Dynamics of Individual Growth in a Recovering Population of Lake Trout (*Salvelinus namaycush*)

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Abstract

In 1976 the Wisconsin Department of Natural Resources established a refuge for a nearly depleted population of lake trout (*Salvelinus namaycush*) at Gull Island Shoal, Lake Superior. The refuge was intended to reduce fishing mortality by protecting adult lake trout. We examined the growth dynamics of these lake trout during the period of recovery by comparing estimates of individual growth before and after the refuge was established. Our estimates are based on an annual mark-recapture survey conducted at the Gull Island Shoal spawning area since 1969. We developed a model that allowed mean growth rates to differ among individuals of different sizes and that accommodated variation in growth rates of individuals of the same size. Likelihood-ratio tests were used to determine if the mean growth increments of lake trout changed after the refuge was established. Our results suggest that growth of mature lake trout (particularly wild fish) decreased significantly in the post-refuge period. This decreased growth may have been associated with a reduction in food availability. We also observed reductions in growth as wild fish grew older and larger, which suggests that the growth of these fish may be adequately approximated by a von Bertalanffy growth model if it becomes possible to obtain accurate ages.

Introduction

Rehabilitation of depleted fish stocks has received widespread attention and motivated research on fish population and community dynamics in the Laurentian Great Lakes. At the species level, rehabilitation typically involves reduction of mortality rates to permit populations to increase in size and ultimately to be self-sustaining. Rehabilitation goals for fish species may sometimes aim to increase population size to support commercial or sport fisheries of a certain magnitude. Rehabilitation goals for the lake trout (*Salvelinus namaycush*), a native fish in the Great Lakes, include such objectives (Hansen 1996).

In the last century, lake trout populations throughout the Great Lakes have undergone extreme fluctuations in abundance, due in part to overfishing and sea lamprey (*Petromyzon marinus*) predation (e.g., Hansen et al. 1995). Such changes resulted in economic loss to the commercial fishery, decreases in genetic diversity, loss of stocks, and generally contributed to unstable trophic conditions in the lakes. One of the few lake trout populations in the Great Lakes to withstand such intense mortality rates was the Gull Island Shoal population in southwestern Lake Superior. Lake trout abundance at Gull Island Shoal was at an all-time low in the early 1960s (Swanson and Swedberg 1980), but the population responded positively to aggressive fishery management measures that increased stock size and reduced mortality rates. Since the early 1960s, stock density of lake trout in Lake Superior was increased through supplemental stocking of hatchery-reared fish, and mortality rates were reduced by controlling sea lamprey predation, placing harvest and effort restrictions on commercial and recreational fisheries, and creating two refuges in Wisconsin waters (Hansen et al. 1995).

The Gull Island Shoal refuge, which encompasses a 70 000 ha area near Gull and Michigan Islands (Figure 1), was established in early 1976 in response to increasing fishing pressure from sport and commercial fishers (Schram et al. 1995). Fishing within the refuge was prohibited. Changes in fishing mortality rates due to the refuge were expected to affect the lake trout population at Gull Island Shoal because many mature fish stay within 40 km of

the refuge and return to the same area to spawn (Rahrer 1968). Marked hatchery-reared fish that were observed up to nine years at liberty exhibited similar movement patterns and tendencies (Pycha et al. 1965).

At Gull Island Shoal, the ratio of wild to hatchery fish changed dramatically through time. In the late 1960s, hatchery fish composed a significant portion of the population (Hansen et al. 1995; Swanson and Swedberg 1980) whereas now, most of the population comprises wild fish (Hansen et al. 1995). Throughout Lake Superior, growth rates of hatchery and wild lake trout were found to differ (Negus 1995; Hansen 1994). If these differences are significant, temporal changes in the proportion of hatchery-raised lake trout may confound any attempt to assess changes in growth over time. To be conservative, we assess the dynamics of growth of these two subpopulations of lake trout separately.

Here we investigate the effects of the Gull Island Shoal refuge on growth rates of lake trout by comparing estimates of growth before the refuge was established with estimates of growth during the period of recovery (i.e., after the refuge was established). We examine the growth dynamics of hatchery and wild fish separately to avoid the potentially confounding effects of changes in stock composition. Our estimates of growth are based on mark-recapture studies of lake trout conducted annually since 1969 at Gull Island Shoal. These lake trout include wild and hatchery fish but may be considered members of a unit stock because we examined only individuals that returned to the spawning site.

Materials and Methods

Mark-recapture

A detailed description of the study area (Gull Island Shoal, Lake Superior) and the mark-recapture survey are given in Schram et al. (1995) and Fabrizio et al. (1996). Briefly, lake trout were captured annually with gillnets set on the spawning reef during the spawning

season (October–November) from 1969 to 1996 (Figure 1). The graded-mesh gillnets (114–178 mm stretch mesh, either nylon or monofilament), which were deployed by personnel from the Wisconsin Department of Natural Resources (DNR), were intended to capture primarily large mature lake trout. Live fish in good condition were measured and tagged with individually numbered anchor tags (Floy tags FD-67, FD-67C, FD-68BC, or FD-94). We used the presence or absence of fin clips to indicate origin of the fish: hatchery fish were fin clipped before stocking in Lake Superior. All recaptures were monitored by DNR personnel; recaptured fish in good condition were re-released after re-tagging. We did not use tag-return information from tribal, commercial, or sport fishers because of uncertainties in reporting (e.g., date of capture, tag number, length measurement) and unknown reporting rates.

In addition to the presence of fin clips, the mark-recapture data included information about dates of initial capture and recapture, initial fish length, fish length at each recapture, and origin of fish (wild or hatchery). Data were examined for the presence of outliers, and observations containing recording or data-entry errors that could not be corrected by consulting field sheets were omitted from further consideration. However, fish that exhibited unusual growth, including apparent shrinkage, were retained in our statistical analysis as their validity could not be ruled out objectively (apparent shrinkage of at least 1 cm was evident in only 1.9% of all observations).

Of the 56 489 lake trout tagged in our sampling efforts, 5 729 fish were recaptured at Gull Island Shoal at least once (Table 1). Growth of lake trout during the pre-refuge period was estimated from observations on 388 fish tagged between 1969 and 1974 and recaptured between 1970 and 1975. Although some of the fish tagged in 1969–1974 were recaptured after 1975, those recapture observations were not considered in our analysis because growth of fish after 1975 was assumed to reflect post-refuge conditions. Growth of lake trout during the post-refuge period was estimated from 5 341 fish tagged in 1975–1995 and recaptured between 1976 and 1996. Some of the fish in our study (pre- and post-refuge periods) were

first captured and recaptured in the same year (i.e., time at liberty < 1 month). In our analysis, we considered the average of these two observations (which usually differed by less than 1 cm) as the size at first capture.

Statistical analysis

Growth rates of fish are commonly estimated by specifying the conditional mean size of an individual as a function of its age or, in the case of marked populations, its time at liberty. In a well-known example of this approach (the von Bertalanffy (VB) growth model), two parameters (the Brody coefficient k and the maximum size L_∞) specify a progressive reduction in growth rate as fish grow older and larger (Fabens 1965).

The VB model is useful in many settings, but it is unlikely to provide an adequate approximation of the sizes of lake trout observed in our study. Our sampling methods were devised to capture primarily large, mature fishes and are not representative of all ages of lake trout in the population. Consequently, estimates of k and L_∞ cannot be interpreted as population averages (applicable to all ages of fish) without potentially falling prey to errors of extrapolation, which are well known in this setting (Knight 1968). Furthermore, the information we have on the growth of each individual is limited to a few observations (typically 1–3 recaptures per fish), and we are concerned that these would be inadequate for computing accurate estimates of the parameters of a VB model modified to include variation in growth of individual fishes (Sainsbury 1980). Our concerns are based, in part, on the mixed success of published analyses of growth data simulated under assumed levels of variation (and correlation) in k and L_∞ among individuals of a marked population (Hampton 1991; Palmer et al. 1991). When the size of an individual is observed only a few times during its lifetime, these studies, as well as our own simulation work, have revealed various difficulties in computing accurate and reliable estimates of VB growth parameters . For example, Hampton (1991) and Palmer et al. (1991) simulated the body sizes of a population of marked animals at the time of release and at the time of a single recapture using assumed

average values of k and L_∞ and assumed levels of individual variation (and covariation) in these parameters. Palmer et al. (1991) estimated k and L_∞ for a single set of simulated data (see Table 6). Their estimates were actually further from the true parameter values than estimates based on Fabens (1965) method, which can produce biased estimates even in large samples (James 1991). Although Palmer et al. (1991) noted the disparity in their estimates, neither the relative frequency of their unsatisfactory results nor the average performance of their estimator can be assessed without conducting additional simulations (and analyses) of data. In a similar but more thorough study, Hampton (1991) showed that average values of k and L_∞ could be estimated reasonably well but levels of individual variation in these parameters were biased and imprecise (see Tables 4 and 5).

Twenty years have elapsed since Sainsbury (1980) demonstrated the dramatic effects that individual variation in growth can have on estimates of average VB growth parameters, yet few investigators have responded to his recommendation that "a topic urgently in need of examination is the form of the joint distribution of k and L_∞ in animal populations." Several methods have been developed for estimating average VB parameters when maximum size (L_∞), but not k, is assumed to vary among individuals in a population (e.g., James 1991; Wang et al. 1995). Sainsbury (1980) noted that this assumption seemed reasonable for many fish species but in other species of fish and in other animals variation in k was also important (e.g., see Xiao 1994). Furthermore, it is not difficult to imagine growth histories that imply a positive correlation between k and L_∞ (e.g., suppose animals that grow faster early in life also tend to achieve larger maximum sizes). In the absence of prior information about differences in growth of individuals, we argue (as did Sainsbury (1980)) that a VB model should include parameters for individual variation (and covariation) in *both* k and L_∞. Fitting the sizes of recaptured animals to less complex VB models can yield biased or overly precise estimates of a population's average growth curve.

Estimation of individual growth increments

As an alternative to models based on the VB growth function, we estimate growth of lake trout using a relatively simple approach that allows the mean growth rate to differ among animals of different sizes. Our approach also accommodates variation in growth among individuals of the same size. The lake trout encountered in our capture-recapture survey were observed at approximately the same time each year; therefore, we develop the following model of the observable sizes of each fish in the year of capture and in each subsequent year when a fish may have been recaptured.

Let Y_j denote a random variable for the size of a fish after j years at liberty. The growth history of an individual fish is represented in the sequence $Y_0, Y_1, \ldots, Y_p$, which we summarize by the vector Y. In our capture-recapture samples an observed value of Y, say y, was generally incomplete because each fish may have been seen only a few times during its p years at large. However, since the size at first capture was measured for every fish, we can represent the observable sizes of any individual as $y = (y_{obs}, y_{mis})'$, where y_{obs} corresponds to the sizes that were actually observed on one or more sampling occasions and y_{mis} corresponds to the sizes that were missing (i.e., unobserved) because the fish was not recaptured in those years.

We estimate growth increments of individuals by modeling the observable growth histories of lake trout whose sizes at first capture were approximately equal. The discretization of sizes at first capture into categories is necessary because the incremental growth of an individual during its time at liberty may depend, in part, on its initial size. We assume that the observable sizes of these lake trout in each of their p years at liberty are normally distributed: $Y \sim N(\mu, \Sigma)$, where μ is a $(p+1)$-dimensional vector of mean sizes and Σ is a $(p+1)\times(p+1)$ matrix of variances and covariances. We deliberately place no restrictions on μ or Σ so that the pattern of growth is fully determined by the data, not by a functional relationship between each element of μ and its corresponding time at liberty (i.e., the VB approach). We

also leave the form of Σ unspecified, which allows the variation in growth among fishes to change with time at large instead of remaining constant. The latter restriction is common in models of repeated measures that assume compound symmetry for Σ (Searle et al. 1992).

We define a p-dimensional vector of individual growth increments, Q, in terms of the parameters of our model:

$$Q = (\mu_1 - \mu_0, \ldots, \mu_p - \mu_0)'.$$

To estimate Q (and Σ, of course), we assume that the observable growth histories of different fishes are independent and that the probability of observing of an individual during each attempted recapture does not depend on the unobserved sizes in y_{mis}. The latter condition, which is equivalent to the missing-at-random assumption commonly entertained in analyses of incomplete data (Little and Rubin 1987; Schafer 1997), ensures that the mechanisms responsible for creating y_{mis} may be safely ignored (i.e., not explicitly modeled) without compromising estimates or inferences about the model parameters (μ and Σ) or Q.

Let (Y_{obs}, Y_{mis}) denote a $n \times (p+1)$ matrix of the observable growth histories of n lake trout from the same size category (i.e., their sizes at first capture were approximately equal). Except in the particular case of $p = 1$, the likelihood of our model's parameters given the observed data, $L(\mu, \Sigma | Y_{obs})$, cannot be factored into a product of independent, complete-data likelihoods, whose parameters are distinct subsets of μ and Σ (Schafer 1997, p. 16). Therefore, it is generally infeasible to compute estimates of model parameters by directly maximizing $L(\mu, \Sigma | Y_{obs})$. Indirect methods, such as the expectation-maximization algorithm or stochastic sampling (specifically, data augmentation), must be used to compute meaningful summaries of the observed-data likelihood (Schafer 1997, sections 5.3 and 5.4).

In our analysis of the sizes of recaptured lake trout, we used the expectation-maximization algorithm to compute maximum-likelihood estimates of μ and Σ. These estimates provided

starting values for data augmentation, which yields a sample of size m from the joint posterior distribution of model parameters and missing data, $p(\mu, \Sigma, Y_{mis}|Y_{obs})$ (see Appendix for computational details). An unbiased estimate of $E(Q|Y_{obs})$ may be computed using the values of μ in the simulated sample:

$$\tilde{Q} = \frac{1}{m}\sum_{t=1}^{m} Q^{(t)}$$

where $Q^{(t)} = (\mu_1^{(t)} - \mu_0^{(t)}, \ldots, \mu_p^{(t)} - \mu_0^{(t)})'$ denotes the vector of mean growth increments in the t^{th} draw of the simulated sample. However, the posterior draws of Y_{mis} also can be used to compute a Rao-Blackwellized estimate of $E(Q|Y_{obs})$ that has equal or smaller variance than $\tilde{Q}$ and is also unbiased (Schafer 1997, p. 98–100). Therefore, we computed the Rao-Blackwellized estimate as follows:

$$\begin{aligned} \bar{Q} &= \frac{1}{m}\sum_{t=1}^{m} E(Q|Y_{obs}, Y_{mis}^{(t)}) \\ &= \frac{1}{m}\sum_{t=1}^{m} \hat{Q}^{(t)} \end{aligned} \tag{1.1}$$

where $\hat{Q}^{(t)} = (\bar{y}_1^{(t)} - \bar{y}_0, \ldots, \bar{y}_p^{(t)} - \bar{y}_0)'$ and $\bar{y}_j^{(t)}$ = the mean size of fishes recaptured in year j. Note that $\bar{y}_j^{(t)}$ is based on the observed sizes of fish that were recaptured in year j *and* on the imputed sizes of fish that were at large, but not seen, in year j.

To compute confidence intervals for Q, we require an estimate of the $p \times p$ covariance matrix of $\bar{Q}$. Using results of probability theory for calculating unconditional variances from conditional expectations, Rubin (1987, chapter 3) showed that an estimate of the covariance matrix of $\bar{Q}$ depends on the average of the conditional covariance matrices estimated for each of the m sets of complete data $(Y_{obs}, Y_{mis}^{(t)})$ and on the variation among the m complete-data posterior means, $\hat{Q}^{(t)}$. Specifically, an estimate of the total covariance matrix is

$$T = \bar{U} + (1 + m^{-1})B \tag{1.2}$$

where the average of the within-imputation conditional variance matrices is

$$\begin{aligned} \bar{U} &= \frac{1}{m}\sum_{t=1}^{m} V(Q|Y_{obs}, Y_{mis}^{(t)}) \\ &= \frac{1}{m\,n}\sum_{t=1}^{m}(-1_p,\, \mathrm{I}_p)\, S^{(t)}\, (-1_p,\, \mathrm{I}_p)' \end{aligned} \tag{1.3}$$

and the variation among complete-data posterior means is

$$B = \frac{1}{(m-1)}\sum_{t=1}^{m}(\hat{Q}^{(t)} - \bar{Q})\,(\hat{Q}^{(t)} - \bar{Q})'. \tag{1.4}$$

In equation (1.3) 1_p is a p-dimensional vector of ones, I_p is a $p \times p$ identity matrix, and $S^{(t)}$ is the sample covariance matrix of the observed and imputed sizes of fish in the tth draw of the simulated posterior distribution of Y_{mis}. We use equations (1.1)–(1.4) to calculate a $100(1-\alpha)\%$ confidence interval for the average growth increment of lake trout recaptured after j years at liberty as follows:

$$\bar{Q}_j \pm t_{\nu,1-\alpha/2}\sqrt{T_{jj}} \tag{1.5}$$

where the degrees of freedom of the t distribution is

$$\nu = (m-1)\left[1 + \frac{\bar{U}_{jj}}{(1+m^{-1})B_{jj}}\right]^2$$

(Rubin 1987, chapter 3), illustrating the dependence of ν on the size of the simulated sample and on the relative increase in variance due to the incompletely observed growth histories.

Comparison of growth increment estimates

We wish to compare the estimated growth increments of lake trout that were marked and recaptured during the pre-refuge period with those of lake trout that were marked and recaptured during the post-refuge period. Provided the comparison includes lake trout that were the same size initially (i.e., in the same size category at first capture), we may use a likelihood-ratio test, modified for incomplete data (Meng and Rubin 1992), to assess whether the mean growth histories of these two groups of fish are significantly different. Let (Y_{obs}, Y_{mis}) be the $(n_1 + n_2) \times (p+1)$ matrix of observable sizes (the first n_1 rows correspond to fish from group 1 (pre-refuge); the remaining rows correspond to fish from group 2 (post-refuge)). We compare a model in which mean sizes in each year of recapture differ between the two groups ($Y_{i\in\{1,\ldots,n_1\}} \sim N(\mu_1, \Sigma)$; $Y_{i\in\{n_1+1,\ldots,n_1+n_2\}} \sim N(\mu_2, \Sigma)$) to a model where the mean sizes at recapture are identical for both groups ($Y_{i\in\{1,\ldots,n_1+n_2\}} \sim N(\mu, \Sigma)$). The complete-data likelihood ratio statistic for testing $H_0 : \mu_1 = \mu_2 = \mu$ is

$$d_L = 2\left[l(\hat{\mu_1}, \hat{\mu_2}, \hat{\Sigma}_*|Y_{obs}, Y_{mis}) - l(\hat{\mu}, \hat{\Sigma}|Y_{obs}, Y_{mis})\right] \tag{1.6}$$

where $\hat{\mu_1}$, $\hat{\mu_2}$, and $\hat{\Sigma}_*$ are parameter estimates that maximize the complete-data log likelihood $l(\mu_1, \mu_2, \Sigma|Y_{obs}, Y_{mis})$, and $\hat{\mu}$ and $\hat{\Sigma}$ are estimates that maximize the complete-data log likelihood $l(\mu, \Sigma|Y_{obs}, Y_{mis})$.

To simplify notation, let $\hat{\psi}_* = \{\hat{\mu_1}, \hat{\mu_2}, \hat{\Sigma}_*\}$ and $\hat{\psi} = \{\hat{\mu}, \hat{\Sigma}\}$. Therefore, using this notation the likelihood ratio statistic in equation (1.6) is

$$d_L(\hat{\psi}_*, \hat{\psi}|Y_{obs}, Y_{mis}) = 2\left[l(\hat{\psi}_*|Y_{obs}, Y_{mis}) - l(\hat{\psi}|Y_{obs}, Y_{mis})\right]$$

The test statistic proposed by Meng and Rubin (1992) requires computation of the maximum-likelihood estimates, $\hat{\psi}_*$ and $\hat{\psi}$, and the likelihood ratio test statistic for each of the m sets of complete data created by data augmentation. Denoting these by $\hat{\psi}_*^{(t)}$, $\hat{\psi}^{(t)}$, and $d_L(\hat{\psi}_*^{(t)}, \hat{\psi}^{(t)}|Y_{obs}, Y_{mis}^{(t)})$, respectively, for the t^{th} complete data set, we compute their average values over all m data sets as follows:

$$\begin{aligned}
\bar{\psi}_* &= \frac{1}{m}\sum_{t=1}^{m}\hat{\psi}_*^{(t)} \\
\bar{\psi} &= \frac{1}{m}\sum_{t=1}^{m}\hat{\psi}^{(t)} \\
\bar{d}_L &= \frac{1}{m}\sum_{t=1}^{m} d_L(\hat{\psi}_*^{(t)}, \hat{\psi}^{(t)}|Y_{obs}, Y_{mis}^{(t)})
\end{aligned}$$

We also compute an average of the complete-data likelihood ratio statistic evaluated at $\bar{\psi}_*$ and $\bar{\psi}$ as follows:

$$\tilde{d}_L = \frac{1}{m}\sum_{t=1}^{m} d_L(\bar{\psi}_*, \bar{\psi}|Y_{obs}, Y_{mis}^{(t)}).$$

The test statistic proposed by Meng and Rubin (1992) for testing $H_0 : \mu_1 = \mu_2 = \mu$ is

$$D_L = \frac{\tilde{d}_L}{(p+1)(1+r_L)},$$

where

$$r_L = \frac{m+1}{(p+1)(m-1)}(\bar{d}_L - \tilde{d}_L).$$

The p-value associated with D_L is

$$p = P(F_{p+1,\nu_L} \geq D_L),$$

where the degrees of freedom parameter of the reference distribution is

$$\nu_L = \begin{cases} 4 + (q-4)[1 + (1-2q^{-1})r_L^{-1}]^2 & \text{if } q = (p+1)(m-1) > 4 \\ (q/2)\,[1 + (p+1)^{-1}](1 + r_L^{-1})^2 & \text{otherwise.} \end{cases}$$

Results

To accommodate size-specific differences in growth of lake trout, we estimated the mean growth increments of individuals in six size categories: ≤ 60 cm, 60–65 cm, 65–70 cm, 70–75 cm, 75–80 cm, and > 80 cm. Fish were assigned to a size category based on their length at first capture, and most were between 60 cm and 80 cm at first capture (Figure 2). Although the size distributions of hatchery and wild lake trout were similar during the pre- and post-refuge periods, hatchery fish tended to be somewhat larger during the pre-refuge period (Figure 2).

To determine the number of years available for estimating mean growth increments, we examined annual recapture rates of lake trout in each of their first six years at liberty (Table 2). Within each recapture period (pre- and post-refuge) wild and hatchery fish exhibited similar patterns in the distribution of recaptures with time at liberty. Although more fish were recaptured over more years during the post-refuge period, this may simply be a result

of the difference in number of years available for actual observation (the maximum for the pre-refuge period was 6, and the maximum for the post-refuge period was 21). In this study, recapture rates of lake trout on the spawning grounds were influenced by apparent survival and by factors affecting catchability such as behavior (particularly spawning behavior). For a given recapture period, hatchery and wild fish appeared to be equally susceptible to capture, thus growth increment estimates are not thought to have been influenced by differences in behaviors or apparent survival. We included for statistical analysis only the sizes of lake trout observed in their first three years at liberty owing to the limited number of recaptures in years 4–6 of the pre-refuge period.

Wild fish

Mean growth increments of wild lake trout in each of their first three years at liberty were significantly different during the pre- and post-refuge periods in five of the six size categories examined (Table 3). Estimates of growth during the pre-refuge period generally exceeded estimates of growth during the post-refuge period (Figure 3). The smaller numbers of fish tagged and recaptured during the pre-refuge period contribute to wider confidence intervals. Note also that confidence intervals are narrowest for mean growth increments estimated after one year at liberty and widest for those after three years at liberty, reflecting an increase in uncertainty as recapture rates declined (and missingness increased) with time at liberty (Table 2).

Mean growth increments of wild fish in a given size category decreased with increasing time at liberty (Figure 3). This result is consistent with the growth pattern specified by the von Bertalanffy model, which is based on size at age. Although we did not explicitly account for fish age, our approach accommodated the pattern of decreasing growth with increasing age. In addition, the variance of the mean growth increment increased with time (Figure 3), but this likely reflected fewer recaptures after two or more years at liberty. We also observed a reduction in estimated annual growth with increasing size at first capture. Thus, larger

(older) fish grew at slower rates than the smaller (younger) fish in our samples. Together, these results suggest that growth of wild lake trout may be adequately described by the von Bertalanffy growth model if it becomes possible to obtain accurate ages.

Hatchery fish

Mean growth increments of hatchery-raised lake trout in each of their first three years at liberty were significantly different during the pre- and post-refuge periods in only two of the six size categories (Table 2). In both of these cases, growth increments were greater in the pre-refuge period than in the post-refuge period (Figure 4). Due to the increased variability associated with smaller numbers of fish and fewer recaptures, growth patterns of hatchery fish were more difficult to discern, but appeared similar to those of wild fish. For example, during the post-refuge period, mean growth increments of hatchery fish in the most abundant size categories (65–70 cm and 70–75 cm) decreased with increasing time at liberty (Figure 4).

Discussion

Size-at-age-based growth estimates

In the Laurentian Great Lakes, growth of lake trout (or simply mean length at age) is often reported as an indicator of the general condition of the population, and only gross comparisons of growth have been attempted. Mean length at age appears to differ among populations in different areas of a lake (e.g., see Hansen 1994) and fluctuations in average length appear to occur through time; however, no formal statistical analyses have been attempted in these investigations. Yet, lake trout growth is an important consideration for fishery managers because one of the fish community objectives for Lake Superior is to "maintain a predator-prey balance in the lake that allows the normal growth of lake trout"

(Busiahn 1990). Furthermore, in the restoration plan for Lake Superior lake trout, Hansen (1996) recommended that a "more meaningful expression of lake trout growth than length at age 7" be developed because average length at age was thought to be insensitive to true changes in growth.

Individual growth of lake trout may be affected by a number of factors including population abundance, composition of the forage base, forage abundance, and water temperature. In Minnesota waters of Lake Superior, growth rates of lake trout were shown to be sensitive to prey availability (Negus 1995). This sensitivity is relevant to the management of lake trout, which now may compete for food resources with nonindigenous salmonids in Lake Superior. The bioenergetics approach is being extended to encompass lake trout populations throughout Lake Superior (Negus 1995), but such modeling clearly requires a better understanding of lake trout growth and corroboration by field studies of growth (Ney 1993). For example, Negus (1995) noted that the observed discrepancy between bioenergetic estimates of biomass consumed by predators and estimates of available prey derived from bottom-trawl surveys may be partially explained by changes in lake trout growth rates, which were not modeled. Representative data (i.e., model inputs) are critical to improving the accuracy of model outputs (Ney 1993). Our study provides additional insight into growth dynamics of the Gull Island Shoal population as well as further evidence for growth differences among hatchery and wild lake trout.

Mark-recapture-based growth estimates

Growth analyses are often based on measures of size at age, but scale-based estimates of age (and hence, growth rates) are biased for large, mature lake trout (Schram and Fabrizio 1998). Age determinations of mature lake trout are more reliable when otoliths are used to determine age. However, this requires sacrificing the fish - an untenable proposition when rehabilitation is sought. In contrast, estimates of growth derived from mark-recapture studies are not affected by uncertainties in age determinations. Unfortunately, in the absence of

information on ages of marked fish, mark-recapture-based growth estimates are not interchangeable with growth estimates derived from traditional length-at-age analyses (Francis 1988).

One of the assumptions necessary to estimate growth of individual fish in a mark-recapture study is that the tagging procedure or tag have no effect on growth. The effects of anchor tags on the growth of mature lake trout have not been studied, but we believe that such effects were minor and possibly undetectable in our study. Growth rates of brook trout, a closely related species, were suppressed only during the first three months after tagging with anchor tags (Floy FD-67); thereafter, growth rates of tagged fish were similar to those of untagged fish (Carline and Brynildson 1972). Studies that reported retardative effects of tags shared one or more of the following conditions: (1) tag type or size was inappropriately matched to fish size (e.g., Manire and Gruber 1991); (2) tags were applied to young life stages which have relatively high growth rates (e.g., 2-year-old lake trout, Eschmeyer 1959); (3) tags (jaw tags) interfered with feeding (e.g., Warner 1971); or (4) stress due to spawning (Gunn et al. 1979) or the presence of wounds (e.g., Carline and Brynildson 1972) contributed to decreased growth rates. In addition, retardative effects are likely to be significant only when growth is studied over short (< 1 year) periods of time (Carline and Brynildson 1972). In the absence of these conditions and when tagging effects are assessed over long periods of time, growth of tagged and untagged individuals is similar.

An additional assumption in our comparison of growth histories of hatchery and wild fish is that fin clipping does not affect growth. In our study, only the hatchery-reared lake trout were subjected to this treatment, which occurred at the yearling stage just before the fish were stocked. Fin clipping, a common method of marking large numbers of fish, generally has no significant effect on fish growth, but may reduce growth rates in young fish (< 90 mm; Coble 1967). Extensive testing with fingerling lake trout less than 90 mm in length (average size ranged from 74 mm to 83 mm) indicated no appreciable effect on growth when the following fins were clipped: adipose, dorsal, right pectoral, or right pelvic (Shetter 1950).

In these studies, lake trout growth rates were monitored in hatchery conditions over periods ranging from two to four and a half years (Shetter 1950). Additionally, in the only study of its kind, the combination of fin clipping and anchor tagging appears to have no significant effect on growth of largemouth bass (Tranquilli and Childers 1982). Together, these studies support the notion that fin clipping and anchor tagging of adult lake trout in Lake Superior have no effect on growth as estimated from our tagging experiment.

Our observations on decreasing growth increment with increasing time at liberty and with increasing size at capture suggest that growth rates of mature lake trout decline with age and size. Mature lake trout at Gull Island Shoal (particularly wild fish) continued to increase in length (in some cases appreciably) even after two, three, or more years at liberty. Even during the post-refuge period, when growth was relatively slower, wild fish in our largest size category grew by 0.87 cm ($\pm$0.14, SE) during the first year at liberty. This suggests that mature lake trout may still experience appreciable growth and that growth rates of lake trout in the Gull Island Shoal area permit these fish to attain large sizes.

Are our conclusions about growth of lake trout robust to the discretization of size at capture and years at liberty? If the discretization of sizes into categories is too coarse, many ages of fish may be included in each category, and we will be unable to detect changes in growth over time. Conversely, if size categories are too narrow and contain too few fish, our growth increment estimates will be imprecise, again leading to difficulties in detecting changes in growth. We believe that the use of 5 cm size categories for mature lake trout appears to strike a balance between the risks of including too many age classes and excluding too many fish. In our study, even the largest mature lake trout exhibited annual growth increments that were significantly greater than zero (as noted earlier).

Dynamics of individual growth of Lake Superior lake trout

In Lake Superior the diet of lake trout shifted from one dominated by lake herring *Coregonus artedi* and deepwater ciscoes *Coregonus* spp. (before the 1950s) to one dominated by

rainbow smelt *Osmerus mordax* by the early 1960s (Conner et al. 1993). This switch paralleled observed changes in the composition of prey fishes in the lake. Although lake herring are now more abundant than rainbow smelt, lake trout preferentially consume rainbow smelt (Mason et al. 1998). For example, between 1985 and 1987 in the Apostle Islands area, rainbow smelt composed about 27% of the prey fish biomass, but lake trout diets were 66-78% rainbow smelt by weight (Conner et al. 1993). Growth (as indicated by mean length at age) of lake trout from Michigan waters of Lake Superior appeared to decline between 1980 and 1989, somewhat coincident with the decline in rainbow smelt abundance that began in the late 1970s (Hansen 1994). However, a closer examination of the relation between prey fish abundance and lake trout growth in Lake Superior revealed that growth rates of hatchery fish during 1979–1984 were poorly associated with abundance of prey fish (Eby et al. 1995). Furthermore, consumption rates of lake trout from several Great Lakes were shown to have been similar even though prey fish abundance differed by a factor of 100 among lakes (Eby et al. 1995). An age-structured model that combined bioenergetics modeling and foraging theory also supported the notion that growth of lake trout, particularly for fish 4 years and older, was not entirely regulated in a density-dependent manner (Mason et al. 1998).

Effect of the Gull Island Shoal refuge

Our observations of the growth dynamics of lake trout at Gull Island Shoal cannot be used to determine whether density-dependent or density-independent mechanisms were responsible for the changes in individual growth rates; however, the evidence does indicate that growth responses of hatchery and wild fish were similar. After the refuge was established, the lake trout population at Gull Island Shoal increased in abundance and average annual growth increments of individual fish decreased significantly. This reduction in growth may have been associated with a reduction in food availability, but we cannot be certain about the cause(s) of reduced food for lake trout given the limitations of our observational study and the paucity of other supporting evidence. More specifically, we are unsure whether food

availability may have decreased because of the increased abundance of lake trout during the post-refuge period (a density-dependent response) or because of changes in environmental conditions that just happened to coincide with the establishment of the refuge (a density-independent response).

Refuges, sanctuaries, reserves, and other 'no-take' areas are increasingly considered as options for managing overexploited fisheries (e.g., Johnson et al. 1999) or as an aid to rehabilitating native species (e.g., Schram et al. 1995). An expected proximate result is a decrease in fishing mortality rates allowing slow-growing fish to achieve maturity and spawn. The ultimate results of such sanctuaries - increased population abundance, expanded size and age structures, dispersal of recruits to areas outside the sanctuary - have been assessed only recently. In addition to our study of lake trout, Johnson et al. (1999) reported that in coastal marine areas protected from fishing, several species of large, slow-growing fishes increased in abundance and average size. Growth rates were not estimated, so it is unknown if the observed changes in the population were accompanied by changes in individual growth. In Gull Island Shoal, Lake Superior, the establishment of a refuge was followed by an increase in abundance of lake trout and a decrease in their individual rates of growth. Further studies of the potential ultimate effects of refuges and sanctuaries may provide additional insights into the dynamics of recovering fish populations.

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A Appendix: Simulating a Sample from the Joint Posterior Distribution of Model Parameters and Unobserved Sizes of Fish

We use a stochastic sampling algorithm called data augmentation (Tanner and Wong 1987; Gelfand and Smith 1990) to simulate an arbitrarily large number of draws from the joint posterior distribution of model parameters and missing data (i.e., unobserved sizes of fish). Although the joint posterior density $p(\mu, \Sigma, Y_{mis}|Y_{obs})$ is difficult to compute or sample directly, it may be sampled indirectly by computing recursive draws from conditional distributions that are easier to sample. For example, given an initial guess of the parameter values, say $\mu^{(t)}$ and $\Sigma^{(t)}$, data augmentation begins by drawing a random value from the conditional predictive distribution of Y_{mis},

$$Y_{mis}^{(t+1)} \sim p(Y_{mis}|Y_{obs}, \mu^{(t)}, \Sigma^{(t)}). \tag{A.1}$$

Then, conditioning on $Y_{mis}^{(t+1)}$, new values of μ and Σ are randomly drawn from the complete-data posterior,

$$\mu^{(t+1)}, \Sigma^{(t+1)} \sim p(\mu, \Sigma|Y_{obs}, Y_{mis}^{(t+1)}). \tag{A.2}$$

Tanner and Wong (1987) showed that repeating equations (A.1) and (A.2) from arbitrary starting values $\mu^{(0)}$ and $\Sigma^{(0)}$ yields a stochastic sequence

$$\{(\mu^{(t)}, \Sigma^{(t)}, Y_{mis}^{(t)}) : t = 1, 2, \dots\}$$

whose stationary distribution is the joint posterior $p(\mu, \Sigma, Y_{mis}|Y_{obs})$.

The data augmentation algorithm is particularly easy to implement for our complete-data model of the observable sizes of lake trout (i.e, the multivariate normal model). In the absence of prior information about the values of μ or Σ, we adopt a uniform prior for μ and Jeffrey's prior for Σ (i.e., $p(\mu, \Sigma) \propto \det(\Sigma)^{-(p+2)/2}$), as recommended by Schafer (1997, p. 154). As a consequence of these priors, a draw from the complete-data posterior (A.2) is obtained by computing random draws from the Inverse-Wishart and Normal distributions (in that order) as follows:

$$\begin{aligned} \Sigma^{(t+1)}|Y_{obs}, Y_{mis}^{(t+1)} &\sim \text{InverseWishart}(n-1, (nS)^{-1}) \\ \mu^{(t+1)}|\Sigma^{(t+1)}, Y_{obs}, Y_{mis}^{(t+1)} &\sim N(\bar{y}, n^{-1}\Sigma^{(t+1)}) \end{aligned}$$

wherein $\bar{y}$ and S denote the sample mean vector and covariance matrix, respectively, of the matrix of observed and imputed sizes of fish from the $(t+1)$-th random draw.

A random draw from the conditional predictive distribution (A.1) is also relatively easy to compute because the rows of (Y_{obs}, Y_{mis}), which correspond to growth histories of individual fishes, are conditionally independent; therefore, a random draw from (A.1) is obtained by drawing

$$y_{i(mis)}^{(t+1)} \sim p(y_{i(mis)}|y_{i(obs)}, \mu^{(t)}, \Sigma^{(t)}) \tag{A.3}$$

independently for $i = 1, \ldots, n$. For our model of lake trout growth histories, Schafer (1997, p. 181) shows that (A.3) represents a draw from a conditionally multivariate normal distribution whose mean and covariance matrix may be computed in terms of $y_{i(obs)}$, $\mu^{(t)}$, and $\Sigma^{(t)}$. Concise

expressions for the conditional mean and covariance matrix are difficult to write down in any generality because they depend on the particular elements of y_i that are observed; however, the parameters of the conditional multivariate normal are easily specified and evaluated in terms of sweep operators (Schafer 1997, p. 159–163, 181).

We computed a sample of $m = 100$ draws from the joint posterior density $p(\mu, \Sigma, Y_{mis}|Y_{obs})$ using a software package called NORM, which implements the data augmentation algorithm described above and is available at the World Wide Web address, `www.stat.psu.edu/~jls/` (Schafer 1997). The data augmentation algorithm was initialized with maximum-likelihood estimates of μ and Σ, which were computed using expectation-maximization in NORM. To help ensure that data augmentation had been run sufficiently long to have converged to a stationary distribution, we ran the algorithm for 2 000 draws and discarded the first 1 000 draws as a "burn-in" period. Our simulated sample was obtained by selecting every tenth draw of the remaining 1 000 draws to avoid dependencies between successive elements of the sequence of model parameters and imputed values of Y_{mis}.

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Table 1: Number of lake trout tagged and released annually in the Gull Island Shoal area of Lake Superior. For the pre-refuge period, the number of fish that were tagged and recaptured at least once excludes those that were recaptured after 1975.

Year	Number released		Number recaptured at least once following the year of release	
released	Hatchery	Wild	Hatchery	Wild
			Pre-refuge	
1969	478	232	22	39
1970	1189	369	18	30
1971	709	548	16	46
1972	842	1454	22	45
1973	420	692	21	49
1974	633	1578	17	63
Total	4271	4873	116	272
			Post-refuge	
1975	291	583	19	105
1976	412	1143	20	208
1977	541	1775	20	311
1978	484	2412	31	435
1979	653	2060	36	384
1980	294	2124	26	390
1981	361	1957	31	422
1982	397	1913	18	281
1983	256	2525	12	295

1984	513	1918	46	223
1985	402	2098	22	171
1986	355	1747	17	166
1987	247	1457	19	173
1988	252	2538	12	293
1989	339	2586	29	342
1990	201	1951	14	189
1991	220	2075	13	168
1992	229	2088	18	181
1993	236	2150	10	107
1994	199	1888	4	54
1995	85	1390	1	25
Total	6967	40378	418	4923
Grand Total	11238	45251	534	5195

Table 2: Annual recapture rates (% of lake trout that were recaptured at least once) in each of the first six years at liberty.

Fish	Recapture	Number	Number of years at liberty					
origin	period	of fish	1	2	3	4	5	6
hatchery	pre-refuge	116	70.7	24.1	12.1	2.6	0.0	0.0
wild	pre-refuge	272	72.4	23.5	7.7	1.8	3.3	0.4
hatchery	post-refuge	418	38.8	29.9	17.2	13.2	8.4	3.8
wild	post-refuge	4923	39.6	31.4	19.2	11.7	8.0	5.2

Table 3: p-values for testing if mean growth increments of lake trout during their first three years at liberty were equal during the pre- and post-refuge periods. Numbers of fish from each size category in pre- and post-refuge periods are indicated by n_{pre} and n_{post}, respectively. NA indicates that the number of fish was insufficient to compute a p-value.

Size at first	Wild			Hatchery		
capture (cm)	n_{pre}	n_{post}	p-value	n_{pre}	n_{post}	p-value
≤ 60	16	228	0.02	2	15	NA
60–65	60	1089	< 0.01	24	77	0.26
65–70	78	1744	< 0.01	25	147	< 0.01
70–75	62	1178	< 0.01	35	89	< 0.01
75–80	25	440	0.37	19	48	0.56
> 80	31	244	< 0.01	11	42	0.10

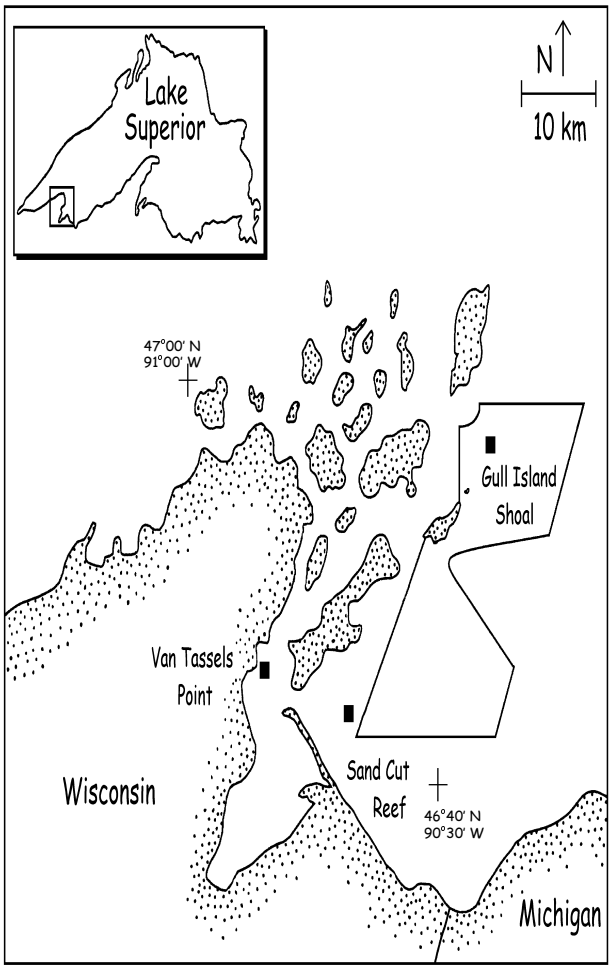

Figure 1: Study site showing the location of the 70 000 ha refuge (bordered by solid line) and gillnet sampling sites (■) in the Gull Island Shoal area of Lake Superior.

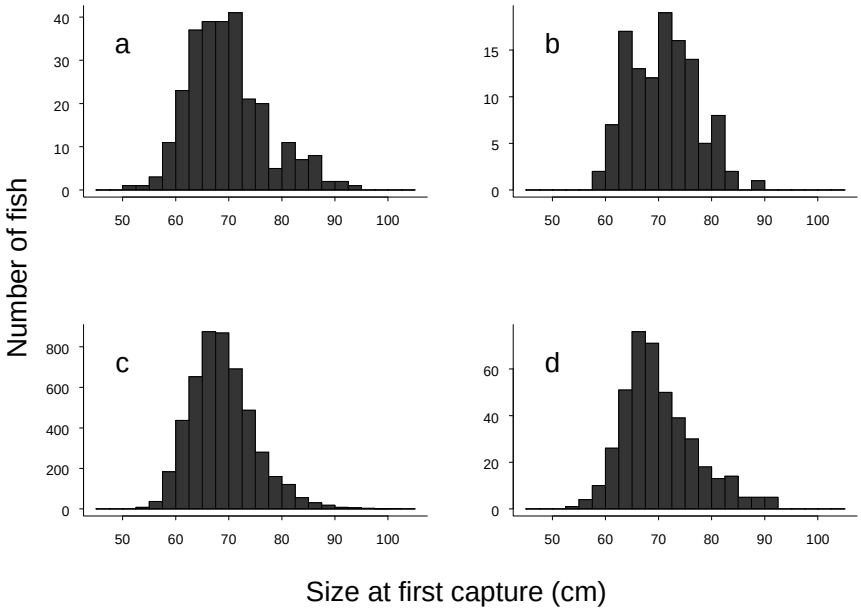

Figure 2: Size distributions of lake trout at first capture. a. wild fish, pre-refuge period, b. hatchery fish, pre-refuge period, c. wild fish, post-refuge period, d. hatchery fish, post-refuge period.

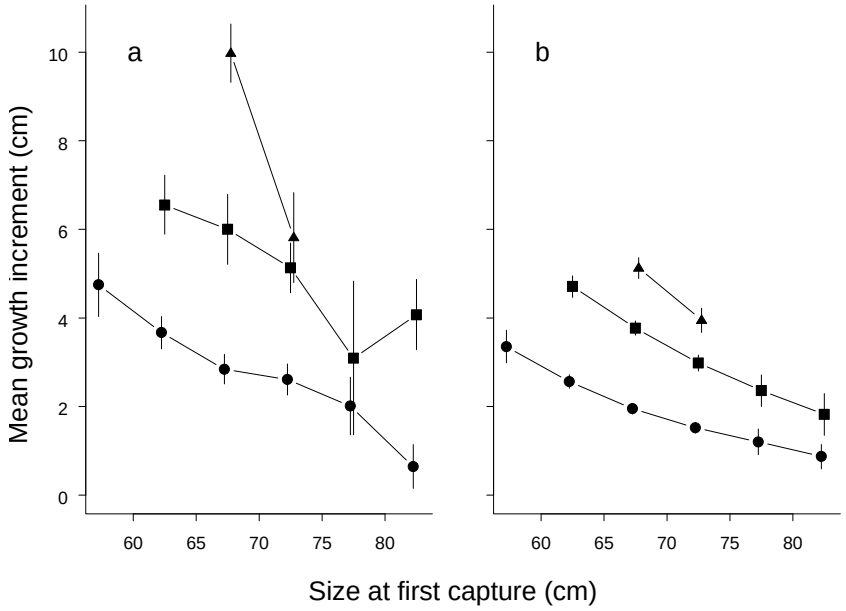

Figure 3: Size-specific estimates and 95% confidence intervals of individual growth increments of wild lake trout during the pre-refuge (a) and post-refuge (b) periods. Estimates of growth after one, two, or three years at liberty are distinguished by symbol type (circle, square, or triangle, respectively).

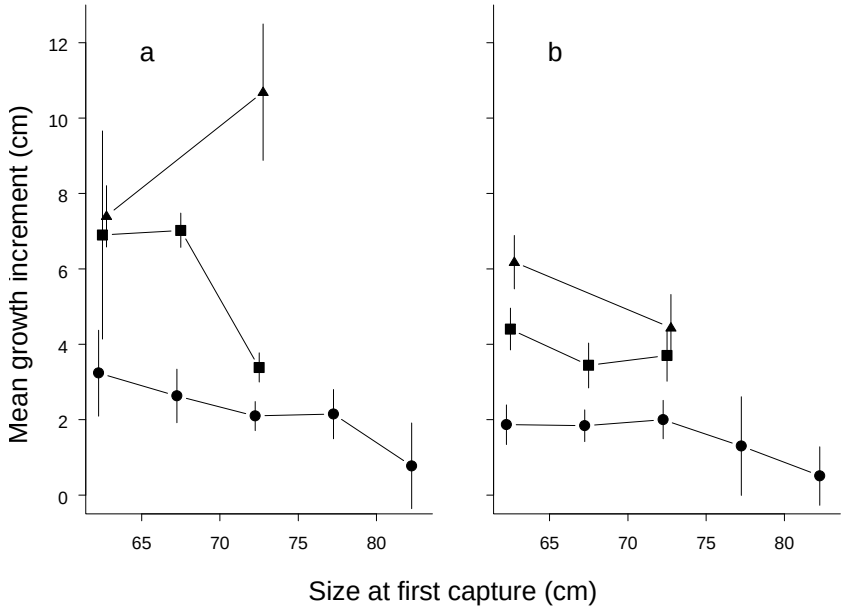

Figure 4: Size-specific estimates and 95% confidence intervals of individual growth increments of hatchery-reared lake trout during the pre-refuge (a) and post-refuge (b) periods. Estimates of growth after one, two, or three years at liberty are distinguished by symbol type (circle, square, or triangle, respectively).