

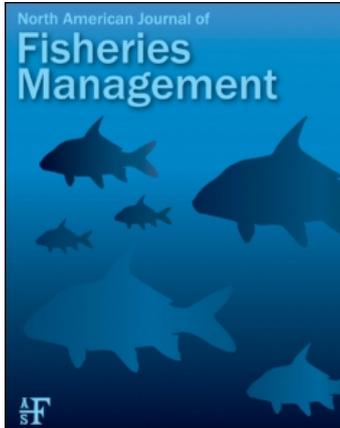
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## Assessing the Effects of Catch-and-Release Regulations on a Brook Trout Population Using an Age-Structured Model

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**Abstract.**—As populations of wild brook trout *Salvelinus fontinalis* decline across the species' native range in North America, angling regulations such as fly-fishing only and catch and release are being used by management agencies to conserve fish while maintaining angling opportunities. Postrelease (hooking) mortality may significantly shift the age structure and size structure of populations. To assess the possible influence of catch-and-release fishing on brook trout population structure, we applied data from several sources to build a deterministic population model that included age-classes up to age 5. To assess the potential effect of fishing, we examined the changes in population density and age structure at varying levels of angler effort (0–400 angler-hours·ha<sup>-1</sup>·year<sup>-1</sup>) and hooking mortality rates (0–14%). Assuming a low (5%) hooking mortality rate, trophy brook trout density (ages 4 and 5) decreased by 50% at an angling intensity of 160 angler-hours·ha<sup>-1</sup>·year<sup>-1</sup>. As angling effort increased, the proportion of older fish (ages 3–5) declined further. At very high levels of angling effort (>300 angler-hours·ha<sup>-1</sup>·year<sup>-1</sup>), age-4 and age-5 fish were eliminated from the population. Increases in postrelease mortality rates resulted in similar declines for older age-classes. The results of this simulation indicate that hooking mortality rates as might be common in catch-and-release fisheries may significantly shift the age structure of a population, thus reducing trophy angling potential.

Many populations of brook trout *Salvelinus fontinalis* throughout the species' native range have been negatively affected by a combination of habitat degradation, the introduction of exotic species, and overexploitation (Hudy et al. 2008). Today, Maine contains more than twice the number of intact subwatersheds for brook trout as the other 16 states in the eastern range combined. Wild brook trout populations in Maine and the eastern region, however, are declining. Most of the large rivers that historically produced brook trout are no longer self-sustaining, and the quality of the fisheries—both in terms of fish size and fish number—has diminished (Karas 1997; Bonney 2006; Hudy et al. 2008). In response to high fishing pressure, many states including Maine have relied upon more restrictive fishing regulations (i.e., fly-fishing only and catch and release [CR]) to provide protection and maintain sustainability (Boucher 2005). Management agencies have increasingly relied upon

CR fishing regulations to promote sustainable fisheries in areas where exploited populations are at risk (Quinn 1996; Bartholomew and Bohnsack 2005; Cooke and Suski 2005). The ultimate success of this type of fishing regulation depends on ensuring high release survival rates (Bartholomew and Bohnsack 2005).

Several field assessments have examined postrelease mortality (hereafter, hooking mortality) of salmonids subjected to CR angling, but the results are equivocal and reported mortality rates vary greatly. Conventional wisdom of management agencies has been that fish caught on flies suffer lower mortality rates than those caught on artificial lures or bait (Schisler and Bergersen 1996; Bachman 2001). In his review of hooking mortality literature, Wydoski (1977) reported that the mean hooking mortality of fish caught on artificial flies was 4% (range = 0–11.3%) and that the mean mortality of fish caught on artificial lures was 6.1% (range = 1.7–42.6%). A second study by Mongillo (1984), which was based on much of the same literature, excluded nonsalmonid fish species. This study concluded that there was no difference in hooking mortality between trout caught on flies and those caught on lures (range = 5–10%) but that hooking mortality of trout caught on bait was significantly higher (30–50%). More recently, Schisler and Bergersen (1996) reported that hooking

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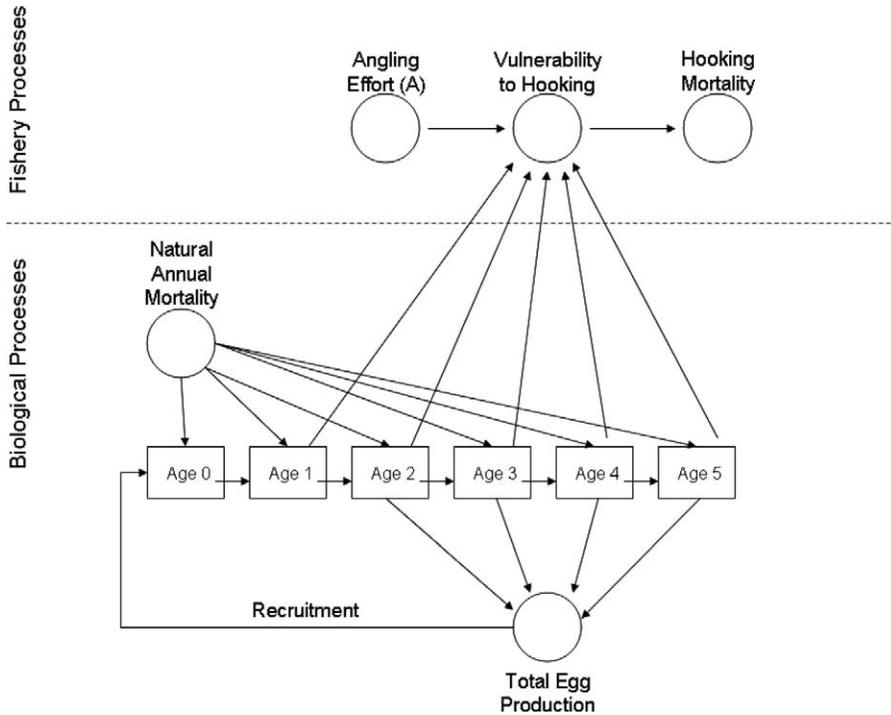


FIGURE 1.—Simplified structure of the trophy brook trout fishery modeled in this study.

mortality of rainbow trout *Oncorhynchus mykiss* was 3.9% (range = 1–14%) for fly-caught fish, 21.6% (range = 9–29%) for fish caught on actively fished artificial bait, and 32.1% (range = 19–45%) for fish caught on passively fished artificial bait. Schisler and Bergersen (1996) also concluded that the lengths of time for which the fish were played (i.e., time from hooking to landing) and held out of water contributed to mortality, as did increasing water temperatures and bleeding intensity.

Few hooking mortality studies reflect the effects of common angling practices on wild trout. Researchers commonly use hatchery fish (Warner 1976; Hulbert and Engstrom-Heg 1980; Schisler and Bergersen 1996) or wild fish that are captured by electrofishing and held in hatchery raceways (Warner and Johnson 1978). Others have used fasted fish (Hulbert and Engstrom-Heg 1980) or fish that are intentionally allowed to swallow the bait (Mason and Hunt 1967). The limited studies comparing hooking mortality of wild, stream-caught trout on flies suggest that mortality is very low (<5%; Shetter and Allison 1955, 1958; Pavol and Klotz 1996). Other data, however, indicate that brook trout may be more sensitive to hooking mortality than other trout species (Shetter and Allison 1958; Taylor and White 1992).

In heavily fished areas, even small changes in mortality rates may alter the age structure and size structure of a fishery, truncating the natural pyramid of age-classes and reducing size at maturity and longevity (Longhurst 2002). Such populations have unstable dynamics and are vulnerable to stochastic events (Longhurst 2002; Anderson et al. 2008). The purpose of this work was to assess the potential effects of CR fishing on an adfluvial brook trout population by using a heuristic approach. An individual-based brook trout population model (Power and Power 1995) was constructed to examine age-class structure at increasing mortality rates (due to angling pressure and postrelease mortality) as might be experienced under fly-fishing-only and CR regulations.

**Methods**

*Design.*—An individual-based model was constructed using STELLA software (Isee Systems 2010). Specific life history (see Figure 1 for a conceptual diagram) input variables included length at age ( $L_a$ ), critical life stage recruitment relations, juvenile survival, adult survival, and size–fecundity relationships. The fishery component consisted of age-specific vulnerability to hooking ( $v_a$ ), catchability ( $q_a$ ), angling effort ( $A$ ), and hooking mortality ( $m_h$ ). Data were scaled to a

TABLE 1.—Age-specific variable set for an age-structured fishery model representing an adfluvial trophy brook trout population per hectare. See text for definitions.

Variable	Age						Source <sup>a</sup>
	0	1	2	3	4	5	
Initial population	3,771	1,565	279	100	69	55	1
Natural annual mortality ( $m_a$ )	0.4	0.5	0.55	0.55	0.55	1.0	1
Proportion of reproductive individuals ( $e$ )	0	0	0.9	0.9	0.9	0.8	1
Catchability ( $q$ )	0	0.01	0.05	0.05	0.01	0.01	2
Mean length ( $L$ , mm)	82	135	176	253	281	314	1

<sup>a</sup> Source 1: variables were heuristically chosen such that with zero mortality due to angling, age structure and total population fluctuated normally about an equilibrium similar to that observed in a quality brook trout population (McFadden et al. 1967). Source 2: variables were developed to approximate the contribution of each age-class to the annual catch statistics observed from a catch-and-release brook trout river (Clark et al. 1981).

representative 1.0-ha system. Variables were estimated as described below.

*Life history.*—We developed an age-structured population model with a maximum age of 5 years and an age at maturity of 2 years (Figure 1); these attributes are typical of adfluvial brook trout populations that support fisheries for large, or “trophy,” brook trout in Maine (Bonney 2006). All processes modeled were based on an annual time step from the spawning period in the fall. At each time step, individuals of the maximum age (5 years) spawn and die, whereas mature individuals of all other ages spawn and then experience a constant per capita mortality rate (natural annual mortality  $m_a$ ; Table 1). Age-0 individuals recruit into the population annually as detailed later.

The initial population and age structure (Table 1) were primarily based on age-class data from a 14-year study of brook trout in Hunt Creek, Michigan (McFadden et al. 1967). The adult distribution in this system was dominated by ages 2 and 3 (as determined by scales), with very few fish of ages 4 and 5 (Table 1). We manipulated (decreased) values of  $m_a$  for adult fish (ages 2–4; compare Tables 1 and 2) so that the model supported a greater proportion of ages 4 and 5. In doing so, we sought to (1) offset the bias of aging through scale analysis in age-2 and older brook trout (Stolarski and Hartman 2008) and (2) better reflect the propor-

tions of older age-classes that have been observed in other self-sustaining populations (e.g., Murphy 2006).

*Size at age.*—Mean length of fish at age  $a$  ( $L_a$ ) was constant (Table 1). Length-at-age values were obtained directly from McFadden et al. (1967) and were in accordance with other data reported in the literature (Clark et al. 1981; Hutchings 1993; Paul et al. 2003) and with data obtained from the Rapid River, Maine (Murphy 2006). We tested the sensitivity of the model to proportional changes in  $L_a$  from 0.7 to 1.5 times the static values.

*Maturity rate.*—Proportions of reproductive individuals ( $e$ ) at age  $a$  were also constant variables (Table 1) estimated from Halfyard et al. (2008) and were consistent with average fecundity-at-length data reported by McFadden et al. (1967). Sensitivity of the model to these variables was also tested over the range 0.0–1.0 for each age-class (ages 2–5) separately.

*Fecundity.*—Egg production was calculated as a function of individual female length with a size–fecundity relationship. Fecundity was calculated by assuming that 50% of the population was female (a 1:1 sex ratio) and that mature age-2 and older fish spawned annually (Table 3; McFadden et al. 1967; Post et al. 2003; Halfyard et al. 2008):

$$E = \sum_{a=2}^5 [N_a(eL_a^f) \times 0.5],$$

TABLE 2.—Age-specific natural annual mortality rates ( $m_a$ ) of brook trout as reported in the literature.

Source	Age					
	0	1	2	3	4	5+
McFadden et al. (1967)	0.54	0.63	0.59	0.74	0.90	0.99
Hatch and Webster (1961)			0.51	0.51	0.51	0.51
Brasch et al. (1982)			0.45	0.45	0.45	0.45
Hutchings (1993)	0.41	0.41				
Nuhfer and Alexander (1994)			0.53	0.53		
van Zyll de Jong et al. (2002)		0.33	0.45	0.45	0.45	0.45
Curry et al. (2003)		0.29	0.35	0.82	0.90	1.00
Petty et al. (2005)	0.54	0.54	0.62	0.62	0.62	

TABLE 3.—Non-age-specific variable set for an age-structured fishery model representing an adfluvial brook trout population. See text for definitions.

Variable	Value	Source <sup>a</sup>
Fecundity ( $E$ )	$E = \sum [N_a (eL_a) \times 0.5]$	1
$e$	$3.0 \times 10^{e3}$	
$f$	2.2	
Recruitment	$R = \alpha E e^{-\beta E}$	2
$\alpha$	0.162202	
$\beta$	$1.77394 \times 10^{-5}$	
Hooking mortality ( $m_h$ )	0.05 (0.00–0.14)	3
Angler effort ( $A$ )	0–400 angler-hours $\cdot$ ha <sup>-1</sup> $\cdot$ year <sup>-1</sup>	4

<sup>a</sup> Source 1: variables were developed to approximate observations of a quality brook trout population in a major tributary system (Halfyard et al. 2008). Source 2: recruitment was modeled using a Ricker stock–recruitment function (Ricker 1975) and recruitment data from a quality brook trout population (Hunt Creek; McFadden et al. 1967). Source 3: hooking mortality rates used here vary over the range of hook-and-release mortality rates for salmonids as reported in literature (Shetter and Allison 1955; Warner 1978; Dotson 1982; Schisler and Bergersen 1996). Source 4: we varied angler effort over the range of 0–400 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup>; angler effort over 240 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup> has been observed in brook trout fisheries in western Maine (Boucher 2005).

where  $E$  is egg number calculated by summing over all mature females,  $e$  is the proportion of mature (spawning) adults,  $f$  is a constant describing the fecundity of an individual of length  $L_a$ , and  $N_a$  is the total number of age- $a$  fish.

**Recruitment.**—For salmonids, early life stage recruitment is often described by a dome-shaped, density-dependent stock–recruitment curve (Elliot 1989). Recruitment from population fecundity ( $E$ ) to age-0 juveniles was modeled by using a Ricker (1975) stock–recruitment relationship (Table 3; Figure 2):

$$R = \alpha E e^{-\beta E},$$

where  $R$  is recruitment of age-0 fish,  $\alpha$  is the y-intercept of the stock–recruitment relationship, and  $\beta$  is the slope of the stock–recruitment relationship. The necessary data to derive such a stock–recruitment relationship were obtained directly from McFadden et al. (1967) and scaled to produce a stable age-class structure as defined above. Sensitivity of the model to the stock–recruitment relationship was tested at  $\alpha \pm$  SD and  $\beta \pm$  SD.

**Natural mortality.**—Natural annual mortality was represented as a constant instantaneous rate of 0.50 for age 1, 0.55 for ages 2–4, and 1.00 for age 5 (Table 1). Natural mortality for age-0 fish was determined by two components: the stock–recruitment relationship (Figure 2) and a constant  $m_a$  of 0.40 (Table 1). The stock–recruitment relationship, as described previously, determines the number of young brook trout that survive from hatching to the fall fingerling stage. These fall fingerlings are then subject to an  $m_a$  of 0.40 before

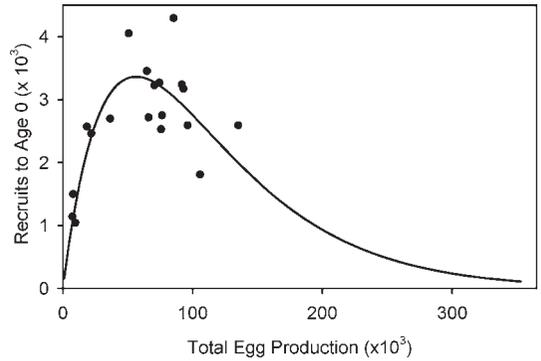


FIGURE 2.—Stock–recruitment relationship with a Ricker (1975) curve fitted for brook trout. Solid line represents the fitted Ricker curve (where  $\beta = 1.77394 \times 10^{-5}$  and  $\alpha = 0.162202$ ). Data are from McFadden et al. (1967).

recruiting into the population at age 1 the next year. This accords with brook trout mortality rates reported in the literature (Table 3; Hutchings 1993; van Zyll de Jong 2002; Curry et al. 2003; Paul et al. 2003), but higher mortality rates for brook trout were reported by McFadden et al. (1967; Table 2). As stated above, the age-class structure in this model includes greater proportions of ages 3–5 than were observed by McFadden (i.e., to represent northern adfluvial populations; Murphy 2006). Stabilizing this population structure required survival between age-classes to be greater than those values calculated by McFadden et al. (1967; Tables 1, 2). Sensitivity of the model to  $m_a$  over the range of 0.00–0.90 was tested separately for age 0, age 1, and ages 2–4. It was assumed that there was no immigration or emigration in this population.

**Fishing variables.**—Age-specific vulnerability to hooking ( $v_a$ ) was modeled at constant rates scaled from 0.0 (completely invulnerable) to 1.0 (completely vulnerable; Table 1). Based on data reported by McFadden et al. (1967) and Boucher (2005) for the Rapid River, age-0 fish were invulnerable to angling ( $v = 0.0$ ). Size-dependent vulnerability for brook trout indicates that they first become vulnerable to angling at 125 mm; therefore, age-1 and older fish were completely vulnerable ( $v = 1.0$ ) to angling. Catchability values for individual age-classes ( $q_a$ ) to the fishery were constant rates (Table 1). The number of age- $a$  fish that were actually caught ( $C_a$ ) was determined by the equation

$$C_a = q_a A v_a,$$

where  $v_a$  is the total number of fish of age  $a$  that were vulnerable to angling,  $q_a$  is the catchability of the total population at age  $a$ , and  $A$  is angler effort (angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup>). We assumed  $q_a$  values that were

lower than those reported in the literature (range = 0.07–0.12; Quinn et al. 1994; Curry et al. 2003; van Zyll de Jong et al. 2002) to be conservative with respect to the effect of  $q_a$  on the model and to examine the effects of  $A$  and  $m_h$  on the population density.

Assuming that the practice of fly-fishing results in lower  $m_h$  than the use of other common types of angling gear, we used a baseline  $m_h$  of 5% (Table 3). Hooking mortality was additive to  $m_a$  such that recruitment to the next age-class was calculated as

$$N_{a+1} = (1 - m_a)(N_a - C_a m_h).$$

The sensitivity of the population to  $m_h$  was tested over the range 0–14%, which is the range reported in the literature (Shetter and Allison 1955; Warner and Johnson 1978; Dotson 1982; Schisler and Bergersen 1996).

Angler effort was applied in the model by defining the number of persons angling for brook trout in one season (1 year). We assumed that each angler who “visits” the system will spend 4 h fishing. Therefore, when the input was 10 persons, the actual  $A$  was 40 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup>. To assess the effects of CR angling on a brook trout population, we examined population density and age structure over a range of 0–400 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup> in increments of 20 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup>. While the upper extent of this range is beyond the  $A$ -values commonly applied to brook trout fisheries (Quinn et al. 1994; Paul et al. 2003), an  $A$  of more than 240 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup> has been observed in brook trout fisheries in western Maine (Boucher 2005).

*Running the model.*—At the end of one time step (1 year), the model censuses the existing population in each age-class and calculates the required summary statistics, including total number, adult number, number of each age-class (ages 0–5), total mortality, and total  $E$ . The model then repeats all calculations for the next year. Population statistics were calculated for 50 years. Data from years 1–10 were omitted from calculations to allow the population to reach an equilibrium oscillation about the mean population density.

Local sensitivity of the model to the estimated life history parameters was evaluated. Parameters included  $m_a$  for juveniles (ages 0 and 1) and adults (ages 2–4), proportion of reproductive individuals ( $e$  for ages 2–5),  $L_a$  (for all age-classes), and the stock–recruitment parameters  $\alpha$  and  $\beta$ . Changes in mean population density and the range of population fluctuation (hereafter, oscillation about the mean) for both juveniles and adults after a 1% increase in life history parameters were calculated. Sensitivity ( $S$ ) was defined as

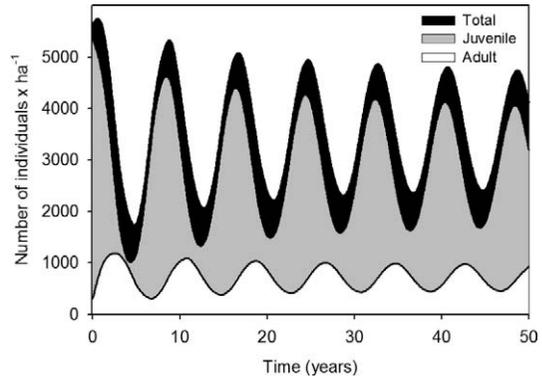


FIGURE 3.—Simulated brook trout population densities (mean total, juvenile, and adult densities) over time for a trophy fishery at an angler effort of zero and with life history variables set at baseline estimates (see Tables 1, 3).

$$S = [(R_a - R_n)/R_n]/[(P_a - P_n)/P_n],$$

where  $R_a$  is the model result for the altered parameter,  $R_n$  is the model result for the unaltered parameter,  $P_a$  is the altered parameter, and  $P_n$  is the nominal parameter (Haefner 2005). Density was considered highly sensitive to a given parameter if  $|S|$  was greater than 1.00. Analysis was conducted on life history variables when  $A$  was set to zero.

To assess the effect of varying levels of  $A$  on the simulated brook trout population,  $m_h$  was set to 5% and life history variables were set as described in Tables 1 and 3. Effect of  $m_h$  was assessed under a fixed  $A$ -value of 40 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup> and with life history variables set at the values in Tables 1 and 3.

### Results

The model was run with life history variables as described (Tables 1, 3) and with  $A$  set to zero to establish the baseline population density and age structure of our model brook trout fishery. For the base model and the range of parameters tested, the model stabilized to an oscillation about a mean for each age-class rather than at a fixed value (Figure 3). Mean and range (averaged over 30 years) of total density, adult density, total  $E$ , and proportion of age- $a$  fish were generally consistent with the means and ranges reported by McFadden et al. (1967).

#### Sensitivity Analyses

Mean juvenile and adult densities exhibited low to moderate levels of sensitivity to changes in  $m_a$  (Table 4). For both juvenile and adult  $m_a$ , the equilibrium adult density decreased as  $m_a$  increased. Changes in juvenile  $m_a$  had a greater effect on the mean population

TABLE 4.—Sensitivity (*S*) of brook trout population density to changes in adult natural annual mortality rate ( $m_a$ , ages 2–4), juvenile  $m_a$  (ages 0–1), length at age  $a$  ( $L_a$ ), maturity rate of adult fish ( $e$ , ages 2–4), and parameters of the stock–recruitment relationship ( $\alpha$  and  $\beta$ ). Variables for which sensitivity was high ( $|S| > 1.00$ ) are indicated in bold.

Density	Adult $m_a$	Juvenile $m_a$	$L_a$	$e$	$\alpha$	$\beta$
<b>Sensitivity of mean</b>						
Adult	–0.254	–0.949	<b>–1.071</b>	–0.458	0.503	<b>–1.001</b>
Juvenile	0.219	0.619	<b>–1.108</b>	–0.495	0.504	–0.997
Total	0.103	0.235	<b>–1.099</b>	–0.486	0.504	–0.998
<b>Sensitivity of oscillation amplitude</b>						
Adult	<b>–2.361</b>	–0.949	0.556	0.278	<b>1.458</b>	<b>–1.181</b>
Juvenile	0.155	0.619	0.386	–0.086	<b>1.222</b>	<b>–1.325</b>
Total	<b>–1.018</b>	<b>–1.033</b>	0.665	0.244	<b>1.385</b>	<b>–1.038</b>

density than changes in adult  $m_a$ . Equilibrium total density was positively related to  $m_a$  (increasing with higher  $m_a$ ) within the narrow window tested because oscillation about the mean was highly (and negatively) sensitive to changes in  $m_a$  for both juveniles and adults. Increases in  $m_a$  resulted in a decreased amplitude of oscillation.

Increases in the maturity rate  $e$  for ages 2–5 produced decreases in both the adult and total mean densities (Table 4). These changes were of a low magnitude. The amplitude of oscillation about the population mean had low sensitivity to  $e$ . Equilibrium juvenile and adult densities were highly sensitive (negative values of  $S$ ) to  $L_a$ , but oscillations about the mean had low values of  $S$  (Table 4).

Model outputs were sensitive to changes in stock–recruitment parameters. Equilibrium total density, adult density, and juvenile density were positively (but modestly) associated with an increase in the value of  $\alpha$  (Table 4). Oscillation about the mean (for both juveniles and adults) was highly sensitive to increases in  $\alpha$ . Equilibrium juvenile and adult densities were moderately to highly sensitive (negative values of  $S$ ) to an increase in the value of  $\beta$  (Table 4). Oscillation about the mean for both juveniles and adults was also highly sensitive to increases in  $\beta$ . Proportions of each age-class (ages 0–5) were relatively unaffected by changes in either  $\alpha$  or  $\beta$ .

*Sensitivity to Angling*

For the base model without any angling pressure ( $A = 0$  angler-hours  $\cdot$  ha $^{-1}$   $\cdot$  year $^{-1}$ ), the population comprised fish of ages 0–5 (Figure 4). Angler effort had a strong negative relationship with adult density and the proportion of older age-classes (ages 3–5). At an  $A$  of 160 angler-hours  $\cdot$  ha $^{-1}$   $\cdot$  year $^{-1}$ , age-4 and age-5 fish declined by more than 50%; fish of these ages were no longer present at 300 angler-hours  $\cdot$  ha $^{-1}$   $\cdot$  year $^{-1}$ . The precipitous decline in ages 4 and 5 under high  $A$  was caused by a rapid dampening of the oscillation pattern as these age-classes neared zero. Angler effort was

positively related to equilibrium total density; however, at high levels of  $A$ , the population was dominated by fish of ages 0–2.

Increases in  $m_h$  were associated with decreases in the proportion of large fish (ages 3–5; Figure 4). Older age-classes persisted in the population when  $m_h$  was as high as 14%, although ages 4 and 5 were 28% lower than base model levels. An increase in  $m_h$  was positively

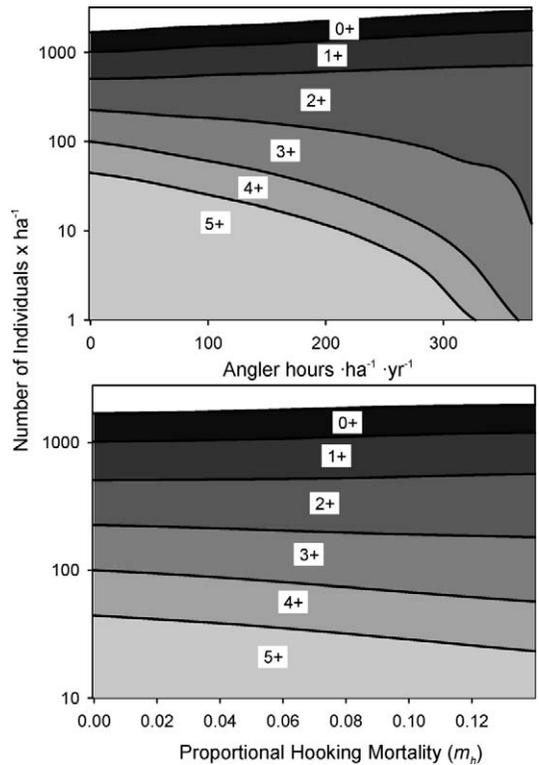


FIGURE 4.—Simulated brook trout densities (ages 0–5) under 5% hooking mortality at varying levels of angler effort (upper panel) and under varying levels of hooking mortality at a fixed angler effort of 40 angler-hours  $\cdot$  ha $^{-1}$   $\cdot$  year $^{-1}$  (lower panel).

associated with an increase in equilibrium total density; however, the population mostly comprised ages 0–2 (Figure 4). An increase in  $m_h$  also resulted in an increase in the amplitude of oscillation about the mean population density over the simulated 50 years.

### Discussion

The results of this modeling study indicate that modest increases in the hooking mortality rate as might be associated with CR fisheries (7–14%) were sufficient to strongly shift the age structure of a brook trout population to one dominated by early age-classes. In this model,  $A$  and  $m_h$  both affected the observed age structure in a parallel fashion. These results are consistent with other trout systems that experience high fishing pressure. For example, mean age and age diversity of brown trout *Salmo trutta* are reduced with increased fishing pressure (Almodovar and Nicola 2004). Even when the fishery is restricted to CR, native salmonid populations (cutthroat trout *O. clarkii* and bull trout *Salvelinus confluentus*) may decline (Paul et al. 2003).

Many brook trout fisheries throughout the species' range are poorly characterized with respect to angling pressure (e.g., Marschall and Crowder 1996); however, the values used in this model were consistent with those observed in other salmonid fisheries (e.g., Vincent 1987; Weiland and Hayward 1997). Even when hooking mortality was fixed at a conservatively low level ( $m_h = 5\%$ ), our results indicate that an angling pressure of only 160 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup> would be sufficient to cause a decline in density of older or larger fish (to < 50% of base levels). A very high angling pressure of 300 angler-hours  $\cdot$  ha<sup>-1</sup>  $\cdot$  year<sup>-1</sup> would be sufficient to eliminate fish of ages 4 and 5.

The catchability of brook trout used in this model was conservative. Clearly, catchability links the vulnerable fish population to the fishery, and the magnitude of catchability contributes to the level of effect (e.g., Quinn et al. 1994; Shuter et al. 1998). In our model, catchability was a constant rate within each age-class (Table 1). It has been suggested that an inverse density-dependent rate is more appropriate than a constant rate (Shuter et al. 1998). If this is the case, then our loss due to hooking mortality may be overestimated for each age-class. The relationship is ambiguous, however, as other research has suggested that this relationship is random (Curry et al. 2003) or constant (Ricker 1975). Regardless, the age-dependent values used for this model ( $q_a = 0.00$ – $0.05$ ) were conservative in comparison with other estimates of catchability for salmonids (range = 0.07–0.86; Anderson and Nehring 1984; Post et al. 2003) and for brook

trout in particular (range = 0.07–0.12; Quinn et al. 1994; van Zyll de Jong et al. 2002; Curry et al. 2003).

Of the variables that influence angling-related mortality, hooking mortality has the greatest range of reported values. Empirical estimates of hooking mortality vary widely (range = 0–14%) for fly-caught fish. Mortality is higher for fish caught on artificial lures (2–43%) and bait (9–50%; Wydoski 1977; Mongillo 1984; Schisler and Bergersen 1996). While our baseline  $m_h$  (5%) was conservative with respect to this range of mortality rates for CR fly-fishing only, a small error would significantly influence the magnitude of the results but not the trends. For lure and bait fishing, the effects can be assumed to be greater.

The actual hooking mortality rate is dependent upon many factors, including the lengths of time for which fish are played and held out of water (Schisler and Bergersen 1996; Cooke and Suski 2005). During the time played, a fish experiences a combination of aerobic and anaerobic exercise resulting in depletion of energy stores, accumulation of lactate, acid–base changes, and osmoregulatory disturbances (Wood 1991). Elevated metabolic rates reduce the ability of the fish to respond to other stressors, such as air exposure, or to engage in predator avoidance (Priede 1985). Because fish size is positively correlated with the duration of the playing event (Thorstad et al. 2003), larger age-classes may be at an increased risk. Efforts by anglers to intentionally prolong playing time through the use of light line or rods could also increase both the hooking mortality rate and the sublethal physiological effects.

Air exposure occurs when anglers remove hooks, weigh and measure fish, or hold fish for photo opportunities. During a fish's time out of water, the gill lamellae collapse, leading to adhesion of the gill filaments (Boutillier 1990), and several major physiological changes occur. In rainbow trout, blood oxygen tension and the amount of oxygen bound to hemoglobin declined by over 80% during brief air exposure, causing severe anoxia, compared with fish that were exercised but not removed from water (Ferguson and Tufts 1992). Further, when rainbow trout were caught by artificial lures and exposed to air for 30 or 60 s after the angling event, mortality increased to 38% and 72%, respectively.

Studies of the consequences of angling-related stress for fecundity and spawning are relatively few (Cooke and Suski 2005). However, because successful spawning is essential for generating offspring to contribute to the population, it is only logical that sublethal effects must be minimized during the spawning season to allow the maximum contribution of offspring to subsequent year-classes. In aquaculture, there is

evidence that salmonids exposed to acute and chronic stressors exhibit endocrine alterations that depress fitness and reduce gamete quality (Campbell et al. 1992). Largemouth bass *Micropterus salmoides* that were exposed to angling stress prior to spawning produced fewer and smaller offspring than control fish (Ostrand et al. 2004). It is not unreasonable to hypothesize that phenotypic traits may shift in populations under heavy angling pressure (Edeline et al. 2007; Hendry et al. 2008).

Hooking mortality is also correlated with temperature (Dotson 1982; Schisler and Bergersen 1996). Angling at especially high water temperatures is associated with increased physiological disturbances, and the probability of mortality increases exponentially (Cooke and Suski 2005), especially as water temperatures approach the species' lethal limit (Thorstad et al. 2003). For coldwater fish species such as brook trout, any angling pressure (including CR) may pose a severe risk of hooking mortality in fisheries conducted at high temperature. Brook trout have a lethal limit of 23°C (Power 1980). Many brook trout rivers are exposed to higher-than-optimal temperature regimes due to habitat degradation, global climate change (Magnuson et al. 1990; Meisner 1990; Shuter and Post 1990), and flow regulation (Jackson and Zydlewski 2009).

Although increased mortality has a strong effect on older age-classes, the population in this model persisted with a lower age structure; increased hooking mortality produced a shift from a population with six age-classes to a population composed only of ages 0–2. Interestingly, the total number of fish in this model population increased due to the density-dependent survival of eggs to age 0. This contrasts with the results obtained by model simulations of bull trout and cutthroat trout populations, where modeled hooking mortalities exceeding 2.5% resulted in lower total abundance of these native species (Paul et al. 2003). Later maturity and larger size at maturity of these species may account for this difference.

In the present model, fishing mortality was additive and we assumed that  $m_a$  was constant for each age-class. While not accounted for in this model, compensatory mechanisms may also come into play. Donald and Alger (1989) found that under exploitation, brook trout recruitment to age 1 increased, offsetting increased mortality. Jensen (1971) and Donald and Alger (1989) observed that exploited populations of brook trout exhibited altered fecundity and maturity schedules that compensated for increased mortality of older individuals. These results suggest that relative to other trout species, brook trout may be extremely resilient to angling, given their ability to mature at

small sizes and early ages (Paul et al. 2003). Further application of this model would likely require more site- and species-specific estimations of the recruitment relationships and the nature of population regulation during early life stages.

The purpose of this study was to construct a testable model system rather than to describe the population at a specific site. The stock–recruitment relationship we used in this model allowed for total brook trout abundance to increase due to a decrease in egg production (a density-dependent relationship; Ricker 1975). Density-dependent mortality has been suggested for salmonid early life stages in streams (McFadden et al. 1967) and is often best described by a dome-shaped stock–recruitment curve (Elliot 1989). However, not all stream populations exhibit this type of density dependence (Grant and Kramer 1990). The biological variables used to define recruitment relationships are poorly characterized for most species, including brook trout (Quinn et al. 1994). While derived from the best available data, uncertainty (and error) in this relationship will greatly affect the outcome. Indeed, such relationships are site-specific and vary annually (Elliot 1989).

In spite of these caveats, our results suggest that hooking mortality can be significant for brook trout fisheries. This mortality can have the unanticipated effect of shifting the age structure to younger fish. While CR fly-fishing has been implemented in many wild brook trout fisheries, heavy angling may limit trophy potential. This work demonstrates that such fisheries may be sustainable only at low intensities of angling. Given the implications, an important next step will certainly be field verification of the model in a setting where angling pressure can be quantified and controlled. Accurate estimates of hooking mortality would be useful to managers. In practice, the success of CR fishing is in the prevention of angling-related mortality. Reducing mortality in this CR model requires a reduction of catchability, fishing pressure, or hooking mortality, the first of which is not readily managed. In addition to limiting the season, managers may wish to reduce mortality by engaging anglers. Education of anglers in the importance of limiting playing times and fish exposure to air (especially at high temperatures) may represent a low-effort management action that would decrease hooking mortality rates due to CR angling.

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