Genetic Consequences of Size-Selective Fishing: Implications for Viability of Chinook Salmon in the Arctic-Yukon-Kuskokwim Region of Alaska

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Abstract.—Selective fishing targets potential breeders with particular characteristics, hence, it can change a population in ways that affect its abundance and productivity. Chinook salmon Oncorhynchus tshawytscha show a wide range of sizes and ages at adulthood and are exposed to fishing during much of their lives. Size-selective fishing can remove the largest and oldest individuals from a population. What is the role of fishing as a factor affecting size, and what are the genetic consequences of change in size for life history and viability? To address these questions for Chinook salmon in the Arctic-Yukon-Kuskokwim region of Alaska, evolutionary and demographic models of long-lived, large-bodied Chinook salmon are linked to assess the effects of two idealized fishing regimes on age-specific length, spawner abundance, and yield to the fishery. The lengths for fish of each age are treated as distinct but correlated traits. The models showed that a constant exploitation rate above a minimum fish size reduces abundance and yield within 100 years unless genetic variation for, and stabilizing natural selection on, length are sufficient to permit adaptation. Because lengths at age were correlated, fish in all age groups, including those under weak selection, responded to selection by declining in length, and abundance and yield both decreased. When fishing removed fish between a minimum and maximum size limit, fish increased in length during adaptation to fishing, and the population could achieve higher abundance after 100 years than that predicted by a non-genetic model. Under both fishing regimes, the population showed evidence of adaptation to fishing if length was heritable and natural selection on length was evident. Management intervention through aggressive reduction of exploitation rate allowed the population to eventually achieve or exceed pre-fishing abundances and stable catches in both regimes. When sufficiently strong and selective, fishing can cause fish size to evolve rapidly, with potential consequences for viability.
Introduction

Human-induced changes in ecosystems that support fish are receiving increased attention, and there is a growing concern that factors such as habitat degradation or fragmentation, climate change, production of hatchery fish, and fishing may be altering life histories in ways that reduce their ability to cope with future change (Law 2000; Hutchings and Reynolds 2004; Birkeland and Dayton 2005; Hutchings and Fraser 2008; Fenberg and Roy 2008). Human actions like fishing may be altering life histories by selectively restricting breeding to individuals of certain sizes, ages, or maturity status. Within a population, a trait can evolve in response to selection when there is a genetic component to its variability, as indicated by a nonzero heritability. A number of recent studies have attempted to attribute life history changes in both marine and freshwater species to genetic effects of fishing (Olsen et al. 2004; Hutchings 2005; Olsen et al. 2005; Swain et al. 2007). Such changes often appear to involve size and age at maturation, traits with a strong influence on fitness in natural environments (Kuparinen and Merilä 2007). The form of fishing selection, whether directional, disruptive or stabilizing, may also affect trait evolution because it may differ in form and strength from those of natural selection. For example, a study of Windermere pike in the U.K. by Carlson et al. (2007) and Edeline et al. (2007) showed that selection imposed by fishing can drive changes in body size that differ from those imposed by natural selection, increasing the intensity of stabilizing natural selection on the phenotype.

Biologists have recognized for over 100 years that fishing-induced evolutionary change could also affect size and life history in anadromous salmonids (Hard et al. 2008). As is the case for other fishes, direct evidence for evolution in salmon in response to fishing is largely circumstantial; it is restricted to retrospective analyses of phenotypic trends (Hard et al. 2008). In an early study, Vaughan (1947) speculated that fishing might have delayed run timing in southeastern Alaska pink salmon Oncorhynchus gorbuscha. Ricker’s (1981, 1995) seminal work on Pacific salmon in Canada was, in the end, unable to link changes in mean harvested fish size directly to fishing, but the selective effects of fishing remain as concerns for several populations of these species. Since Ricker’s studies, successful attempts to detect genetic effects of fishing on salmon have been rare, in large part because discriminating the effects of selective fishing from environmental causes, such as changes in density-dependent growth, is exceedingly difficult (Hard et al. 2008). Helle and Hoffman (1995, 1998) observed a decrease in body size and an increase in age at maturation for two chum salmon O. keta stocks between 1980 and the early 1990s, a trend that showed some association with a major ocean climate regime shift in the North Pacific Ocean in 1976–77. An increase in size at maturity since the mid-1990s may indicate sensitivity to a subsequent change in ocean conditions (Helle and Hoffman 1998). Clearly, density-dependent growth may reflect variable patterns of environmental change, shifts in inter- and intra-specific interactions, or production of hatchery fish. As a result, at least two key issues remain unresolved for salmon populations. First, the impacts of fishing selection on traits correlated with size that affect productivity are not well understood. We are aware of only a handful of studies that have addressed the importance of the architecture of life history on the evolutionary response of salmon to selective fishing (e.g., Healey 1986; Riddell 1986; Hard 2004), and only one of these (Hard 2004) examined the role of correlations among life history traits (see also Walsh et al. 2006). Second, although an evolutionary response to fishing is thought to incur consequences
for viability (Policansky 1993a, 1993b; Law 2007), the demographic and ecological consequences of such genetic change have not been evaluated quantitatively. The present study is intended as a start toward addressing these knowledge gaps.

Each approach that has been employed to evaluate the consequences of selective fishing on life history and productivity has its limitations. Model system approaches, such as those employed by Conover and Munch (2002), Munch et al. (2005), and Walsh et al. (2006), have several advantages over simulation but they may have questionable relevance to commercial, recreational, artisanal, or subsistence fishing. The primary value of such approaches is in characterizing responses to selection for fish with simplified life histories in controlled environments. Empirical approaches with species of interest are desirable but are almost always impractical logistically or contentious politically to implement. Modeling or simulation approaches (Law 1991; Hard 2004; Bromagin et al. 2008) can identify important effects that might be difficult to predict in real populations, but they typically suffer from restrictive, and often unrealistic, assumptions. Nevertheless, such approaches can guide future research and can be valuable in providing a systematic means of identifying the range of potential responses to selection in predictable environments. These models can be useful in evaluating distinctly different scenarios, such as alternative harvest management regimes.

In this paper, we evaluate the potential genetic effects of size-selective fishing on the viability of Chinook salmon *O. tshawytscha* in the Arctic-Yukon-Kuskokwim (AYK) region of Alaska (Evenson et al. 2009, this volume) with a simulation model that focuses on long-lived, large-bodied fish—such as those found in the Yukon River. In recent years, some Yukon River salmon fishermen have expressed concern that adults returning to the river in successive generations have declined in average size. Although evidence for such a trend is mixed (Hyer and Schleusner 2005), such a trend would raise the question whether declining size could reduce viability, possibly by reducing female fecundity or offspring survival. Our approach is one of the first to analyze both evolutionary and demographic aspects of selection and its response for salmon, thereby incorporating evolutionary considerations directly into an analysis of population viability. Our primary objectives were to identify the genetic consequences of size-selective fishing for abundance and yield of Chinook salmon in the AYK region, and to explore the contributions of genetic variability and natural selection on size to mitigate these effects.

**Methods**

Our assessment of the short-term evolutionary effects of size-selective fishing on Chinook salmon life history involved combining evolutionary and demographic models to determine how selection imposed by fishing alters size and age structure and, consequently, abundance and yield of fish from a population characterized by long life and large size at maturation. By linking these complementary models, we attempted to capture the semelparous reproduction, age and size structure, and inheritance of correlated life history traits for Chinook salmon, based on published estimates and empirically obtained genetic and phenotypic data from this species. Models were used to predict the responses of length at age to selection imposed by two idealized fishing scenarios. More general and sophisticated models, notably those developed by Barton and Turelli (1989) and Kirkpatrick et al. (2002), provide a comprehensive means to evaluate inheritance and evolution of polygenic characters under selection. However, we employed a simple additive genetic model because many of the
genetic parameters required for the general models have not been estimated empirically for any population of Chinook salmon.

Selection on length at age.—Potential genetic effects of selection on size was first quantified with a multivariate age-structured model of evolutionary response. This deterministic model integrated nonequilibrium age-structured demography and multivariate response to selection to follow the response of mean age-specific length over time. For our analysis, the changes in \( z \) age-specific lengths were tracked for each age, to a maximum age \( x = 8 \), for \( t = 100 \) years. (It was assumed that length at each age was normally distributed and that the population’s age structure was constant over this period; both assumptions may often be violated in natural populations but we did not explore these effects.) The annual changes in age-specific lengths in the population were determined using the matrix formulas developed by Law (1991):

\[
X_{t+1} = (X_t + PP_0^{-1}S_t)T_t C + A_{t+1} C'
\]

and

\[
A_{t+1} = (A_t + GP_0^{-1}S_t)T_t
\]

where \( X_t \) and \( X_{t+1} \) are matrices of order \( z \) by \( x + 1 \) of age-specific lengths corresponding to years \( t \) and \( t + 1 \), \( P \) is the phenotypic covariance matrix for the lengths expressed at different ages, \( P_0 \) is a modification of \( P \) that has nonzero elements on the diagonal corresponding to traits that are expressed at the same age (\( P_0^{-1} \) its inverse), \( S_t \) is the matrix of selection differentials on length at age, \( T_t \) is a transition matrix that represents the aging of present cohorts through the life history to age \( x \), \( C \) and \( C' \) are diagonal matrices of order \( x + 1 \) by \( x + 1 \) that allow lengths and their breeding values to be updated each year, and \( A_t \) and \( A_{t+1} \) are the matrices, of order \( z \) by \( x + 1 \), of breeding values for all age-specific lengths corresponding to years \( t \) and \( t + 1 \) (Law 1991).

These relationships represent a modification of the discrete-generation multivariate breeder’s equation, \( \Delta z = GP^{-1}s \) (Lande 1979) to accommodate direct and correlated responses to selection in an age-structured population with iteroparous reproduction. In this equation, \( \Delta z \) is a vector of lengths corresponding to matrix \( X \), \( s \) is a vector of selection differentials corresponding to the matrix \( S \), and the genetic covariance matrix \( G \) is equivalent to matrix \( A \) in the equations above. Hard (2004) described this model, its components, and the computation of breeding values, selection differentials, and fitnesses associated with length at age under both directional and disruptive selection scenarios.

To conduct the analysis with realistic estimates of selection and response, we used variance component estimates obtained from a Chinook salmon population at Grovers Creek Hatchery near Suquamish, Washington (Hard 2004; in press) into the model. Table 1 summarizes other values for key parameters that were used to represent Chinook salmon from the AYK region of Alaska. Unlike Grovers Creek Hatchery fish, which is an ocean-type population, AYK Chinook salmon are stream-type populations that generally spend an additional year in freshwater, live longer (up to 8 years) and reach larger sizes (exceeding 1 m in length) at maturation. We recognize this disparity between them but genetic estimates for AYK Chinook salmon life history traits are not available. As Bromaghin et al. (2008) did in a similar study involving stochastic simulation, the genetic estimates from the Grovers Creek population were combined with available phenotypic information from the Yukon River population to represent the key features of AYK Chinook salmon in the life history represented in Figure 1. Two modifications were also made to Law’s model to simulate the life history and exploitation of AYK Chinook salmon. First, the model was adapted
Table 1. Parameter estimates used for Chinook salmon *Oncorhynchus tshawytscha* in the fishing selection model. Estimates were made from available Chinook salmon data from the Arctic-Yukon-Kuskokwim region of Alaska or were generated in an attempt to produce a life history reflecting a long-lived, large-bodied population, while producing a stable population age structure and growth rate in the absence of fishing. Initial abundances reflect the expected abundances after 100 years in the absence of fishing (1−θ = 0), subject to the empirical age-specific survival, maturation, and fecundity data and the parameters of the stock-recruitment function for the population. Annual growth rates were determined by the breeding values for age-specific length. BV = breeding value; SD = phenotypic standard deviation. Estimates of parameters are for Chinook salmon from several published and unpublished sources (Ratner et al. 1997; Kareiva et al. 2000; Hard 2004; Hyer and Schleusner 2005; Zabel et al. 2006).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$h^2$ of length at ages 1–8</td>
<td>0, 0.34, 0.5</td>
</tr>
<tr>
<td>Correlation, $r_p$, of lengths at age t</td>
<td>0.48 (0.01 in absence of data)</td>
</tr>
<tr>
<td>Initial abundance at age 0, $N_0$</td>
<td>810,642,355</td>
</tr>
<tr>
<td>Initial abundance at age 1, $N_1$</td>
<td>17,834,132</td>
</tr>
<tr>
<td>Initial abundance at age 2, $N_2$</td>
<td>1,599,559</td>
</tr>
<tr>
<td>Initial abundance at age 3, $N_3$</td>
<td>1,266,851</td>
</tr>
<tr>
<td>Initial abundance at age 4, $N_4$</td>
<td>903,011</td>
</tr>
<tr>
<td>Initial abundance at age 5, $N_5$</td>
<td>487,626</td>
</tr>
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<td>Initial abundance at age 6, $N_6$</td>
<td>87,773</td>
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<tr>
<td>Initial abundance at age 7, $N_7$</td>
<td>21</td>
</tr>
<tr>
<td>Initial abundance at age 8, $N_8$</td>
<td>0</td>
</tr>
<tr>
<td>Initial BV for length at age 0, $A_0$ (SD)</td>
<td>40 (1.225)</td>
</tr>
<tr>
<td>Initial BV for length at age 1, $A_1$ (SD)</td>
<td>70 (8.062)</td>
</tr>
<tr>
<td>Initial BV for length at age 2, $A_2$ (SD)</td>
<td>230 (50.000)</td>
</tr>
<tr>
<td>Initial BV for length at age 3, $A_3$ (SD)</td>
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</tr>
<tr>
<td>Initial BV for length at age 4, $A_4$ (SD)</td>
<td>555 (91.191)</td>
</tr>
<tr>
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<td>704 (126.500)</td>
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<td>Initial BV for length at age 6, $A_6$ (SD)</td>
<td>827 (127.173)</td>
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<tr>
<td>Initial BV for length at age 7, $A_7$ (SD)</td>
<td>860 (90.373)</td>
</tr>
<tr>
<td>Initial BV for length at age 8, $A_8$ (SD)</td>
<td>900 (94.868)</td>
</tr>
<tr>
<td>Proportion female at age 2 (0 at ages &lt; 2)</td>
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</tr>
<tr>
<td>Proportion female at age 3</td>
<td>0.001</td>
</tr>
<tr>
<td>Proportion female at age 4</td>
<td>0.15</td>
</tr>
<tr>
<td>Proportion female at age 5</td>
<td>0.25</td>
</tr>
<tr>
<td>Proportion female at age 6</td>
<td>0.75</td>
</tr>
<tr>
<td>Proportion female at age 7</td>
<td>0.80</td>
</tr>
<tr>
<td>Proportion female at age 8</td>
<td>0.80</td>
</tr>
<tr>
<td>Proportion returning to spawn at age 0</td>
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</tr>
<tr>
<td>Proportion returning to spawn at age 1</td>
<td>0</td>
</tr>
<tr>
<td>Proportion returning to spawn at age 2</td>
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</tr>
<tr>
<td>Proportion returning to spawn at age 3</td>
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</tr>
<tr>
<td>Proportion returning to spawn at age 4</td>
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</tr>
<tr>
<td>Proportion returning to spawn at age 5</td>
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</tr>
<tr>
<td>Proportion returning to spawn at age 6</td>
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</tr>
<tr>
<td>Proportion returning to spawn at age 7</td>
<td>0.99</td>
</tr>
<tr>
<td>Proportion returning to spawn at age 8</td>
<td>1.00</td>
</tr>
<tr>
<td>Survival to age 1, $s_1$</td>
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</tr>
<tr>
<td>Survival to age 2, $s_2$</td>
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</tr>
<tr>
<td>Annual survival to ages 3–8, $s_3$–$s_8$</td>
<td>0.8</td>
</tr>
</tbody>
</table>
Figure 1. Generalized life history of stream-type Chinook salmon *Oncorhynchus tshawytscha* from the Arctic-Yukon-Kuskokwim region of Alaska, depicting the combination of age structure and semelparous reproduction. $N_{xi}$ is the abundance of immature individuals at age $x$; $N_{xm}$ is the number of individuals maturing and returning to freshwater to spawn at that age. The probability of immature individuals surviving to the next age-class is $s_x$; the proportion of individuals maturing and returning to spawn the following year is $b_x$ (years range from 0 to 8). Fecundity of mature females at age $x$ is $f_x$. Harvest occurs on these fish after they initiate maturation and begin upstream riverine migration in their final year of life.
to a semelparous life history by changing the elements of the first column of the transition matrix $T_t$ to 0 except for the last element (which we set to 1). This alteration limits annual updates of breeding values to those contributed by adults maturing at their terminal age. Second, the matrix of breeding values $A_t$ were altered so that these values are updated only for newborn individuals each year; an alteration that better reflects a terminal fishery on returning adults.

It was assumed that all genetic variance for length at age was additive (e.g., no net dominance, epistatic genetic effects, maternal effects). For genetic parameter values, the following was assumed: heritability ($h^2$) of length at age = 0.34, and correlation among lengths = 0.48 (estimated from empirical data; Hard 2004). The covariance matrices and matrix of selection differentials were considered constant over the 100 years monitored.

Selection imposed by fishing took one of two general, idealized forms (Figure 2). The left panel of Figure 2 depicts directional selection mediated by capture of fish above a fixed length threshold, $k$ (a “minimum size” scenario). The panel on the right depicts disruptive selection mediated by capture of fish between two length thresholds, $k_1$ and $k_2$ (a “slot limit” scenario). The mean length at age $j$ is $\mu_j$ (Figure 2 depicts the case for a single age). In each case, the fraction of fish longer than $k$ that escape fishing is $\theta$; the fraction removed by fishing is $1-\theta$. Length at age $j$ is normally distributed with phenotypic standard deviation $\sigma$. The parameter $\omega$ defines the width of the fitness function corresponding to length, expressed as the deviation of the inflection point from the optimum in the current generation before fishing. The strength of stabilizing natural selection on size were varied between absent ($\omega = 0$) and weak ($\omega = 3\sigma$) to simulate natural selection countervailing that imposed by fishing (Hard 2004). Selection on size imposed by fishing affects adults maturing at mixed ages, which are represented by overlapping normal distributions of lengths at age. For the minimum size regime, the value of $k$ was set to 600 mm; for

![Figure 2](image-url)
the slot limit regime, $k$ was set to 550 mm and $k_2$ to 850 mm. We varied $h^2$ of length at age among three values: 0.0, 0.34, and 0.5, which bracket the range of expected values (see Carlson and Seamons 2008; 0.0 was included to provide a contrast with the other values that represented high environmental variability, and 0.34 is the $h^2$ estimate measured in Chinook salmon by Hard 2004). The annual proportions of fish removed by fishing $(1-\theta)$ was varied from 0 to 100%, but focused on values of 55% for a minimum size fishing regime and 65% for a slot limit regime for comparison. These values are not equivalent to an annual exploitation rate in a terminal fishery; the exploitation rate is the fraction of maturing fish available and susceptible to fishing annually that are captured rather than survive to spawn, i.e., catch/(catch + escapement), whereas $1-\theta$ is the fraction of all fish susceptible to fishing in a given year (on the basis of length, regardless of maturation state) that are removed by fishing (it therefore also varies with the rate of natural mortality). Actual values of $\theta$ are not known for AYK Chinook salmon, but catch estimates of the total Yukon River Chinook salmon run from 1995–2005 averaged 25.5% for the subsistence fishery and 31.7% for the commercial fishery (“2006 Yukon River Salmon Fisheries Outlook,” Alaska Department of Fish & Game and U.S. Fish & Wildlife Service, Anchorage, unpublished data). We selected values of $\theta$ for the model to be consistent with recent estimates of the annual total exploitation rate for Yukon River Chinook salmon.

*Population abundance and fishery yield.*—Linking the genetic and demographic models allowed us to explore how size-selective removal might influence abundance and viability. The demographic trajectory of the Chinook salmon population proceeded in the following steps: 1) the freshwater and marine environments were populated with fish aged 0–8 years; 2) a fraction of fish aged 3–8, representative of the length distribution for their age-class, matured and returned to freshwater; 3) size-selective fishing was imposed on the fish returning to freshwater; 4) spawning occurred among the mature fish that survived fishing, and the fecundity of females at each age was determined by the mean length of the age-class after selection (with breeding values of the newborn progeny determined according to the values in Table 1); and 5) simultaneously, immature fish in each age-class aged by one year with the same mean breeding values for length with which they were born—with only those for newborn progeny updating as a result of selection.

To follow the dynamics of the population under fishing through time, we modified the basic approaches used by Ratner et al. (1997), Kareiva et al. (2000) and Zabel et al. (2006) for stream-type Chinook salmon that are based on a Leslie population projection matrix (Leslie 1945; Caswell 2001). The model, a discrete-time model with intervals of one year, accommodates the semelparous reproduction and complex breeding age structure of Chinook salmon (Figure 1). Male and female Chinook salmon from populations like that in the Yukon River may show up to nine age classes ($x = 0–8$ years). The number of individuals at age $x$ in year $t$, $N_x(t)$, depends on age-specific survival and maturity rates; the probability of surviving from age $x–1$ to $x$ is $s_x$; the probability of these individuals maturing at age $x$ is $b_x$ (Table 2; Figure 1). Expected female fecundity at age $x$ is $f_x$, which is estimated as a linear approximation to the relationship between fish length and fecundity estimated by Healey and Heard (1984) for Yukon River Chinook salmon, 450 mm and longer.

The propensity to mature at each age adhered to the following schedule for males and females (corresponding % mature female in parentheses): 0% of fish aged one year and younger mature (<1%), 1% of age-3 fish mature (1%), 10% of age-4 fish mature (15%),
Table 2. Population projection matrix for Chinook salmon assuming a maximum age of 8 years. The survival propensities (1-natural mortality) from one year \((t)\) to the next \((t+1)\), \(s_t\), are given along the off-diagonal of the matrix below the top row. Proportions of fish maturing and returning to spawn \((b_t\), assumed to be independent of length) are given along the top row, as are female fecundities \((f_t)\). Survival rates and maturation proportions used in the model are given in Table 1. We estimated fecundities from a linear approximation to the function estimated for Yukon River Chinook salmon > 450mm by Healey and Heard (1984). Survival estimates assume no mortality due to upstream adult migration.

\[
\begin{array}{cccccccccc}
  & t & & & & & & & & t+1 \\
 0 & 0 & 0 & 0 & b_4 f_4 & b_5 f_5 & b_6 f_6 & b_7 f_7 & b_8 f_8 & N_0 & N_0 \\
 s_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & N_1 & N_1 \\
 0 & s_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & N_2 & N_2 \\
 0 & 0 & (1-b_2)s_3 & 0 & 0 & 0 & 0 & 0 & 0 & N_3 & N_3 \\
 0 & 0 & 0 & (1-b_3)s_4 & 0 & 0 & 0 & 0 & 0 & N_4 & = N_4 \\
 0 & 0 & 0 & 0 & (1-b_4)s_5 & 0 & 0 & 0 & 0 & N_5 & N_5 \\
 0 & 0 & 0 & 0 & 0 & (1-b_5)s_6 & 0 & 0 & 0 & N_6 & N_6 \\
 0 & 0 & 0 & 0 & 0 & 0 & (1-b_6)s_7 & 0 & 0 & N_7 & N_7 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & (1-b_7)s_8 & 0 & N_8 & N_8 \\
\end{array}
\]
25% of age-5 fish mature (25%) 70% of age-6 fish mature (75%), 99% of age-7 fish mature (80%), and 100% of age-8 fish mature (80%). The breeding age distribution was determined by these values and the annual survival rates given in Table 1; these rates were assumed to be independent of fish size for each age-class. Table 2 shows the structure of the population projection matrix corresponding to the age-specific survival rates, fecundities, and maturation propensities. The model employed is deterministic and did not incorporate either demographic or environmental stochasticity into it.

A hockey stick function was used to represent the population’s spawner-recruit relationship (Barrowman and Myers 2000). The hockey stick is an alternative to the Ricker and Beverton–Holt functions. It relaxes the assumption of a close linkage between survival to reproduction and spawner density. Use of the hockey stick assumes that recruits increase with spawner abundance in linear fashion to a threshold, above which recruitment is constant at the carrying capacity, regardless of increasing spawner density. A carrying capacity of 11.8 million age-1 recruits was assumed corresponding to a spawner density of 250,000–300,000, then parameterized the model with the initial age-specific abundances shown in Table 1. These values reflect the expected abundances after 100 years in the absence of fishing \((1–\theta = 0)\), subject to the empirical age-specific survival, maturation, and fecundity data and the parameters of the stock–recruitment function for the population (Table 1). Estimated population growth rate \((\lambda)\) in the absence of fishing, given these parameters, was approximately 1.15.

The fitnesses, selection differentials, and responses to selection in the two fishing scenarios were calculated by tracking phenotypes for maturing fish aged 3–7 years under varying levels of heritability and stabilizing natural selection; fish aged 0–2 were not vulnerable to fishing and no fish survived to age 8 in these scenarios (Table 1). Selection differentials, responses to selection, and changes in abundance for 100 years (McElhany et al. 2000) were monitored, with an opportunity for management intervention after 30 years.

**Results**

**Effects of selective fishing on length at age**

The complicated age structure of Chinook salmon modeled in these simulations tended to produce complex responses in length at age, because size-selective fishing imposed different selection differentials on lengths of fish of distinct ages. As expected, when length was not heritable, directional selection imposed by size-selective fishing, under a minimum size limit of 600 mm and a fraction of harvestable fish caught \((1–\theta)\) of 55%, resulted in negative selection differentials on length but no evolutionary response when length at age was not heritable. When length was heritable \((h^2 = 0.34)\) and no stabilizing natural selection on length was present \((\omega = 0)\), lengths declined only slightly (Figure 3). When length was heritable and stabilizing natural selection on length was weak but present \((\omega = 3\sigma)\), negative selection differentials produced modest phenotypic changes in length (Figure 3). Initial selection differentials were nearly –3.5 mm for 3-year old fish, over –8 mm for 4- and 6-year old fish, and over –10.5 mm for 5-year old fish; these selection differentials showed little trend over time under constant selection. Mature fish of all five ages showed declines in length, ranging from more than –4 mm (age 3) to nearly –8 mm (ages 5 and 6) in 50 years and between –8 and –15 mm in 100 years, with the largest responses expected for 5- and 6-year old fish (–15 mm) (Figure 3). When \(h^2 = 0.5\) and \(\omega = 3\sigma\), the phenotypic responses in length were about 50% larger than those for \(h^2 = 0.34\) (results not shown).
Fishing under a slot limit between 550 and 850 mm with $1 - \theta = 65\%$ resulted in both negative and positive selection differentials on length at age. Fishing produced negative selection differentials for 3- and 4-year old fish but positive selection differentials for older fish. When length was heritable ($h^2 = 0.34$) and no stabilizing natural selection on length was present ($\omega = 0$), the selection differential increased over time for five-year old fish from about $+6$ mm to over $+25$ mm after 100 years (Figure 4). However, when length was heritable and stabilizing natural selection on length was present ($\omega = 3\sigma$), selection differentials were much smaller and phenotypic changes in length correspondly weaker than when $\omega = 0$ (Figure 4). The initial selection differential was approximately $-4$ mm for 3-
and 4-year old fish, nearly 0 mm for 5-year old fish, and over +2.5 mm and +4.3 mm for 6- and 7-year old fish, respectively. Mature fish of all five ages increased in length, ranging from +6 mm for three-year old fish to over +11 mm for five- and six-year old fish after 100 years (Figure 4). When $h^2 = 0.5$ and $\omega = 3\sigma$, the phenotypic responses in length were nearly 50% larger than those for $h^2 = 0.34$ (results not shown).

**Effects of selective fishing on abundance and yield**

Size-selective fishing at high exploitation rates led to rapid reductions in total run abundance and yield to the fishery, especially under a minimum-size limit scenario. Under a minimum length limit of 600 mm and a fraction of harvestable fish caught (1–$\theta$) of 55%, size-selective fishing caused total run abundance and fishery yield to decline rapidly when stabilizing natural selection on length was absent ($\omega = 0$), regardless of the heritability (Figure 5). The reductions in run abundance and yield were greatest if length was heritable ($h^2 = 0.34$) and $\omega = 3\sigma$; run abundance declined about 30% and yield 35% over 100 years. Mean annual exploitation rate was stable over this period at slightly less than 30%.

Under a length slot limit between 550 and 850 mm and $1–\theta = 65\%$, size-selective fishing caused total run abundance and fishery yield to decline initially when stabilizing natural selection on length was absent ($\omega = 0$) (Figure 5); the rate of change depended on the heritability. If length at age was not heritable, the declines in run size and yield were monotonic, with run size dropping to about 20% of the level before fishing began and catch to about 50% of the initial level. If length at age was heritable ($h^2 = 0.34$), abundance and yield began to recover after 50 years, reaching over 80% of initial levels after 100 years (Figure 5). With $h^2 = 0.5$, recovery was complete within 75 years (results not shown). With $h^2 \geq 0.34$ and $\omega = 3\sigma$, total run size and catch increased to the maximum levels within 50 years; the annual exploitation rate rose to a cap of 17% over the period (Figure 5).

The potential to adapt to size-selective fishing conferred a greater demographic benefit when fishing mortality was high. Figure 6 illustrates the effects of fishing on total run size over 100 years when $h^2$ of length is 0.34 or when $h^2$ is 0 ($\omega = 0$). Under a minimum size limit of 600 mm, relative run size ($\text{abundance}_{h^2 = 0.34}/\text{abundance}_{h^2 = 0}$) declined initially at all harvest levels but began to increase after 5 years at harvest rates greater than 40%. Relative run size was highest when harvest rates exceeded 70%; at this rate, the relative run size nevertheless began declining gradually after about 35 years, although after 100 years it still exceeded 1.0 (Figure 6). By contrast, under a slot limit of 550–850 mm, relative run size exceeded 1.0 under all harvest rates, reaching maximum values at harvest rates exceeding 50% within 5 years and at harvest rates lower than 50% within 35 years.

**Responses to reduced fishing rates**

One form of management intervention might correspond to a substantial reduction in harvest rate, such as could occur with elimination of a commercial fishery and leaving subsistence as the only allowable harvest. When represented as a reduction in the proportion of harvestable fish caught (1–$\theta$) after 30 years, management intervention produced dramatic changes in selection differentials and responses in lengths at age and in abundance under both fishing regimes. Under the minimum size regime, a reduction in $1–\theta$ from 55% to 25% reduced selection differentials by as much as 70% to less than –12 mm for four- and five-year old fish and less than –4 mm for six-year old fish. Declining trends
Figure 4. Trends in selection differentials on lengths at age (upper panels) and changes in length at age (lower panels) for Chinook salmon *Oncorhynchus tshawytscha* (ages 3–7 years) from the Arctic-Yukon-Kuskokwim region of Alaska under a slot limit fishing regime (disruptive selection) over 100 years of fishing. The minimum length is 550 mm and the maximum length is 850 mm in the slot; the fraction of fish removed by fishing (1–θ) is 65%. The strength of stabilizing natural selection on length is either absent (ω = 0; left panels) or relatively weak (ω = 3σ; right panels).
\( \omega = 0 \) \hspace{2cm} \omega = 3\sigma

**Figure 5.** Trends in total run size (prespawning abundance), yield of mature adults, and % mature caught, for Chinook salmon *Oncorhynchus tshawytscha* from the Arctic-Yukon-Kuskokwim region of Alaska, under minimum size (upper panels) and slot limit (lower panels) fishing regimes over 100 years of size-selective fishing. The fraction of fish removed by fishing \((1-\theta)\) under the minimum size limit (minimum length 600 mm) is 55%; the fraction of fish removed by fishing under the slot limit (minimum length 550 mm, maximum length 850) is 65%. The strength of stabilizing natural selection on length is either absent \((\omega = 0;\) left panels\) or relatively weak \((\omega = 3\sigma;\) right panels\).
Figure 6. Effect of genetic variation for length at age on final abundance, after 100 years, for Chinook salmon *Oncorhynchus tshawytscha* from the Arctic-Yukon-Kuskokwim region of Alaska, under size-selective fishing under minimum size or slot limit fisheries. The graphs depict the ratio of final abundance (total run size) when heritability of length at age is moderate ($h^2 = 0.34$) to final abundance when length is determined entirely by environmental factors ($h^2 = 0$). Directional selection is represented by a minimum size limit of 600 mm (left panel); disruptive selection is represented by a slot limit of 550–850 mm (right panel). The proportion of harvestable fish removed by fishing ($1-\theta$) under each regime varies from 0 to 100%.
in length diminished accordingly when length at age was heritable. Total run size and catch began to increase immediately after the adjustment in harvest rates; run size eventually exceeded prefishing levels and annual catch stabilized at its new level (~35%) within 50 years (Figure 7). These patterns were qualitatively similar when stabilizing natural selection on length was absent (although rates of increase were slower; Figure 7), reflecting the overriding effect of exploitation rate on abundance.

Under the slot limit regime, a reduction in $1-\theta$ from 65% to 25% reduced selection differentials by as much as 65% to less than −11 mm for four-year old fish and + 14 mm for six-year old fish (Figure 7). As in the minimum size scenario, increasing trends in length diminished accordingly under the slot limit scenario when length at age was heritable. Total run size increased sharply after the adjustment in harvest rates; run size exceeded prefishing levels and annual catch stabilized at its new level (~20%) within 10 years. As in the minimum-size fishery, these patterns were qualitatively similar under the slot limit when length at age was absent, but changes in run size and catch took longer in that case (Figure 7).

**Discussion**

A deterministic genetic-demographic model was used to explore how size-selective fishing is likely to affect abundance and yield in an exploited Chinook salmon population, with characteristics like those found in populations from the AYK region of Alaska. An evident decline in the frequency of very large (>900 mm) Chinook salmon from some areas of the Yukon River in recent years (Hyer and Schleusner 2005; Evenson et al. 2009), as well as a more general perception that mean size and age have declined in this population since the 1970s, has precipitated concern that fishing or another factor is changing the characteristics of AYK Chinook salmon. Subsistence fishing on the run has existed for centuries; exploitation of the population by commercial fisheries, which began in 1918 and has been continuous since 1932, was at peak levels from the early 1960s until the late 1990s (Vania et al. 2002; Evenson et al. 2009). This fishery shares similarities to both regimes simulated here, but probably more closely resembles key features of the minimum-size scenario. In 1998, the exploitation rate was curtailed but since 2001 it has increased again and, although run sizes are not showing consistent trends, fish size has continued to decline. Whether this decline and the disappearance of older fish have resulted from the fishery or from environmental factors that affect growth and maturation is the subject of considerable controversy, and at present neither of these putative factors can be ruled out.

Fishing can impose selection on salmon size, and if sufficient genetic variability underlies variation in size for a population, that population can respond in mean body size (and potentially in other traits) to fishing selection. Whether the population will respond to fishery selection depends on several factors (Law 1991; Hard 2004, in press). First, fishing must be sufficiently strong to impact breeding population size; under constant fishing vulnerability, selectivity, and genetic variability, high harvest rates are more likely than low harvest rates to elicit an evolutionary response. Second, fishing selectivity must be sufficiently high to impose a detectable selection differential. A fishery that removes fish that deviate substantially in size from the population mean, e.g., only the largest fish, is more likely to alter the size and age structure of an exploited population than a fishery that captures a broad range of fish sizes. Removal of the largest fish will have a disproportionate impact because of the contribution of their high fertility to population growth rate (Birkeland and Dayton 2005; Hutchings and Fraser
Genetic Consequences of Size-Selective Fishing

Minimum size (1-$\theta$ = 55→25%)

Slot limit (1-$\theta$ = 65→25%)

Figure 7. Responses of abundance (run size and yield) and catch rate in Chinook salmon *Oncorhynchus tshawytscha* from the Arctic-Yukon-Kuskokwim region of Alaska to a reduction in fishing mortality after 30 years. The left panels depict responses under a minimum size limit (minimum length 600 mm) when 1–$\theta$ is initially 55%, then reduced to 25%; the right panels depict responses under a slot limit (minimum length 550 mm, maximum length 850 mm) when 1–$\theta$ is initially 65%, then reduced to 25%. The upper panels depict responses when natural selection on length is absent ($\omega = 0$), and the lower panels depict responses in the presence of relatively weak natural selection on length ($\omega = 3\sigma$). In both cases, $h^2$ of length at age is 0.34.
Third, in order to detect a response to fishing, the environmental variability that has contributed to observed variation in fish size and size at age must be relatively small. Because of the plasticity of many fish characteristics, single genotypes can produce a range of phenotypes when environmental variation is high.

Like the findings of Law (1991) and Hard (2004), our results indicate that size-selective fishing can produce a detectable evolutionary response in size at age if the harvest rate and selectivity are both sufficiently strong. Bromaghin et al. (2008) found similar responses in their analysis of size-selective exploitation of Yukon River Chinook salmon using a stochastic, individual-based model integrating phenotypic evolution and population dynamics. Under a minimum-size limit for harvestable fish, the lengths of fish of most ages (3–7 years old) declined under selection within 100 years even if the selection differentials on fish of particular ages were small, due to the correlated heritabilities of lengths expressed at different ages. This pattern reflects the genetic and phenotypic covariance structure of length at age; in the unlikely event that lengths at different ages were not under the influence of the same genes, we would expect to see an evolutionary response only in the length of fish belonging to those age groups directly selected upon. Under the minimum size regime, growth is likely to respond to selection as fish become smaller. Adaptation to the regime could take one of two general forms: growth rate increases and fish mature at younger ages, or growth rate declines. Growth rate and length at age in Chinook salmon appear to be positively genetically correlated (Hard 2004); consequently, selection against large size may reduce growth rates. However, for anadromous salmonids, growth rate might accelerate during adaptation to selection on length as a consequence of earlier age at maturity, as these traits also tend to be positively correlated.

Under the slot limit regime, selection differentials on length show different patterns for young versus old fish (selecting for small young fish and large old fish). The responses tend to be toward larger fish at age, especially at older ages. The patterns of change in length suggest that growth would increase under selection on length to avoid the slot. These results are contingent on the specific range of the length thresholds, the selection differentials, and harvest rates (as well as the genetic influences on length at age) evaluated here, but they clearly demonstrate the potential of size selectivity in a fishery to alter the size distribution of a long-lived, large-bodied Chinook salmon population like that in the Yukon River.

The results indicated that, under some circumstances, an evolutionary response to fishing selection could reduce population viability lower than expected due to the immediate demographic reduction caused by harvest. Under a minimum-size limit, both run size and fishery yield of the population can decline detectably within several generations when heritabilities of length at age are greater than zero. If length at age is heritable and stabilizing natural selection on length is weak (through natural or sexual selection on size of breeding adults), these declines tend to be modest; if stabilizing natural selection is absent, these declines are rapid and substantial. Under a slot limit, both run size and yield decline if stabilizing natural selection on length is absent, but show signs of recovery within several decades if length is heritable. If stabilizing natural selection on length is weak, run size and yield increase within 40 years under size-selective fishing at the harvest intensities evaluated here. Therefore, given sufficient genetic variability, a population can adapt to fishing selection to reach a higher abundance, but how a population adapts to fishing depends on its life history characteristics and the type of fishing regime it experiences. In some cases adaptation to a minimum-size
fishing regime may reduce future yield (e.g., through a reduction in mean size or age at first spawning).

Aggressive management of harvest to reduce fishing mortality appears to precipitate rapid demographic responses. Management intervention through reduction of exploitation rates after 30 years allowed the population to restore its total run abundance rapidly under both fishing regimes. The responses to reduced fishing mortality allowed the population to achieve or exceed prefishing abundances and catches within several decades under the minimum size regime and in less than a decade under the slot limit regime. As expected, substantial changes in harvest rates are likely to overshadow other management options in effectiveness, including fishing selectivity.

Considerable discussion in the literature has focused on the merits of minimum size limits, slot limits, and other fishing strategies as means to maintain current and preserve future yields. Some researchers have argued that minimum size limits tend to lead to “recruitment overfishing,” whereas practices that increase catch of small, young fish tend to lead to “growth overfishing,” which is often thought to have less deleterious impacts on productivity and yield (Ricker 1976; Larkin 1978, 1981; Nelson and Soulé 1987). Our results are consistent with these arguments. That said, such arguments often overlook the importance of the level of genetic variation for size and associated life history traits, and the strength of natural selection on them, to the resilience of an exploited population (Allendorf et al. 2008). The results of this study clearly show that a modest genetic influence on size at age can permit adaptation to fishing selection. Such adaptation will take time, however, and during adaptation to fishing selection a population could be highly vulnerable to natural selection affecting growth, size and age at maturation, especially if environmental conditions for survival or growth worsen.

What are the wider implications of these patterns for conservation and management of Arctic-Yukon-Kuskokwim Chinook salmon? Because uncertainty about the condition of these populations may be high, the simplest answer to this question is to permit exploited populations sufficient opportunity to cope evolutionarily with the ecological and evolutionary pressures posed by fishing (see Gerrodette et al. 2002). Because resistance among the public to reducing fishing rates is likely to remain high in most circumstances, it is important to consider reducing fishing selectivity as well as reducing exploitation rates. A timely reduction in exploitation rates in response to declining abundance or productivity is a powerful tool available to management, but reducing selectivity on length can also increase the size or maintain the yield of an exploited population. Our findings indicated that reducing selectivity on size, by allowing a greater proportion of large, old fish to escape harvest, can help to maintain preharvest abundance and yield to the fishery, as well as conserve life history variability. This benefit will be greatest when diminished gear selectivity is combined with substantially reduced exploitation rates (see also Bromaghin et al. 2008). However, the most effective modifications for sustainable fishing are not yet completely clear, and the influence of gear selectivity and the dependence of selectivity on time and area closures or other feasible strategies are two issues that would clearly benefit from additional research.

Management options such as these might not always have the desired effect. The consequences of environmental variation for fish growth, size, and age at maturity might easily—at least in some years—overwhelm the impacts of fishing. Indeed, what cannot be determined yet is whether the selection imposed by fishing, the evolutionary response to it, and any attendant effects on viability will be sufficiently large to detect and therefore
require some form of management intervention. Regrettably, our understanding of within-population fishery selection in salmon has not changed appreciably since the commentaries of Larkin (1978, 1981) and the review by Nelson and Soule (1987). We are not yet able to say with certainty when fishing selection on a particular salmon population, such as those in Alaska’s AYK region, will pose a serious problem for long-term management and conservation. Effects of habitat conditions that alter density-dependent growth and maturity may override the selective effects of fishing that reduce abundance or productivity. Nevertheless, fishing selection is likely to compound problems originating from other sources, and the effects of this selection will be cumulative. Some populations which have weakened resilience due to other variables may be especially vulnerable to fishing selection. Such selection could represent a “tipping point” for viability. Cumulative evolutionary changes imposed by fishing along the lines illustrated here could eventually erode a population’s capacity to respond to future environmental challenges. Prudent fishery managers should recognize this possibility and attempt to reduce the intensity and selectivity of fishing practices to maintain salmon life history diversity and productivity over the long term.

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