No. 462

FACTORS LIMITING JUVENILE STEELHEAD SURVIVAL IN STREAMS TRIBUTARY TO MINNESOTA WATERS OF LAKE SUPERIOR

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FACTORS LIMITING JUVENILE STEELHEAD SURVIVAL IN STREAMS TRIBUTARY TO MINNESOTA WATERS OF LAKE SUPERIOR

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Abstract.—Numbers of adult steelhead spawning in many of Minnesota's tributary streams to Lake Superior have declined. Restrictive regulations have been implemented to attempt to halt the decline and information is being collected to develop rehabilitation strategies. Increasing smolt yield from tributary streams may increase steelhead abundance but factors limiting the smolt yield are poorly understood. Survival rates were estimated and potential limiting variables measured to develop a linear regression model relating parr survival to environmental factors. Survival rates through two summers of growth varied from 0.7% to 9.0%. Flooding shortly after stocking, substrate diameter, early winter snowfall, summer discharge, and the amount of woody debris were correlated with survival. If increasing smolt yield is desirable, riparian forests should not be logged and beaver should be removed from streams rearing steelhead. Planting conifers in riparian zones is suggested as a long term strategy to discourage beaver infestation. These strategies will probably be implemented most effectively if fisheries managers are members of multidiscipline resource management teams. Experimental addition of woody debris is recommended to verify its limiting effect, and to determine how it functions to improve survival of steelhead parr.

INTRODUCTION

Angler catches of adult steelhead (Oncorhynchus mykiss) during the spring spawning runs have declined in Minnesota's tributaries to Lake Superior during the last two decades. Adult returns to the French River fish trap have also declined since 1991. The Minnesota DNR developed a steelhead management plan in 1991 with the goal to "...stop the decline of adult steelhead, and to gather the necessary information to rehabilitate wild steelhead stocks" (MNDNR 1991). Harvest restrictions were imposed to attempt to stop the decline, virtually eliminating legal angling harvest. To successfully rehabilitate, we need to determine how limiting factors such as habitat, weather, predation and competition limit steelhead abundance and then mitigate their effects. In the interim, increasing the smolt yield may improve fishing and assist with rehabilitation. However, factors limiting the

1 This project was funded in part by the Federal Aid in Sport Fish Restoration (Dingell-Johnson) Program. Completion Report, Study 677, D.J. Project F-26-R Minnesota.
smolt yield are poorly understood. The focus of this work was on the factors limiting smolt yield.

After the factors limiting smolt yield are identified, habitat management may be instituted to increase yield and the utility of the habitat management will require evaluation. Evaluation is possible only when pretreatment densities and survival rates are known. Precise estimates of survival rates from stocking through two summers of growth were lacking. One objective of this study was to determine expected densities and survival rates of parr through two summers of growth in North Shore streams before habitat is altered.

A second objective of this study was to develop a multiple regression model of steelhead parr survival in Minnesota to identify limiting factors. Elements of a regression model are either limiting factors or correlates of limiting factors, serving as focal points for habitat management or additional research.

**METHODS**

**Study Area**

Our study area was in the Minnesota portion of the Lake Superior watershed, an area known as the North Shore (Figure 1). North Shore watersheds are dominated by second growth forests and have little groundwater input. Channel substrates are rocky and fish species are few. Our study reaches were principally inhabited by one or more of the following species: blacknose dace (*Rhinichthys atratulus*), longnose dace (*Rhinichthys cataractae*), slimy sculpin (*Cottus cognatus*), creek chub (*Semotilus atromaculatus*), and brook trout (*Salvelinus fontinalis*). A few brown trout (*Salmo trutta*) or specimens of other minnow species were also found. Selected data typical of the water chemistry and geomorphology of North Shore streams is presented in Table 1.

Figure 1. Study stream locations on the North Shore of Lake Superior, Minnesota.
Table 1. Selected weather and geomorphology data measured in four study reaches from 1991-1995 in four streams tributary to Lake Superior, Minnesota. Units of measure are in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Amity Creek</th>
<th>French River</th>
<th>Stewart River</th>
<th>Two Island River</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hydraulic Structure</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Very sallow fast</td>
<td>29.5</td>
<td>14.5</td>
<td>58.5</td>
<td>15.7</td>
</tr>
<tr>
<td>% Shallow fast</td>
<td>46.0</td>
<td>46.2</td>
<td>9.5</td>
<td>66.3</td>
</tr>
<tr>
<td>% Deep fast</td>
<td>0.0</td>
<td>2.3</td>
<td>0.4</td>
<td>8.5</td>
</tr>
<tr>
<td>% Very shallow slow</td>
<td>1.9</td>
<td>0.5</td>
<td>8.6</td>
<td>1.1</td>
</tr>
<tr>
<td>% Shallow slow</td>
<td>16.1</td>
<td>21.1</td>
<td>20.9</td>
<td>4.8</td>
</tr>
<tr>
<td>% Deep slow</td>
<td>6.4</td>
<td>15.4</td>
<td>2.0</td>
<td>3.5</td>
</tr>
<tr>
<td>% Forest debris</td>
<td>0.0</td>
<td>1.3</td>
<td>0.2</td>
<td>0.8</td>
</tr>
<tr>
<td>Mean channel width (m)</td>
<td>5.3</td>
<td>4.0</td>
<td>4.5</td>
<td>6.3</td>
</tr>
<tr>
<td>Sector gradient (m·km(^{-1}))</td>
<td>20.6</td>
<td>11.9</td>
<td>11.5</td>
<td>12.2</td>
</tr>
<tr>
<td><strong>Substrate</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Muck-detritus</td>
<td>0.0</td>
<td>0.6</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>% Silt-Clay (&lt;0.062 mm dia.)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.6</td>
</tr>
<tr>
<td>% Sand (0.062-3.2 mm dia.)</td>
<td>0.0</td>
<td>21.3</td>
<td>0.0</td>
<td>5.3</td>
</tr>
<tr>
<td>% Gravel (3.2-64 mm dia.)</td>
<td>31.3</td>
<td>50.5</td>
<td>38.6</td>
<td>34.8</td>
</tr>
<tr>
<td>% Cobble (64-128 mm dia.)</td>
<td>20.0</td>
<td>13.1</td>
<td>31.2</td>
<td>23.3</td>
</tr>
<tr>
<td>% Rubble (128-256 mm dia.)</td>
<td>16.0</td>
<td>7.9</td>
<td>16.8</td>
<td>15.5</td>
</tr>
<tr>
<td>% Small boulder (256-508 mm dia.)</td>
<td>13.9</td>
<td>5.7</td>
<td>8.1</td>
<td>12.1</td>
</tr>
<tr>
<td>% Large boulder (&gt;508 mm dia.)</td>
<td>10.1</td>
<td>1.0</td>
<td>5.3</td>
<td>8.3</td>
</tr>
<tr>
<td>% Ledge rock</td>
<td>8.7</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Weighted mean substrate diameter (mm)</td>
<td>189</td>
<td>74</td>
<td>146</td>
<td>172</td>
</tr>
<tr>
<td><strong>Discharge (open water)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Highest discharge (m(^3)·sec(^{-1}))</td>
<td>7.412</td>
<td>11.744</td>
<td>89.776</td>
<td>15.307</td>
</tr>
<tr>
<td>Lowest discharge (m(^3)·sec(^{-1}))</td>
<td>0.030</td>
<td>0.0</td>
<td>0.052</td>
<td>0.862</td>
</tr>
<tr>
<td>Median discharge (=50% exceedence, m(^3)·sec(^{-1}))</td>
<td>0.191</td>
<td>0.072</td>
<td>0.693</td>
<td>1.515</td>
</tr>
<tr>
<td><strong>Stream Temperature</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Highest recorded (°C)</td>
<td>24.8</td>
<td>24.4</td>
<td>25.1</td>
<td>17.8</td>
</tr>
<tr>
<td><strong>Water Chemistry</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chlorophyll a accrual rate (mg tile(^{-1})·week(^{-1}))</td>
<td>14.27</td>
<td>*</td>
<td>15.56</td>
<td>16.5</td>
</tr>
<tr>
<td>Total alkalinity (mg(\text{L}^{-1}))</td>
<td>94</td>
<td>54</td>
<td>80</td>
<td>*</td>
</tr>
<tr>
<td>Total dissolved solids (mg (\text{L}^{-1}))</td>
<td>248</td>
<td>104</td>
<td>132</td>
<td>*</td>
</tr>
<tr>
<td>Total phosphorus (mg (\text{L}^{-1}))</td>
<td>&lt;0.005</td>
<td>0.015</td>
<td>&lt;0.005</td>
<td>*</td>
</tr>
<tr>
<td>Nitrate nitrogen (mg (\text{L}^{-1}))</td>
<td>0.028</td>
<td>0.017</td>
<td>0.016</td>
<td>*</td>
</tr>
<tr>
<td>Nitrite nitrogen (mg (\text{L}^{-1}))</td>
<td>&lt;0.001</td>
<td>0.0015</td>
<td>&lt;0.001</td>
<td>*</td>
</tr>
<tr>
<td>pH</td>
<td>8.17</td>
<td>7.78</td>
<td>7.71</td>
<td>*</td>
</tr>
<tr>
<td>Sulfates (mg (\text{L}^{-1}))</td>
<td>9</td>
<td>&lt;1</td>
<td>6</td>
<td>*</td>
</tr>
<tr>
<td>Chlorides (mg (\text{L}^{-1}))</td>
<td>58</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>*</td>
</tr>
<tr>
<td><strong>Riparian Morphology</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean forest canopy density at stream center (%)</td>
<td>36.5</td>
<td>70.3</td>
<td>32.0</td>
<td>52.6</td>
</tr>
</tbody>
</table>

*a* Oswood and Barber (1982)
*b* Not available
Data Collection

Single study reaches in four North Shore streams were stocked with steelhead fry and monitored (Table 2, Figure 1). Study reaches in each of two streams were stocked in June each year from 1991-1994 with unfed steelhead fry at various stocking rates. Natural barriers of various kinds prevented upstream migration of rainbow trout into the study reaches and no fry were stocked upstream of the study reaches. Steelhead parr are protected from angling by a minimum size limit of 40 cm, and angling was minimal in the study reaches.

Dependent Variable

Survival rate through two summers of growth was selected as the dependent variable for multiple regression analysis. Smolt yield would have been the preferred dependent variable but estimating smolt yield was precluded by the absence of smolt traps. Smolt traps capable of surviving floods are costly structures requiring considerable maintenance, and are visually objectionable to many people. As a result, the oldest presmolt age group that could be accurately measured in most streams was the age 1 population in the fall.

Table 2. Steelhead fry stocking schedule from 1991-1994 and study reach descriptions for four streams tributary to Lake Superior, Minnesota.

<table>
<thead>
<tr>
<th>River</th>
<th>Year class</th>
<th>Number stocked</th>
<th>Stocking rate (no./100m²)</th>
<th>Length (km)</th>
<th>Low Flow Surface Area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amity Creek</td>
<td>1992</td>
<td>10,600</td>
<td>67</td>
<td>2.9</td>
<td>1.59</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>20,000</td>
<td>126</td>
<td></td>
<td></td>
</tr>
<tr>
<td>French River</td>
<td>1991</td>
<td>38,700</td>
<td>645</td>
<td>1.5</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>15,000</td>
<td>251</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stewart River</td>
<td>1991</td>
<td>95,600</td>
<td>595</td>
<td>3.6</td>
<td>1.62</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>43,200</td>
<td>267</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Two Island River</td>
<td>1992</td>
<td>13,000</td>
<td>103</td>
<td>2.0</td>
<td>1.27</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>25,600</td>
<td>202</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
the age 1 population estimate, so the entire
reach was electrofished using a mark and
recapture technique. Fish captured during the
marking run were marked by removing the
dorsal tip of the caudal fin. The second
electrofishing encounter for marked fish
followed approximately 48 h after they were
marked. This was sufficient time for fish to
recover and randomly mix with unmarked fish,
and assured equal catchability with unmarked
fish (Peterson and Cederholm 1984). When
marked mortalities were found, a fish of
similar size was removed from the "marked"
data set. All salmonids were measured to the
nearest millimeter total length and released
near the point of capture. Salmonid population
sizes were estimated using the smoothing spline
based methods of Anderson (1995) to reduce
potential bias due to size selection by sampling
gear. The age 1 survival rate was the
estimated population size from the second.
assessment divided by the estimated population
size of YOY from the first assessment. Adult
minnows and sculpins had a narrow size range,
so populations were estimated using the
modified Chapman mark and recapture model
(Ricker 1975).

**Independent Variables**

We evaluated an extensive number of
potential limiting variables in the four represen-
tative streams. The independent variables that
we measured can be included in one of three
general categories: geomorphology, weather,
and competition/predation. One study reach
was established in each stream and year to year
variation in geomorphology was assumed to be
negligible, thus, the geomorphology variables
had four observations. All other independent
variables had eight observations.

Several variables were measured to
assess the limiting effect of in-stream and
riparian geomorphology (Table 2). Water
depth, channel width, water velocity, and
overhead cover were measured during June
through August using methods of Oswood and
Barber (1982) which were slightly modified to
include a very shallow (≤15 cm) depth cate-
gory. This method was selected because it was
rapid and objective, and because stream fea-
tures are categorized similarly in Minnesota's
stream surveys, minimizing the data collection
needed to apply our survival model in other
North Shore streams. Substrates were also
quantified categorically. Channel gradient was
determined from USGS quadrangle topographic
maps. Water samples were collected in August
1991 and analyzed at the Department of Agri-
culture (DOA) laboratory in St. Paul. Riparian
canopy density (Carlson et al. 1990, Li et al.
1994) was estimated at center stream using a
convex forest canopy densiometer (Lemmon
1957).

The chlorophyll a accrual rate (Grimm
and Fisher 1986) during a six week low flow
period was measured to compare primary
production rates in the four study streams.
Thirty-six 75mm X 75mm X 10 mm quarry
tiles were placed in each study sector at equal
depths with equal solar illumination. Six tiles
were randomly selected from each stream
weekly and frozen for later chlorophyll a
analysis at the DOA laboratory.

Stream stage, water temperature, air
temperature, and snowfall were measured to
assess the limiting effect of weather. Stage and
water temperature (Table 2) were measured at
5 s intervals with a temperature-pressure trans-
ducer and means were logged hourly on a data
logger. Stage-discharge functions were calcu-
lated for each stream. Mean hourly stage
could then be used to estimate mean hourly
discharge. Air temperature and snowfall data
were collected at the US Weather Bureau
station at Duluth International Airport and at
private weather stations near Isabella and
Finland Minnesota.

Competition and predation within each
reach were assessed by measuring steelhead
parr growth, competitor densities, and predator
densities (Table 3). Measurements of total
length (mm) and weight (g) were collected
from a random sample of 50 or more YOY
steelhead. Densities (number·100m-2) of YOY
steelhead, adult minnows, sculpins, brook
tROUT, and YOY brook trout were also esti-
mated.
Table 3. Selected competition/predation data measured in four study reaches from 1991-1995 in four streams tributary to Lake Superior, Minnesota. Two data separated by a comma represent means of the first, and second year classes stocked. Two data separated by a dash represents the range of the four observations.

<table>
<thead>
<tr>
<th>Age 0 steelhead, mean weight (g)</th>
<th>Amity Creek</th>
<th>French River</th>
<th>Stewart River</th>
<th>Two Island River</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.987, 4.910</td>
<td>3.147, 2.820</td>
<td>3.358, 4.290</td>
<td>2.451, 2.380</td>
<td></td>
</tr>
<tr>
<td>Age 0 steelhead, mean condition factor (g 10^5·mm^3)</td>
<td>1.018, 1.068</td>
<td>0.902, 0.961</td>
<td>0.941, 1.018</td>
<td>1.052, 0.969</td>
</tr>
<tr>
<td>Adult brook trout (&gt;age 0, number 100 m^-2)</td>
<td>0.20 - 1.00</td>
<td>2.48 - 7.40</td>
<td>0.21 - 6.00</td>
<td>2.0 - 22.1</td>
</tr>
<tr>
<td>Age 0 brook trout 0.00 - 2.91 (number 100 m^-2)</td>
<td>0.00 - 8.60</td>
<td>0.00 - 0.30</td>
<td>4.40 - 22.51</td>
<td></td>
</tr>
<tr>
<td>Slimy sculpin (number 100 m^-2)</td>
<td>17.60 - 65.10</td>
<td>0.00</td>
<td>0.00</td>
<td>26.60 - 41.20</td>
</tr>
<tr>
<td>Blacknose dace (number 100 m^-2)</td>
<td>10.70 - 21.80</td>
<td>20.00 - 34.45</td>
<td>5.00 - 12.58</td>
<td>0.00</td>
</tr>
<tr>
<td>Longnose dace (number 100 m^-2)</td>
<td>0.00</td>
<td>0.00 - 0.80</td>
<td>28.20 - 56.84</td>
<td>0.00</td>
</tr>
<tr>
<td>Creek chubs (number 100 m^-2)</td>
<td>0.00 - 3.00</td>
<td>5.70 - 15.79</td>
<td>0.90 - 2.47</td>
<td>0.00</td>
</tr>
<tr>
<td>Northern redbelly dace (number 100 m^-2)</td>
<td>0.00</td>
<td>0.00 - 11.10</td>
<td>0.00 - 1.40</td>
<td>0.00</td>
</tr>
</tbody>
</table>

**Data Analysis**

We assumed that mortality increased dramatically as discharge increased above some threshold value. To identify thresholds, discharge data were expressed as a series of redundant variables: frequency and percent of time that discharge equaled or exceeded the 1% exceedence value; the 5% exceedence value; the 10% exceedence value; etc. Exceedence is an index of relative discharge (Bedient and Huber 1988). One percent exceedence, for example, was a very high discharge that was exceeded only 1% of the time during the four years of study in the reach. Similar variables were developed to determine low flow thresholds.

We developed variables that were composites of the measured variables, and some that integrated the duration and intensity of a variable. For example, the mean specific stream power index (MSSPI) was a composite variable integrating discharge, gradient, and channel width to evaluate a stream's energy or power to displace fish.

\[
\text{MSSPI} = Q \cdot S \cdot W^{-1}
\]

Where: \( Q \) = discharge (m³·s⁻¹) \( S \) = slope (gradient) of the reach (m·km⁻¹) \( W \) = mean bank full width (m)

The MSSPI value was calculated for each mean hourly discharge and is proportional to a metric called the specific stream power, described in the hydraulics literature (Ferguson 1987). Regressors integrating the magnitude and duration of extreme air temperatures were developed (e.g., \( \sum \) daily low temperatures \( \leq 17.8^\circ \)C, Seelbach 1987). Stressful stream temperatures were expressed as degree-hours.
of water temperature $<5^\circ C$ or $>23^\circ C$. The effects of cold water temperatures (Cunjak and Power 1987a, Smith and Griffith 1994) and high water velocities (Cunjak 1988) were integrated as degree-hours of water temperature $\leq 5^\circ C$ when the discharge was also greater than the 25% exceedence discharge.

Environmental variables were grouped to facilitate analysis. Variables were divided into four groups categorized as Discharge, Climate, Geomorphology, and Competition/predation assuming that the variables in each category were likely to be correlated. Variables in each variable category were then allocated to one of two subsets: one to develop a "YOY survival model," and a second subset to develop an "age 1 survival model." The YOY survival model subset contained data collected exclusively during the interval from stocking to the first electrofishing assessment. The age 1 survival model data set contained data collected exclusively during the interval between the first and second electrofishing assessments. Geomorphology data were common to both intervals, so both subsets contained the variables.

The number of variables in each subset was then reduced to a more tractable number of regressors. It was clear after inspection of the data sets that survival was not correlated with the MSSPI index, stream water chemistry, or the chlorophyll $a$ accrual rate, so they were eliminated from further analyses. Simple correlation matrices were then developed for each variable group. Scatter plots of the variables most correlated with survival were developed and inspected. Variables with few data points or with influential outliers were eliminated from the analyses. When two or more variables were correlated with survival and with each other, one variable was selected for regression based on some practical consideration such as ease of measurement. Variables that were most correlated with the appropriate survival rate were selected from among the four categories for stepwise forward and backward regression analysis (Table 4). Alpha to enter and remove was 0.15. Statistical significance of the model coefficients was defined at the 0.05 level.

Table 4. Variables included in the stepwise linear regression analyses and their simple correlations ($r$) with survival.

| VARIABLE                                                                 |  
|--------------------------------------------------------------------------|--------------------------------------------------|
| Young-of-the-Year (YOY) Model                                            |  
| % of time discharge $\geq 50\%$ exceedence within 4 weeks of stocking   | -0.629                                           |
| $\sum$ (mean hourly stream temperature $-12^\circ C$) for all mean temperatures $>12^\circ C$ | 0.711                                           |
| % of water surface area containing forest debris                         | -0.658                                           |
| Weighted mean substrate diameter                                         | 0.629                                            |
| Sector gradient                                                          | 0.815                                            |
| Age 1 Model                                                              |  
| Exceedence value on the day that permanent ice cover formation began     | 0.639                                            |
| Discharge during the highest water temperature                           | 0.668                                            |
| Hours of water temperature $\leq 5^\circ C$ and discharge $>90\%$ exceedence | 0.589                                            |
| Total snowfall by 15 January                                             | 0.570                                            |
| Highest annual water temperature                                         | -0.527                                           |
| Total hours of highest water temperature                                 | -0.574                                           |
| % of water surface area containing forest debris                         | 0.629                                            |
| Riparian forest canopy density (%)                                       | 0.581                                            |
| Mean weight of YOY steelhead on 1 October                                | -0.645                                           |
| Variance of the mean weight of YOY steelhead on 1 October               | -0.630                                           |
RESULTS

Survival Rates and Densities

Marked fish were usually vigorous when released during electrofishing assessments and very few mortalities were observed, suggesting that mortalities were insufficient to bias the population estimates. Survival rates were quite variable, ranging from 0.7% to 9.0% through two summers of growth (Table 5). YOY densities ranged from 6.4-81.0 x 100m^2. Age 1 densities ranged from 1.4-14.4 x 100m^2.

YOY Survival Model

Both stepwise forward, and backward procedures resulted in the same model. The model explained 69% (adjusted $R^2$) of the observed variation in the survival rate. YOY survival ($Y$) increased with weighted mean substrate diameter ($X_1$), and decreased with duration (h) of discharge greater than the 50% exceedence (median) discharge within four weeks after stocking ($X_2$). Specifically,

$$Y = 12.719 + 0.126X_1 - 0.269X_2$$

Age 1 Survival Model

Both stepwise forward and backward procedures again resulted in the same model. This model explained 97% (adjusted $R^2$) of the variation in the survival rate. Survival of age 1 parr ($Y$) increased with discharge during the highest mean hourly water temperature of the summer ($X_1$), increased with cumulative snowfall before 15 January ($X_2$), and increased with the percentage of the stream surface area occupied by forest debris ($X_3$). Specifically,

$$Y = -24.24 + 2.26X_1 + 1.32X_2 + 14.96X_3$$

Predicted survival through two summers of growth is obtained by the product of the YOY and age 1 model survival estimates.

DISCUSSION

Model predictions should be viewed with caution if weather or habitat measurements from the stream where prediction is desired are outside the ranges of the data used to develop the models (see Tables 2 and 3). Our study reaches were representative of North

<table>
<thead>
<tr>
<th>Stream</th>
<th>Year</th>
<th>Survival(%) age 0 to age 1</th>
<th>YOY density: number·100m^2</th>
<th>Survival(%) age 1 to age 2</th>
<th>Age 1 density: number·100m^2</th>
<th>Overall survival rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amity Creek</td>
<td>1992</td>
<td>32.4</td>
<td>21.6</td>
<td>28.3</td>
<td>6.1</td>
<td>9.0</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>17.8</td>
<td>22.4</td>
<td>6.5</td>
<td>1.4</td>
<td>1.1</td>
</tr>
<tr>
<td>French River</td>
<td>1991</td>
<td>1.8</td>
<td>11.8</td>
<td>37.3</td>
<td>4.4</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>8.7</td>
<td>21.7</td>
<td>47.0</td>
<td>10.2</td>
<td>4.1</td>
</tr>
<tr>
<td>Stewart River</td>
<td>1991</td>
<td>13.6</td>
<td>81.0</td>
<td>17.8</td>
<td>14.4</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>5.7</td>
<td>15.1</td>
<td>29.0</td>
<td>4.4</td>
<td>1.7</td>
</tr>
<tr>
<td>Two Island River</td>
<td>1992</td>
<td>6.3</td>
<td>6.4</td>
<td>63.6</td>
<td>4.1</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>13.2</td>
<td>26.7</td>
<td>22.3</td>
<td>6.0</td>
<td>2.9</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>12.4</td>
<td>25.1</td>
<td>31.5</td>
<td>5.1</td>
<td>3.9</td>
</tr>
</tbody>
</table>
Shore streams, and weather during the study was considered typical for the area. We did not experience drought, unusually long periods of extreme heat or cold, or winter flow cessation during the study. The survival models developed in this study are inappropriate for these extreme conditions.

**YOY Limiting Factors**

Steelhead may only be susceptible to displacement by floods during a limited period immediately after stocking. Work by Nuhfer et al. (1994) showed that recruitment of brown trout was inversely related to stream discharge during 30 d periods when fry were entering the free feeding stage of development; the stage at which our steelhead fry were stocked. Flood displacement has also been reported for chinook salmon (*Oncorhynchus tshwytsc*) fry by Irvine (1986).

We suspect that after territories were established, and YOY steelhead were acclimated to the stream, they were at much lower risk of displacement by flooding. Lack of a significant flood variable in the age 1 model and recent observations of emigrating steelhead in the French River support this hypothesis. No steelhead were captured in our smolt trap during a flood in 1996 while discharges receded from 9.63 to 1.98 m$^3$/s, but they were captured at discharges less than 1.98 m$^3$/s. Age 1 juveniles were apparently able to avoid flood displacement by seeking cover, but moved downstream of their own volition at the lower discharges.

The significant positive partial regression coefficient of the weighted mean substrate diameter suggests that survival of YOY increased as substrate size increased. Large substrates probably provided lateral cover which prevented YOY steelhead from being displaced during floods, and provided resting sites that minimized energy expenditure during drift feeding (Fausch 1984). Fausch and White (1981) suggested that resting sites can be a "critical and scarce" resource, characteristics of a limiting factor. Invertebrate production is also positively correlated with substrate size (Bell 1969), and more food may enhance growth and survival of fish.

**Age 1 Limiting Factors**

Correct understanding of our Age 1 model requires a caveat: early emigrants are indistinguishable from true mortalities within the study sector. Smolt trap data from French River show that many steelhead parr emigrate at age 1 during their second season of growth. In 1995, for example, 60% of the emigrating steelhead were age 1 parr. Electrofishing of age 1 parr took place in late fall during this study, so our mortality estimates included presmolts that emigrated. We hypothesize that these age 1 migrants were not smolts, and emigrated because habitat was unavailable. Recent analyses of scales from adult steelhead captured in the French River fish trap substantiate the conclusion of Hassinger et al. (1974) that age 1 emigrants survive poorly in Lake Superior and contribute little to the fishery.

The Age 1 model suggests that higher flows may have mitigated the effect of high water temperature (>23°C). Rainbow trout can survive warm temperatures as long as well oxygenated water is available (Scott and Crossman 1973). Increased discharge is almost always accompanied by increased turbulence which may yield higher dissolved oxygen concentrations, and thus, yield greater survival rates. Three of the four study sites were in upstream areas that were well shaded, yet a variable related to high water temperature was significant. The scatter plot of age 1 survival versus this variable, however, was highly influenced by one datum, suggesting that the biological significance of this variable is suspect in our study reaches. Lower reaches of many North Shore streams are often stressfully warm in summer, as evidenced by observations of moribund salmonids during high stream temperatures.

We hypothesize that total snowfall prior to 15 January was positively correlated with survival of age 2 parr because deep snows insulated stream waters from very cold air temperatures. Other workers have found that early winter is a stressful period for stream
dwelling salmonids because maintenance metabolism exceeds energy gain from feeding, reducing lipid reserves (Gardiner and Geddes 1980, Cunjak and Power 1987a, Cunjak 1988). Heavy snow insulates stream waters from cold air temperatures and may mitigate the physiological stress of cold water. Heavy snow cover may also limit anchor ice formation which is known to be destructive to aquatic organisms of all types (Butler 1979).

Our findings suggest that woody debris may be as important for North Shore steelhead as it is for Pacific salmonids in their native range. Heifetz et al. (1986) found that wintering juvenile steelhead preferred deep pools containing cover such as woody debris, root wads, and cobble; riffles, pools, and glides that did not contain such cover were not used. Swales et al. (1986) found that wintering chinook salmon were most abundant in deep pools containing log debris, suggesting such habitat is preferred, and its lack may limit survival. Woody debris often improves habitat for juvenile salmonids by altering a stream's hydraulic morphology (Elliot 1986, Bilby and Ward 1991, Flebbe and Dolhoff 1995). Fausch and Northcote (1992) projected that 80% of the salmonid biomass was forgone in a 332 m long reach due to prior debris removal.

Our analysis indicates that age 1 survival might be increased by the addition of woody debris. If the steelhead population is limited by smolt yield, then an increase in age 1 survival could increase adult steelhead abundance. If, for example, the 1995 catch of emigrant steelhead in the French River is typical (60% age 1), and if the age 1 parr emigrate because of a lack of woody debris, doubling the present amount of woody debris could double the abundance of age 2 presmolts and increase smolt yield.

If fisheries managers wish to increase juvenile steelhead survival, they need to influence management of the entire watershed. Fisheries managers should discourage clear cutting in watersheds of streams containing juvenile steelhead, particularly in the riparian zones. Undisturbed forests retard runoff and moderate floods (Wesche 1993), reduce stream temperatures (Verry 1996), and insure the continuous input of woody debris. They should encourage loggers to leave an undisturbed forest corridor equaling 10-bankfull width + 15 m on both sides of the stream (Verry 1996). Beaver impound and kill trees in large areas, creating beaver meadows and interrupting the supply of woody debris for many years. Beaver should be removed from streams containing steelhead and discouraged from recolonizing by the planting of conifers in the riparian zone. Removal of woody debris from streams should be avoided unless debris blocks upstream migration of fish (AFS 1983, Elliot 1986).

**MANAGEMENT IMPLICATIONS**

Fisheries managers will probably be most effective at implementing land use practices that benefit steelhead by participating on multidiscipline resource management teams. Such teams focus on the ecosystem, giving fisheries equal consideration with other resource products.

Small scale addition of woody debris warrants further study. Limitation of steelhead by woody debris can only be proven if survival rates increase after the addition or decrease after removal of woody debris when compared to an untreated reference stream. It is important to determine the role woody debris plays in juvenile steelhead survival and how its placement may maximize survival before addition of woody debris is considered as a routine management strategy. Work should continue to address the relative importance of smolt yield versus subsequent survival in Lake Superior as limiting factors for steelhead.
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