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EFFECTS OF A SLOTTED SIZE LIMIT ON A MULTISPECIES TROUT FISHERY¹

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Abstract

A slotted size limit was established on a 14-km section of Michigan's Au Sable River. It allowed harvest of any trout between 203 and 305 mm or greater than 406 mm in length. Wild populations of brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and rainbow trout (*Salmo gairdneri*) coexisted in the section. Harvest of brown trout and rainbow trout was formerly restricted by a 305-mm minimum limit and harvest of brook trout by a 203-mm minimum limit. One of the primary purposes of the slotted limit was to help improve the growth rate of brown trout by reducing abundance of 203- to 305-mm fish through harvest.

We compared before- (1974 through 1978) and after-period (1980 through 1983) trout populations, catch, and fishing effort in the study section and in a control section where regulations remained constant. Mark-and-recapture population estimates were conducted annually from 1974 to 1983 to determine abundance and size structure of the populations, and samples of trout scales were aged to determine age structure, survival rates, and growth rates. Stratified, random sampling methods were used to estimate total catch, both harvested and released, and its species and size composition. Finally, we compared the effects of the slotted size limit on brown trout as determined from these field surveys to those predicted earlier with a mathematical model (Clark et al. 1980).

Abundance of brown trout smaller than 203 mm decreased in the study section by 8%, abundance of 203- to 305-mm brown trout decreased by 32%, and abundance of brown trout over 305 mm decreased by 47%. Growth rate of brown trout did not change significantly. Annual fishing mortality rate between ages 2 and 3 increased from near zero to about 30%, and this reduced the number of fish surviving to older ages and larger sizes. However, unfavorable changes in environmental conditions also contributed to decreases in abundance by reducing brown trout recruitment. Brook trout and rainbow trout abundance increased by 63% and 48%, respectively, but these increases were due to environmental factors and not to the change in regulations. For example, recruitment of age-0 brook trout increased 40% in the control section where regulations remained constant. Growth rates of brook trout and rainbow trout remained constant, as did their survival rates at age 1 and older. Total numerical harvest of brown trout increased nearly fivefold but consisted of smaller fish. Catch of 305- to 406-mm brown trout remained constant, despite their reduced abundance in the population. This was apparently due to multiple recaptures of released fish. Total catch of brook trout and rainbow trout increased by about the same amount as their numbers increased in their populations. The model predictions of the size and age structure of the brown trout population were accurate on a per-recruit basis, but the reduction in brown trout recruitment caused by environmental factors could not have been predicted.

The slotted size limit reduced the density of brown trout but did not improve their growth rate. Instead, the reduction in brown trout density may have been compensated, at least in part, by the increase in density of brook trout and rainbow trout. We concluded that the greatest effect of the slotted limit was in reshaping man's use of the trout populations. Biological effects were comparatively unimportant except for their influence on satisfying desires of different factions within the angling community.

Introduction

An experimental fishing regulation was established on a 14-km stretch of the Mainstream of the Au Sable River. The regulation was a slotted size limit which allowed harvest of trout between 203 and 305 mm and greater than 406 mm in size. Wild, self-sustaining populations of brown trout (Salmo trutta), brook trout (Salvelinus fontinalis), and rainbow trout (Salmo gairdneri) coexist in the experimental area. We described the effects of the slotted limit on the brown trout fishery in a previous paper which emphasized basic results and management implications (Clark and Alexander 1984). This paper, which is more comprehensive, presents results for all three trout and concentrates on the technical details of experimental methods and analysis. We also compare effects of the slotted limit on brown trout, as determined from this field study, to effects predicted earlier by mathematical simulation (Clark et al. 1980).

Background

Study Area

The Au Sable River basin is approximately 4,680 square km in size and is located in the north central part of Michigan's lower peninsula (Fig. 1). The river consists of three major branches, the North Branch, the Mainstream (or Middle Branch), and the South Branch, and has three major tributaries, the East Branch, and two different Big Creeks. The soils in the basin are light, composed of much sand and gravel, and are very pervious to water infiltration. As a result, a large part of the average 75 cm of annual precipitation goes to groundwater recharge, and the influx of this groundwater to the stream helps maintain cold temperatures and stable flow conditions for trout.

The slotted size limit was applied to the section of the Mainstream beginning about 9 km downstream from the City of Grayling at Burton's Landing and extends 14 km to Wakeley Bridge (Fig. 1). This stretch of the Au Sable is recognized as one of the best trout fishing areas in the Midwest. Hatchery trout have not been planted in the area since 1954.

Problem

In the early 1970's anglers began complaining that the large brown trout which helped give the Burton-to-Wakeley stretch its reputation were gone. At the time, it was thought an increase in fishing pressure might be causing the decline of the larger brown trout through overharvest, but this could not be confirmed because neither trout population surveys nor creel surveys had been conducted there since 1963. Nonetheless, in response to angler complaints the minimum size limit on brown trout and rainbow trout was increased from 254 to 305 mm in 1973, and the daily creel limit was reduced from 5 to 3 trout per day. Also, the size limit on

brook trout was increased from 178 to 203 mm in 1974. Annual trout population surveys were resumed in 1972 so the effects of the change in size limits could be studied in detail.

By 1977, surveys showed the regulations had failed to bring back large brown trout. The most important reason for the failure appeared to be a significant decline in their growth rate (Alexander et al. 1979). Mean lengths of brown trout of all ages were considerably less in the 1970's than in the 1960's. For example, the average 3-year-old brown trout was 58 mm smaller (287 mm versus 345 mm). This change in growth had a great impact on the fishery. The estimated number of brown trout larger than 305 mm in the population and the estimated number harvested per hour of fishing both decreased by two and one-half times (Alexander et al. 1979).

The size structure of the population seemed to be out of balance under the 305-mm limit with too many mid-sized fish and not enough large fish. It was suggested that harvesting these "overabundant" mid-sized fish and protecting the rarer, more valuable large fish might solve the problem. It might allow the remaining fish in the population to obtain more food per individual, and grow faster. Thus, a slotted size limit was designed to thin the numbers of 203- to 305-mm brown trout by allowing their harvest and to protect 305- to 406-mm brown trout by requiring their release. The slotted size limit went into effect on April 28, 1979.

However, a number of other hypotheses were advanced to explain the decline in growth (Alexander et al. 1979). One of the leading hypotheses was based on an observed decrease in the productivity of the river (Merron 1982). The State of Michigan phased out fish production, with its related waste discharge, at the Grayling Hatchery in the mid-1960's and the town of Grayling stopped discharging sewage effluent into the river in 1971. As a result, nitrogen concentrations decreased in the Burton-to-Wakeley section by about 70% between 1971 and 1972, and phosphorus concentrations decreased by about 10% from 1966 to 1972 (Coopes 1974). Such a loss of nutrients could have been responsible for the reduction in average sizes of trout in the mid-1970's. A second hypothesis was based on population genetics. It suggested the growth potential of brown trout was reduced by selective harvest of larger fish over time (Favro et al. 1980). Of course, if either of these latter two hypotheses is correct, then the slotted size limit could not restore the growth rate of brown trout in the Mainstream.

Methods

Field Experiment

The experiment to evaluate the slotted limit spanned a 10-year period, 1974 through 1983. Specific regulations on the study section (Burton's Landing to Wakeley Bridge) from 1974 through 1978 were artificial flies only, minimum size limits of 305 mm on brown and rainbow trout and 203 mm on brook trout, and a creel limit of 3 trout per day. Specific

regulations from 1979 through 1983 were artificial flies only, harvest of any trout between 203 and 305 mm or over 406 mm permitted, and a creel limit of 5 trout per day. In both periods, the fishing season for harvesting fish was from the last Saturday in April to October 31, but catch-and-release fishing was permitted the rest of the year. A control section was selected on the North Branch of the Au Sable River, where regulations remained constant. Regulations on the control section from 1974 through 1983 were artificial flies only, minimum size limits of 203 mm on brook trout and 254 mm on brown trout, creel limit of 5 trout per day from the last Saturday in April to October 31. The control section was 23 km long, from Sheep Ranch Public Access Site to Kellogg's Bridge near the community of Lovells (Fig. 1). At its farthest point, it is only 25 km from the study section on the Mainstream, and it has similar trout habitat. Rainbow trout were not present in the North Branch, but its brown and brook trout populations compared very well with those in the Mainstream. The same data on trout populations and angler use were collected on both study and control sections.

Trout population sampling

Trout populations were sampled at two stations on the Mainstream, one 0.67 ha in size at Wa Wa Sum and one 0.60 ha in size at Stephan's Bridge (Fig. 1). Three stations were sampled on the North Branch, 1.34 ha at Twin Bridge, 1.00 ha at Eamon's Landing, and 1.23 ha at Dam 4. Sampling stations comprised 3% and 4% of the surface area in the study and control sections, respectively.

Abundance and survival.—Abundance of trout in the the sampling stations was estimated each fall between September 19 and October 30. Direct-current electrofishing gear (220 volts) was used to collect the trout and mark-and-recapture techniques were applied to make the estimates. Separate estimates of population numbers were made for each species and each 1-inch length group (for example, trout from 51 mm to 75 mm were in inch group 2, trout from 76 mm to 101 mm were in inch group 3, and so on). Estimates were stratified in this way to reduce the size-selective bias of the sampling gear. Trout were marked with a fin clip on the first day, their total lengths were recorded, and they were returned to the water. The ratio of marked to unmarked trout of each species and inch group was recorded on the second day.

Trout scales were sampled during the marking run to estimate age composition of each inch group. A quota was set for each station of 10 samples per inch group per species. However, as trout got larger they got fewer, so it was not possible to meet this quota for all inch groups and species. The overall number of trout by age was estimated by multiplying abundance estimates by age composition and summing over inch groups.

Trout Stream Data System (TSDS), a package of computer programs, was developed for data storage and retrieval and to calculate abundance estimates and variances by size and age categories. We used the Bailey formulas for these estimates (Bailey 1951). Estimated numbers

of trout per unit area (hectares) were calculated for each river branch from data collected at their respective sampling stations.

The before period was defined as 1974 through 1978 and the after period as 1980 through 1983. This allowed a 2-year transition period (1978 to 1980) for the population to adjust from the 305-mm limit to the slotted limit. The annual population estimates \hat{N}_{ij} , and their variances, $V(\hat{N}_{ij})$, were treated as means and variances of independent random samples drawn from the true before-period or after-period populations. The before and after period means, $\bar{N}_{.j}$, were estimated from the sample means as:

$$\bar{N}_{.j} = \frac{\sum_{i=1}^n \hat{N}_{ij}}{n},$$

where n was the sample size of years (i) in period j , and the before and after variances, $V(\bar{N}_{.j})$, were estimated from the sample variances as:

$$V(\bar{N}_{.j}) = \frac{\sum_{i=1}^n V(\hat{N}_{ij})}{n^2}$$

Confidence intervals were calculated for these before and after means and any differences observed were considered statistically significant if the confidence intervals did not overlap. We used 90% confidence intervals for these tests.

We also calculated the mean annual survival rate, S_k , and its variance, $V(S_k)$, for each age group k in the before and after periods. The binomial formula was used to estimate these variances. For example,

$$V(S_1) = V(N_2/N_1) = (N_2/N_1)^2 \{ [V(N_2)/N_2^2] + [V(N_1)/N_1^2] \}$$

where $V(S_1)$ was the variance of the survival rate from age 1 to age 2, N_1 was the mean number of 1-year-old trout, N_2 was the mean number of 2-year-old trout, $V(N_1)$ was the variance of 1-year-old trout, and $V(N_2)$ was the variance of 2-year-old trout.

Growth.—We used a second-degree polynomial regression to express average individual growth. That is,

$$Y^{(1/2)} = b_0 + b_1 X + b_2 X^2,$$

where Y was the length in millimeters, X was the age in years, and b_0 , b_1 , and b_2 were parameters. The square-root transformation of the dependent variable was necessary to help adjust for heteroscedacity. That is, to correct for the fact that the variance of length increased with age. We compared before and after growth by testing for equal regressions at the 90% confidence level.

Mean lengths of trout by age were calculated for each year and station. But this only gave mean lengths for the calendar dates of the individual population estimates, and the population estimates for each station were not conducted on the same date every year. They varied by as much as 1 month over the 10 years of study, and they were conducted during a period of rapid trout growth (September and October). Scales were not measured, so lengths of trout could not be back calculated to annulus formation by standard methods. Therefore, we used the seasonal growth data of Cooper (1953) to estimate the proportion of the total annual growth occurring by each calendar date. Then we used the proportions to adjust the ages of trout in relation to annulus formation (growing season). The mean lengths of trout at these computed ages for each year and station were then treated as single observations in developing the polynomial regressions.

Catch and effort surveys

Annual surveys of catch and effort were conducted for 1 year before the slotted size limit, 1976, and 5 years after, 1979 through 1983. To allow for a transition period and to be consistent with our treatment of the population data, we only used the 1980 through 1983 surveys to compute the after period statistics. Unfortunately, two problems limited the conclusions which could be drawn from these creel surveys. First, only 1 year of before data (1976) was available, and we do not know how representative that year was of the entire period. And second, the 1976 survey was conducted before the slotted size limit experiment was designed (Alexander et al. 1979), and no confidence bounds were calculated for its estimates.

These surveys were designed to estimate total catch of trout, both harvested and released, and total man-hours of fishing effort. Stratified, random sampling methods were used (Alexander and Shetter 1967; Merna et al. 1981; or Malvestuto 1983). A clerk made progressive instantaneous counts by floating each section in a canoe and counting the number of anglers at specified times of the day in 1- to 2-km subsections. Catch per hour was obtained by interviewing anglers on the river, usually after their fishing trip was completed.

Anglers were asked the length of their fishing trip and how many trout of each species they had caught and released. Trout in the angler's possession (those harvested) were counted and identified to species. Finally, we estimated total catch by multiplying the total hours fished per day by the average catch per hour per day.

Obviously, estimates of trout caught and released were dependent on the honesty of the anglers; their ability to distinguish between brown, brook, and rainbow trout; and their ability to recall the exact number and species and approximate sizes of trout they caught and released. To help test the accuracy of these catch-and-release reports from the general public, a small group of knowledgeable fishermen was recruited to keep accurate records of sizes and species of trout they caught. These cooperating anglers were not interviewed in the general census, so their catches and the catches of the general public were assumed to be two independent random samples from the same population of trout. Percent species and size composition of these two samples were tested for differences using a simple chi-square test (comparison of proportions from two independent samples, Snedecor and Cochran 1971). We used the 90% significance level for these tests, also.

Model Validation

Prior to imposing the slotted limit, TROUT.DYNAMICS was used to predict its effects on the brown trout fishery (Clark et al. 1980). We compared the real-world data from the fishery to these predictions to help evaluate the validity of the model. More specifically, the size and age structure of the brown trout population and the catch of brown trout predicted by the model were compared to those estimated in the field experiment.

Results and Discussion

Earlier research demonstrated that changes in daily possession limits did not affect trout populations while size limits had strong effects (Shetter 1969; Hunt 1970; Latta 1973). The ineffectiveness of possession limits was due primarily to the rarity of anglers catching their limit of trout. Size limits were effective because they applied to every single trout caught. Therefore, even though the daily possession limit increased from three to five trout, we assumed any effects of the new regulations would be due to the change in size limits.

Field Experiment

Trout population statistics

Brown trout.—The abundance of brown trout of all sizes decreased significantly in both study and control sections (Table 1). In the Mainstream, brown trout smaller than 203 mm decreased 8%, brown trout between 203 and 305 mm decreased 32%, and brown trout 305 mm or larger decreased 47%. In the North Branch, the respective decreases were 19%, 24%, and 44%.

We expected reductions in brown trout abundance in the Mainstream because a greater harvest was permitted under the slotted limit, but we did not expect reductions in the North Branch where regulations remained constant. Apparently, environmental conditions changed in some way, and we were faced with the problem of separating effects of changing fishing regulations from effects of changing environmental conditions. We use "environmental conditions" here in the broad sense to refer to anything not measured in the experiment.

As an approach to separating effects, we examined how the observed size structures were formed through the biological processes of recruitment, survival, and growth. "Recruitment" was defined as the annual number of young fish born and surviving to age 0 (6 months old). We excluded an exceptionally large 1978 year class from our calculations. This year class was twice as large as any other year class for both study and control sections. Including it in the calculations would have inflated mean numbers at age and misrepresented the effects of the regulation. Sample sizes of brown trout scales used to determine the age composition of these populations were 1,097 for the Mainstream and 1,628 for the North Branch in the before period and 1,117 for the Mainstream and 1,564 for the North Branch in the after period.

We found a significant decrease in annual recruitment of brown trout in both study and control sections but no change in annual survival rates, except at older ages where survival was influenced by changes in fishing mortality (Table 2). Average recruitment of age-0 fish decreased 10% in the Mainstream and 23% in the North Branch. Environmental factors such as weather and climate most often affect fish populations through recruitment of young fish (Cushing 1977; Backiel and Le Cren 1978). Perhaps environmental conditions were less favorable for recruitment of brown trout in the after period.

Even without changes in regulations, reduced recruitment alone would have led to reductions in abundance of older, larger brown trout in both streams. However, regulations did change in the Mainstream causing additional mortality of 203- to 305-mm brown trout through harvest. This harvest mortality added to the environmental effect to reduce the number of larger, older brown trout even further. More specifically, the survival rate from age 0 to 1 in the Mainstream did not change. Brown trout of this age were smaller than 203 mm and not affected by harvest. Survival from age 1 to 3 decreased significantly under the slotted limit.

Brown trout of this age were between 203 and 305 mm. Apparently, fishing mortality added to the existing natural mortality and reduced survival.

Survival from age 3 to 4 did not change significantly in the Mainstream (Table 2). About half of the brown trout at this age were smaller and half larger than 305 mm, so about the same proportion of fish in the age group was vulnerable to harvest under each regulation; the smaller half under the slotted limit and the larger half under the 305-mm limit.

In the North Branch, survival of brown trout did not change significantly in the after period until age 2, the age they began to exceed the minimum size limit of 254 mm. Here survival decreased from 0.48 to 0.35 (Table 2). This suggested survival decreased due to an increase in fishing pressure. We could not detect a significant increase in pressure in creel survey data, but the trend in pressure over time was increasing. One result that seemed to contradict this idea, however, was an apparent increase in survival rate from age 3 to 4, from 0.05 to 0.14. If fishing pressure had increased, one would have expected this survival rate to decrease. Nevertheless, we think there probably was an increase in fishing pressure. Both creel survey estimates of fishing pressure and the survival estimate from age 3 to 4, which ran counter to this idea, suffered from low sample sizes. The problems with the creel survey were mentioned earlier. With regard to the survival estimate, the number of age-4 trout averaged only 3 per ha before and 4 per ha after. Also, growth of brown trout was relatively slow in the Au Sable River after age 4, and this made aging of these older trout less reliable (Beamish and McFarlane 1983).

While fishing and environmental factors combined to reduce abundance of brown trout in both study and control streams, this did not lead to an increase in growth rates. Growth of brown trout did not change significantly in the Mainstream, and in the North Branch a slight, but statistically significant decrease in growth was detected. The growth regressions for Mainstream brown trout were:

$$Y^{(1/2)} = 5.71 + 4.95 X - 0.53 X^2,$$

$$R^2 = 0.99,$$

for the before period and

$$Y^{(1/2)} = 6.14 + 4.59 X - 0.47 X^2,$$

$$R^2 = 0.99,$$

for the after period. In each case Y was total length in millimeters and X was age in years. Plots of residuals showed that these regression models were appropriate for the data. The test of equal regressions indicated the lines were not significantly different.

The growth regressions for North Branch brown trout were:

$$Y^{(1/2)} = 5.00 + 5.89 X - 0.64 X^2,$$

$$R^2 = 0.99,$$

for the before period and

$$Y^{(1/2)} = 4.97 + 5.83 X - 0.65 X^2,$$

$$R^2 = 0.99,$$

for the after period. Plots of residuals showed that these regression models were appropriate. The test of equal regressions indicated the lines were significantly different.

The classical inverse relationship between individual growth rate and abundance was not observed in these brown trout populations. There are at least two possible explanations. First, the decreased growth in the North Branch suggested environmental conditions might have acted to reduce growth, along with recruitment, in the after period. If so, the additional reduction in abundance caused by the slotted limit in the Mainstream could have increased growth there, perhaps enough to balance the negative environmental effect and to result in no net change in growth. But even if the regulation did cause this slight improvement in growth, the relatively larger increase in mortality it caused between ages 1 and 3 was clearly the more important effect in determining the abundance of brown trout larger than 305 mm.

Second, while the numbers of brown trout in both streams decreased, the numbers of brook trout and rainbow trout increased. We will give more detail about brook trout and rainbow trout later, but the net result of these shifts in abundance was that the total abundance of all trout increased significantly in both study and control streams. In the Mainstream, abundance of all trout changed from $2,964 \pm 72$ per ha in the before period to $3,236 \pm 76$ per ha in the after period, a 9% increase. In the North Branch, abundance of all trout changed from $3,113 \pm 35$ per ha to $3,711 \pm 45$ per ha, a 19% increase. Thus, overall trout abundance increased substantially more in the North Branch than the Mainstream, and this might explain why a decrease in growth of brown trout was detected in the North Branch. The second hypothesis seems more reasonable than the first, but it is not entirely consistent. We will show later that the growth of brook trout did not change significantly in the North Branch, despite the 19% increase in abundance of all trout that occurred there.

Brook trout.—The abundance of brook trout of all sizes increased significantly in both the Mainstream and the North Branch with the exception of larger fish (203 to 304 mm) in the Mainstream for which no significant change in abundance was detected (Table 3). Brook trout smaller than 203 mm increased by 64% in the Mainstream and 61% in the North Branch. Brook trout from 203 to 304 mm increased 26% in the North Branch. Brook trout 305 mm or larger were extremely rare. Not enough of them were collected to determine if changes in their abundance occurred.

We did not expect to find any changes in the numbers of brook trout in either the North Branch or the Mainstream. We can think of no mechanism by which fishing or fishing regulations could have caused changes in both study and control sections. Apparently, environmental conditions were responsible. Perhaps the same conditions which were detrimental to brown trout recruitment were favorable to brook trout recruitment.

Annual recruitment of age-0 brook trout increased significantly in both study and control sections, a 52% increase in the Mainstream and a 40% increase in the North Branch (Table 4). In addition, the survival rate of these age-0 fish to age 1 increased significantly in both streams. This resulted in a significant, 145% increase in the average number of age-1 brook trout in the Mainstream and a significant, 131% increase in the average number of age-1 brook trout in the North Branch. The number of brook trout older than age 1 also increased significantly in the North Branch, but we could detect no significant change in the number of older fish in the Mainstream. Sample sizes of brook trout scales used to determine the age composition of these populations were 448 for the Mainstream and 1,062 for the North Branch in the before period and 666 for the Mainstream and 1,173 for the North Branch in the after period.

Even though abundance of brook trout increased, no change in their growth was detected in either the Mainstream or the North Branch. The growth regressions for the Mainstream brook trout were:

$$Y^{(1/2)} = 4.73 + 5.60 X - 0.74 X^2,$$

$$R^2 = 0.99,$$

for the before period and

$$Y^{(1/2)} = 5.61 + 4.64 X - 0.54 X^2,$$

$$R^2 = 0.98,$$

for the after period, where X and Y were defined as before. Plots of residuals showed that these regression models were appropriate, and the test of equal regressions indicated the lines were not significantly different.

The growth regressions for the North Branch brook trout were:

$$Y^{(1/2)} = 3.63 + 7.25 X - 1.15 X^2,$$

$$R^2 = 0.98,$$

for the before period and

$$Y^{(1/2)} = 3.89 + 6.78 X - 1.04 X^2,$$

$$R^2 = 0.99,$$

for the after period. Plots of residuals showed that these regressions were appropriate, and the test of equal regressions indicated the lines were not significantly different.

Density-dependent growth was not observed in the brook trout populations. Perhaps the magnitude of the change in abundance observed was not enough to trigger a change in growth. The maximum change in abundance of brook trout was the 63% increase in the North Branch. However, when the reduction in abundance of brown trout is considered, the maximum change in the numbers of all trout was only a 19% increase in the North Branch.

Rainbow trout.—The abundance of rainbow trout smaller than 203 mm increased significantly in the Mainstream (+48%), and an increase in abundance of 203- to 304-mm fish of 54% was nearly significant (Table 5). The average number of rainbow trout larger than 305 mm did not seem to change, but reliable confidence bounds could not be calculated for these larger fish because of small sample sizes. No rainbow trout were collected in the North Branch.

Abundance of rainbow trout of all age groups increased in the after period, although the increases in numbers of 2-year-old and 3-year-old fish were not statistically significant (Table 6). No significant changes in survival rates were detected, so the increase in recruitment of age-0 fish (+86%) was probably responsible for the observed increases in numbers of age-1 and older fish. The sample sizes of rainbow trout scales used to determine the age composition of these populations were 236 and 392 for the before and after period, respectively.

No changes in growth of rainbow trout were detected. The growth regressions were:

$$Y^{(1/2)} = 3.03 + 6.95 X - 0.87 X^2,$$

$$R^2 = 0.99,$$

for the before period and

$$Y^{(1/2)} = 3.91 + 6.38 X - 0.78 X^2,$$

$$R^2 = 0.99,$$

for the after period, where X and Y were defined as before. Plots of residuals showed that these regression models were appropriate, and the test of equal regressions indicated the lines were not significantly different.

Catch and effort statistics

The accuracy of the calculations to separate catch into species and size categories depended on the reliability of the angler interviews, that is, the ability of the anglers to remember and accurately report the number, species, and size of trout they caught and released. Therefore, before interpreting catch estimates we checked the reliability of the interviews by comparing species and size composition of catches reported in them to those reported by cooperating anglers.

We found the cooperators reported catching a significantly greater proportion of brown trout and a smaller proportion of trout less than 203 mm in size than the general public. However, when only fish larger than 203 mm were evaluated, no significant difference was found in the size composition of the brown trout catches from the Mainstream (Table 7). The first result can be interpreted in two ways. First, the general public actually caught trout with the same species and size composition as the cooperators. This would mean they incorrectly identified about 25% of the brown trout they caught and released as brook trout, and they overestimated, by about 25%, the number of sublegal trout they caught and released. Or second, the differences in species and size composition were real because the cooperators were better than average trout fishermen and were able to catch more larger, harder-to-catch brown trout.

We think the second interpretation is correct because the cooperators tended to concentrate their fishing effort in times when larger brown trout were actively feeding (that is,

during fly hatches in the spring and late in the evening during summer). Therefore, we think the species and size compositions reported by the general public were accurate, and we used them without adjustment to estimate total catches and harvests. In any case, estimating the size composition of the catch for brown trout larger than 203 mm was the most important task for evaluating the slotted limit, and no significant differences were found between public and cooperator catches of these larger brown trout.

Brown trout.—Despite the limited before period survey data, it seemed obvious that total harvest of brown trout from the Mainstream changed significantly (Table 8). It increased from an estimated 440 brown trout per year under the 305-mm minimum limit to an average of 2,090 brown trout per year under the slotted limit. Of course, numbers of trout were not the only difference in the total harvest. The average size of fish harvested under the slotted size limit was much smaller than under the 305-mm minimum limit. Almost all the former were between 203 and 305 mm, while the latter were all over 305 mm. For the same time periods, no significant change was observed in total harvest of brown trout in the North Branch (Table 8).

No significant change in total fishing pressure could be detected for either the Mainstream or the North Branch in these data (Table 8), but we think there probably was a modest increase in pressure. The trend in estimates of fishing pressure over time were increasing in both streams.

There were only two other creel survey statistics we can confidently say changed significantly, and those were the changes mandated by law. The number of 203- to 305-mm brown trout harvested increased from near zero under the 305-mm limit to 2,060 under the slotted limit, and the number of 305- to 406-mm brown trout harvested decreased from 410 under the 305-mm limit to near zero under the slotted limit (Table 8). No deliberate effort was made to estimate the illegal harvest, but the creel census clerks did observe a small harvest of illegal-sized fish during the study. Hopefully, this illegal harvest was negligible or was no more severe under the slotted limit than the 305-mm limit.

The estimated catch of 305- to 406-mm brown trout, that is, the sum of harvest and catch and release, was nearly the same in the after period as the before period in both study and control sections—930 before versus 1,050 after in the study section. Yet, the number of brown trout of this size in the population decreased by over 40% (Table 1). Thus, it appears anglers caught the same number of fish, even though fewer fish were available. Either they improved their fishing skills over the years, or they caught, released, and recaptured the average brown trout from one and one-half to two times. The former explanation is flattering, but difficult to accept by those of us who have observed the behavior of anglers over the years. The latter explanation makes the most sense because an increase in the release rate of brown trout in this size category was mandated by the slotted limit on the Mainstream. In the North Branch, it appears in general that the release rate of trout has increased over the years, even

though the fish may be legal to harvest. Anglers reported releasing about 41% of the legal-sized brown trout on the North Branch in 1976 and about 57% in the 1980's. This increase in release rate was probably responsible for maintaining a relatively constant catch of 305- to 406-mm brown trout in the North Branch (730 before versus 830 after) while abundance declined in the population.

Brook trout.—No significant change in the number of brook trout harvested was detected in either study or control sections despite the overall increase in brook trout abundance. However, we found a significant increase in the number of legal-sized brook trout caught and released, assuming the confidence bounds for the 1976 estimates would have been less than $\pm 100\%$ of the estimates (Table 9). Thus, total catch of brook trout, both harvested and released, increased by about the same amount as brook trout abundance.

We found an increasing tendency for anglers to voluntarily release legal-sized brook trout, which was consistent with our findings for brown trout. In the Mainstream, anglers reported releasing 56% of their brook trout catch in 1976, while they reported releasing 80% of their catch from 1980 to 1983. In the North Branch, anglers reported releasing 40% of their brook trout catch in 1976, while they reported releasing 61% of their catch from 1980 to 1983.

Rainbow trout.—We found a significant increase in the total annual catch of legal-sized rainbow trout in the Mainstream, assuming the confidence bounds for the 1976 estimates would have been less than $\pm 100\%$ of the estimates. Anglers caught 140 legal-sized rainbow trout in 1976 and 490 (± 220) per year from 1980 to 1983. Legal-sized rainbows caught in 1976 were all larger than 305 mm, but those caught from 1980 to 1983 were all between 203 and 305 mm. An additional 110 (± 130) rainbow trout per year between 305 mm and 406 mm were caught and released in the after period. The increase in catch of legal-sized rainbow trout was due partly to the change in regulations and partly to the increase in recruitment of juvenile fish, but we cannot separate the effects of these two factors because rainbow trout were not present in the control stream.

Model Validation

Trout population

Brown trout were less abundant under the slotted size limit than we predicted earlier with TROUT.DYNAMICS. The number of brown trout estimated in field surveys was less than the number predicted for every size and age group, and, in no case, did one of the predicted values fall within the confidence interval for its corresponding estimate (Tables 10 and 11). However, predicted survival rates were all within the confidence intervals for their corresponding estimates, except for the survival rate from age 3 to 4 (Table 11). In the latter case, the estimated survival was less than predicted.

Differences between model predictions and field estimates could be due to errors in the model structure or assumptions, errors in estimating model parameters, or errors in field estimates. However, it appeared that the major reason for differences in brown trout abundance was the unexpected decrease in recruitment of young fish in the after period. The number of age-0 brown trout estimated in the field was 28% less than the predicted number (Table 11), and because estimated and predicted survival rates were essentially the same, the difference in the total number of brown trout was about the same as the difference in recruitment (30%). We used parameters for recruitment in the model that were derived from before period data, and they probably gave a good representation of recruitment under the conditions existing then. However, the model was not structured to consider the effects of changing environmental conditions, and even if it was, we could not have predicted the direction of environmental changes. Although, we did evaluate the potential effects of random environmental changes on recruitment in an earlier report (Clark 1984).

On the positive side, it does appear the model did a good job of predicting the changes in the population size and age structure on a per-recruit basis. That is, if we had given the model the same number of recruits as the real fishery, it would have predicted the size and age structure accurately (within the confidence interval of the field estimates). Therefore, the traditional model assumptions we used, that fishing mortality and natural mortality would be additive as competing probabilities of death and that average individual growth would remain constant over time, were valid. Also, our original method of assigning the various components of mortality to each age group based on length frequencies was valid.

Trout catch

We cannot directly compare the catch predicted with the model (Clark et al. 1980) to the catch estimated from the creel survey. The catch from the model represented only the small index areas where trout populations were sampled, while the creel survey represented the entire study section. Trout populations within the index areas were probably close to average for the rest of the study section, but we have no quantitative data to prove it. The main reason the fisheries in the index areas were not representative of the whole section was a difference in fishing effort. Fishing effort per unit area was higher in the index areas than in most other parts of the study section. The index areas were accessible to fishermen from roads and public land, while much of the rest of the section was inaccessible. The fishing rate used in the model was estimated from data collected in the index areas, so the model predicted a greater catch per unit area than the creel survey estimated.

Nevertheless, it was clear that TROUT.DYNAMICS had a major limitation in its ability to predict the number of fish caught and released. The model assumed all the legal-size fish caught would be harvested, but creel survey statistics showed that more legal-size fish were

released voluntarily than harvested (Table 8). We corrected this limitation and evaluated the effects of voluntary catch and release in another report (Clark 1983).

Fishery Management Implications

The greatest effect of the slotted size limit was not in the trout population itself, but in the change in man's use of the trout population. In the Mainstream, anglers traded the harvest of 305- to 406-mm brown trout for about a fivefold increase in the total number of brown trout harvested, although the new harvest consisted of smaller fish (203 to 305 mm). At the same time, they still caught at least as many 305- to 406-mm brown trout, but had to release them.

Is harvesting five trout between 203 and 305 mm worth as much as harvesting one trout larger than 305 mm? Fenske (1984) surveyed the opinions of Michigan trout anglers and found a nearly even split on a question very similar to this one. Of those questioned, 45% thought it was better to catch five 203-mm trout, while 39% thought it was better to catch one 305-mm trout. Is catching and releasing a 305-mm trout worth as much as catching and harvesting a 305-mm trout? We suspect most anglers would answer no to this question, yet there is no doubt catching and releasing a trout has considerable value. The main point of these questions was to suggest that beyond protecting trout populations from extermination, the primary function of fishing regulations is to satisfy different, and often competing, angler preferences. From this standpoint, slotted size limits have the desirable feature of being able to compromise between those who prefer to harvest many small trout and those who prefer to catch fewer larger trout. However, it should also be recognized that this same compromise could be achieved more simply by dividing a stream into two smaller sections; one section having an 203-mm minimum limit for the first group of anglers and one having a 305-mm minimum limit for the second group of anglers. Likewise, a similar compromise could be achieved with a 254-mm minimum limit applied to the whole area.

Based on both the model analysis and field results, the slotted limit allowing harvest of 203- to 305-mm and over 406-mm trout was not as good as a 305-mm minimum size limit in producing larger trout. Harvest mortality had a greater effect in reducing survival of trout to larger sizes than on increasing growth rate. Results of other studies also indicated growth rates of trout in streams were independent of relatively large changes in population density and fishing intensities (Cooper 1949; McFadden et al. 1967; McFadden 1969; Bachman 1984). Furthermore, results of this study suggested that any reduction in density of brown trout might be compensated by an increase in density of competing species, such as brook trout, instead of the desired increase in brown trout growth.

What is the future of slotted size limits in trout fisheries management? This should depend primarily on their popularity among anglers and the need for managers to devise

compromises between total harvest and catching trophy fish. We think slotted limits will always remain in the realm of "special" or "quality" regulations and will only be used on unique or special fisheries. They are just one alternative in a large array of regulations that adequately serve the most important management objective of protecting wild trout stocks from overfishing. Other biological effects of regulations are comparatively unimportant, except for their influence on satisfying the desires of different factions within the angling community.

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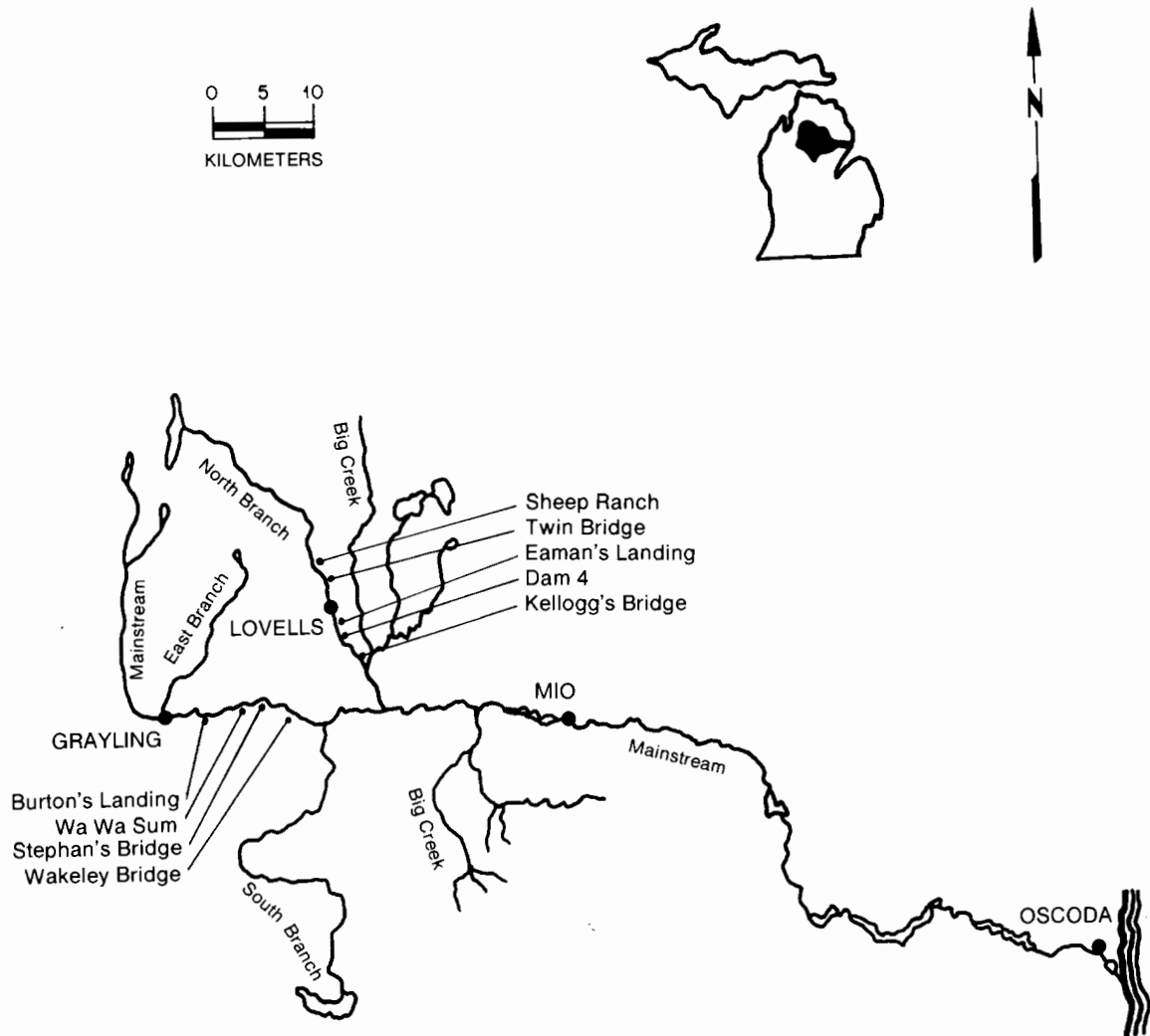


Figure 1. Au Sable River basin in Michigan. The study section was from Burton's Landing to Wakeley Bridge on the Mainstream. The control section was from Sheep Ranch to Kellogg's Bridge on the North Branch.

Table 1. Mean number of brown trout per hectare in fall populations by selected size categories. Confidence bounds for the 90% level of significance are in parentheses.

Stream, time period, (size limit)	Size category			
	Trout smaller than 203 mm	203- to 304-mm trout	305- to 406-mm trout	Trout 406-mm or larger
<u>Mainstream</u>				
1974-1978 (305-mm minimum)	1,485 (±55)	467 (±16)	45 (±6)	2 (-)
1983-1983 (Slotted)	1,374 (±53)	316 (±15)	26 (±4)	<1 (-)
<u>North Branch</u>				
1974-1978 (254-mm minimum)	1,299 (±25)	213 (±7)	58 (±6)	5 (±1)
1980-1983 (254-mm minimum)	1,053 (±29)	162 (±6)	33 (±3)	2 (±1)

Table 2. Mean number per hectare of brown trout by age and annual survival for fall populations. Confidence bounds for the 90% level of significance are in parentheses.

Stream, time period, (size limit)	Age				
	0	1	2	3	4
<u>Mainstream</u>					
1974-1978 (305-mm minimum)					
Number	1,114 (±53)	407 (±20)	283 (±22)	183 (±18)	11 (±4)
Survival rate	0.36 (±0.02)	0.70 (±0.06)	0.65 (±0.07)	0.05 (±0.02)	
1980-1983 (Slotted)					
Number	1,002 (±51)	367 (±24)	197 (±33)	86 (±18)	2 (±1)
Survival rate	0.37 (±0.03)	0.54 (±0.08)	0.44 (±0.09)	0.02 (±0.01)	
<u>North Branch</u>					
1974-1978 (254-mm minimum)					
Number	1,184 (±23)	229 (±9)	107 (±8)	51 (±6)	3 (±1)
Survival rate	0.19 (±0.01)	0.47 (±0.04)	0.48 (±0.06)	0.05 (±0.01)	
1980-1983 (254-mm minimum)					
Number	906 (±29)	194 (±9)	82 (±10)	29 (±7)	4 (±2)
Survival rate	0.21 (±0.01)	0.42 (±0.05)	0.35 (±0.07)	0.14 (±0.07)	

Table 3. Mean number of brook trout per hectare in fall populations by selected size categories. Confidence bounds for the 90% level of significance are in parentheses.

Stream, time period, (size limit)	Size category	
	Trout smaller than 203 mm	203- to 304-mm trout
<u>Mainstream</u>		
1974-1978 (203-mm minimum)	599 (± 35)	10 (± 3)
1980-1983 (Slotted)	980 (± 44)	13 (± 2)
<u>North Branch</u>		
1974-1978 (203-mm minimum)	1,492 (± 26)	46 (± 5)
1980-1983 (203-mm minimum)	2,403 (± 39)	58 (± 5)

Table 4. Mean number per hectare of brook trout by age and annual survival for fall populations. Confidence bounds for the 90% level of significance are in parentheses.

Stream, time period, (size limit)	Age			
	0	1	2	3
<u>Mainstream</u>				
1974-1978 (203-mm minimum)				
Number	522 (±34)	74 (±10)	13 (±3)	- (-)
Survival rate	0.14 (±0.03)	0.17 (±0.07)	0.00 (-)	- (-)
1980-1983 (Slotted)				
Number	792 (±42)	181 (±17)	18 (±5)	1 (±1)
Survival rate	0.23 (±0.03)	0.10 (±0.04)	0.06 (±0.08)	- (-)
<u>North Branch</u>				
1974-1978 (203-mm minimum)				
Number	1,440 (±24)	175 (±10)	24 (±4)	<1 (0)
Survival rate	0.13 (±0.01)	0.14 (±0.04)	0.01 (-)	- (-)
1980-1983 (Slotted)				
Number	2,010 (±34)	404 (±19)	48 (±11)	<1 (-)
Survival rate	0.20 (±0.01)	0.12 (±0.04)	0.01 (-)	- (-)

Table 5. Mean number of rainbow trout per hectare by selected size categories in fall populations in the Mainstream. Confidence bounds for the 90% level of significance are in parentheses. No rainbow trout were collected in the North Branch.

Time period and size limit	Size category		
	Trout smaller than 203 mm	203- to 304-mm trout	Trout 305 mm or larger
1974-1978 (305-mm minimum)	341 (± 35)	13 (± 2)	2 (-)
1980-1983 (Slotted)	506 (± 45)	20 (± 5)	2 (-)

Table 6. Mean number per hectare of rainbow trout by age and annual survival for fall populations in the Mainstream. Confidence bounds for the 90% level of significance are in parentheses. No rainbow trout were collected in the North Branch.

Time period and size limit	Age			
	0	1	2	3
1974-1978 (305-mm minimum)				
Number	314 (± 35)	29 (± 3)	8 (± 2)	1 (-)
Survival rate	0.09 (± 0.03)	0.27 (± 0.12)	0.13 (-)	
1980-1983 (Slotted)				
Number	584 (± 44)	52 (± 9)	14 (± 5)	4 (± 1)
Survival rate	0.09 (± 0.02)	0.27 (± 0.13)	0.29 (± 0.18)	

Table 7. Size composition of brown trout larger than 203 mm reported caught by general public and cooperators in the Mainstream from 1980 through 1983. No significant differences were found in percent size composition.

Size	General public		Cooperators	
	Number	Percent	Number	Percent
203 mm-305 mm	741	88.2	253	91.0
305 mm-406 mm	97	11.6	24	8.6
>406 mm	2	0.2	1	0.4

Table 8. Mean numbers per year of brown trout harvested and caught and released in selected size categories. Confidence bounds for 90% level of significance are in parentheses. No confidence bounds were calculated for the 1976 survey.

Stream, time period, (size limit)	Size categories								Total fishing pressure (hours)
	203 to 305 mm ¹		305 to 406 mm		Over 406 mm		Total ¹		
	Harvested	Released	Harvested	Released	Harvested	Released	Harvested	Released	
Mainstream									
1976 (305-mm minimum)	—	—	410	520	30	40	440	—	30,500
1980-1983 (Slotted)	2,060 (±690)	5,440 (±1,650)	—	1,050 (±530)	30 (±40)	70 (±121)	2,090 (±670)	5,510 (±1,660)	34,500 (±4,700)
North Branch									
1976 (254-mm minimum)	1,110	770	430	300	60	40	1,600	1,110	24,300
1980-1983 (254-mm minimum)	1,030 (±330)	1,360 (±530)	360 (±160)	470 (±230)	50 (±50)	60 (±70)	1,440 (±430)	1,890 (±710)	26,800 (±3,600)

¹For North Branch this includes only trout larger than 254 mm because a 254-mm minimum size limit was in effect.

Table 9. Mean numbers per year of brook trout harvested and caught and released.
Confidence bounds for the 90% level of significance are in parentheses.

Stream, time period, (size limit)	Number of brook trout:	
	Harvested	Released
<u>Mainstream</u>		
1976 (203-mm minimum)	530 (-)	680 (-)
1980-1983 (Slot)	480 (±160)	1,970 (±630)
<u>North Branch</u>		
1976 (203-mm minimum)	1,430 (-)	910 (-)
1980-1983 (Slot)	1,620 (±480)	2,550 (±980)

Table 10. Estimated versus predicted number by size group of brown trout fished under the slotted size limit. Estimates were derived from 1980 to 1983 population surveys, excluding the large 1978 year class. Predictions were made in 1979 using TROUT.DYNAMICS.

Size	Number per hectare	
	Estimated	Predicted
<203 mm	1,374 (±53)	1,872
203 – 305 mm	253 (±12)	448
305 – 406 mm	26 (±4)	39
>406 mm	<1 (-)	2
Total	1,654 (±64)	2,361

Table 11. Estimated versus predicted number and survival rates by age for brown trout fished under the slotted size limit. Estimates were derived from 1980 to 1983 population surveys, excluding the large 1978 year class. Predictions were made in 1979 using TROUT.DYNAMICS.

Age	Number per hectare		Annual survival rates	
	Estimated	Predicted	Estimated	Predicted
0	1,002 (±51)	1,395	0.37 (±0.03)	0.36
1	367 (±24)	502	0.54 (±0.08)	0.62
2	197 (±33)	311	0.44 (±0.09)	0.45
3	86 (±18)	139	0.02 (±0.01)	0.08
4	2 (±1)	14		

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