 0.72; hatchery, 0.69) between 1983 and 1994 are comparable to those reported elsewhere for western Lake Superior. Linton (2002) estimated survival of lake trout between 1980 and 2001 at 0.636–0.744 for wild fish and 0.566–0.72 for hatchery-reared fish. Both our study and Linton's (2002) investigation

reported lower survival rates among hatchery fish relative to wild fish. This apparent difference in survival rates was observed regardless of where the fish were captured (in Linton's [2002] study, lake trout were captured outside the Gull Island Shoal refuge). Krueger et al. (1986) estimated survival rates of 0.45 and 0.35 for wild and hatchery lake trout, respectively, from outside the refuge during spring, 1970–1980. The estimates of Krueger et al. (1986) imply a much larger survival differential between wild and hatchery fish and much lower survival rates, but their study occurred just after the period of lowest abundance of lake trout in the Great Lakes.

The survival estimates from hatchery fish in our study (mean = 0.69) are similar to, but slightly higher than, those reported for adult lake trout populations from northern Lake Michigan (fall tagged fish, 0.67; spring tagged fish, 0.53–0.88; Fabrizio et al. 1997), Six Fathom Bank in Lake Huron (0.52–0.38; Madenjian et al. 2004), and southern Lake Huron (0.61 based on $Z = 0.49$ from Figure 7 in Sitar et al. 1999). All three populations consisted only of hatchery-reared fish, which may have been subjected to higher sea lamprey or fishing mortality rates than were lake trout at Gull Island Shoal.

Wild fish survival rate was dependent on sex and size. The best model indicated both sexes experienced an additive increase in survival with growth, but a model with almost equally good fit suggested that the size-dependence relationship took a different form for each sex. Under this model survival increased as size increased for males, whereas for females survival decreased as size increased. Although sample size for female fish is insufficient to clearly distinguish the better of the two models these results suggest interesting biological hypotheses to consider. Perhaps for females there is some survival penalty to increased size, whereas for males there is not. Alternative hypotheses include large males being more associated with the refuge than small males, and large females being less associated with the refuge than small females.

The possible influence of the refuge on our survival estimates is difficult to assess because this was an observational study and not an experiment. Changes attributable to the refuge are confounded with temporal changes resulting from other extrinsic factors, such as competition or changes in mortality rates. Nevertheless, comparison of the mean survival estimates before (1969–1975) and after (1976–1996) establishment of the refuge (0.70 [SE, 0.08] and 0.80 [SE, 0.03]) suggests that survival was higher after the refuge was established. Further, our survival estimates for fish inside the refuge were higher than those for fish outside

the refuge reported by others (Krueger et al. 1986; Linton 2002). The positive and immediate effects of the fish refuge were demonstrated by an increase in the abundance of wild females after 1976 and the subsequent increase in progeny in 1977 (Schram et al. 1995). The establishment of a refuge was a contributing factor in the recovery of another lake trout population in the Parry Sound area of Lake Huron (Reid et al. 2001).

Future Research

We recommend continuation of double tagging lake trout so that tag loss can be estimated directly and methods to reduce tag loss can be explored. Telemetry tags in combination with tag–recapture methods can give rise to large gains in precision (Nasution et al. 2001; Pollock et al. 2004) as well as other important information such as the tendency of fish to permanently or temporarily emigrate. Use of the robust design (Pollock 1982; Kendall et al. 1997; Kendall and Bjorkland 2001) to examine the assumption of no temporary emigration also would be valuable. The robust design combines closed and open tag–recapture models in one analysis. Unfortunately, it could not be used here as we did not have multiple capture periods within a year. We recommend that this approach be explored in future studies on lake trout and other species.

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