An Investigation of the Potential Effects of Selective Exploitation on the Demography and Productivity of Yukon River Chinook Salmon

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Jeffrey F. Bromaghin, Ryan M. Nielson, and Jeffrey J. Hard

Abstract

Yukon River Chinook salmon (*Oncorhynchus tshawytscha*) have been targeted in large-mesh gill net fisheries for over 100 years. Recent reductions in productivity and perceptions of reduced size and earlier age at maturation have elevated concerns regarding the potential consequences of the selective exploitation of large fish. Investigations associating changes in population productivity and demography, particularly size and age composition, with overharvest and selective exploitation are common in the fisheries literature. However, most such investigations have considered long-lived species repeatedly subject to exploitation, often prior to maturation. Similar investigations concerning semelparous Pacific salmon are comparatively limited in number, and largely inconclusive with respect to cause. Exploratory analyses of data collected during fishery sampling or stock assessment activities may be hampered by the lack of pre-fishery data to provide a baseline, short time series of available data, biased samples obtained via selective gear, and high levels of natural variation. In addition, retrospective analyses of observational data are insufficient to ascribe cause. For these reasons, we chose to investigate the potential long-term effects of large-mesh gill net fisheries on Chinook salmon by stochastic modeling. We constructed an individual-based model integrating population dynamics and the heritability of traits, using information from Yukon River Chinook salmon to guide model construction when possible, and simulated the effects of selective exploitation under a variety of productivity and fishing scenarios. In most cases considered, the mean size and age at maturation declined rapidly for approximately 50 years and stabilized at reduced levels after approximately 100 years. In these cases, subsequent adoption of gill nets with moderately reduced mesh size was not effective in reversing prior declines in mean size and age unless exploitation rates were also reduced. Our results suggest that long-term, selective exploitation of large Chinook salmon is likely to cause reductions in fish size and maturation age, and impair population productivity. The effectiveness of management strategies to reverse prior effects of selective exploitation appears to be enhanced by the concurrent reduction of both exploitation rates and selectivity for large individuals, especially if implemented before large declines in mean size and age have been induced.

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Introduction

There is a growing global concern that fishery management practices are leading to widespread and undesirable changes to the demographic composition and life histories of exploited populations, the reduction of genetic variation and spatial diversity, and even fishery collapse and ecosystem restructuring. Prominent examples include northwest Atlantic cod (*Gadus morhua*; Myers et al. 1997), western Atlantic bluefin tuna (*Thunnus thynnus*; Safina and Klinger 2008), and eastern Pacific groundfish (Levin et al. 2006). Excessive exploitation rates and the selective catch of large individuals have often been implicated as precursors of such population responses (e.g., Jørgensen et al. 2007).

In addition to its immediate demographic consequences, selective exploitation can have genetic effects on exploited populations which lead to declines in future productivity and yield. Exploitation rates are often managed to provide maximum sustainable yield (MSY) to the fishery (Ricker 1958, 1969; Walters and Martell 2004), although management for MSY has frequently been criticized (e.g., Larkin 1977). For many populations, maximum sustainable yield is realized at a fairly high exploitation rate. However, the genetic effects of high and often selective exploitation, which could alter size and age distributions of breeding adults, are seldom considered when fishery managers establish exploitation rates and the methods and timing of fishing. The Food and Agriculture Organization of the United Nations recently estimated that approximately 50% of the world's primary fish stocks were fully exploited and producing close to their maximum yields, while another 25% were in various states of overexploitation (FAO 2004). If evolutionary changes in fish life histories reduce productivity and future fishery yield, the consequences for fishing and population viability could be serious (Heino 1998; Law 2000; Conover and Munch 2002).

Although Hard et al. (2008) concluded that no single study has conclusively demonstrated the occurrence of fisheries-induced evolution in a wild population, considerable theoretical and empirical evidence exists for its occurrence (e.g., Ricker 1981, 1995; Heino 1998; Law 2000; Carlson et al. 2007). Modeling investigations tend to conclude that size- or age-selective fisheries can be a powerful force in modifying population structure (e.g., Kaitala and Getz 1995, Martínez-Garmendia 1998, Ratner and Lande 2001). Conover and Munch (2002) conducted tank experiments in which selective harvests of Atlantic silverside (*Menidia menidia*) led to substantial changes in fish size in as few as three generations. In addition, evidence that evolutionary changes in the life histories of some heavily exploited fish populations may already be widespread is accumulating (e.g., Ricker 1981; Law 2000; Edeline et al. 2007; Kuparinen and Merilä 2007; ICES 2007; Swain et al. 2007). Trippel (1995) concluded that declining abundance in combination with selective exploitation of large individuals generally leads to reduced age at maturity for groundfish populations. However, not all analyses have found such effects. For example, in a meta-analysis of marine fisheries studies, Hilborn and Minte-Vera (2008) evaluated an age-structured model based on a von Bertalanffy structure of differential growth rates, and concluded that the evidence for fisheries-induced change in growth rates was weak. One implication of this finding is that fisheries-induced evolution in size and age at maturation may be difficult to detect.

Investigations into potential fishery-induced evolution on wild populations have necessarily been based on observational data, and therefore have not been able to ascertain cause. For example, none of the investigations involving salmon has been able to exclude the possibility that other factors, such as density dependence or environmental conditions, caused the observed trends in

size or size at age (Hard et al. 2008). Nevertheless, that selective exploitation has had and continues to have a substantial influence on trends in life history remains a strong possibility in at least some populations. If true, the management implications for sustainable fisheries could be serious. The genetic composition of un-fished populations is the net result of counterbalancing evolutionary forces. High and selective exploitation has the potential to substantially decrease genetic diversity (Allendorf et al. 2008) and reduce the capacity of a population to respond to natural evolutionary forces, even if exploitation and the intensity of selection are subsequently reduced. Indeed, the failure of collapsed populations to recover following substantial reductions in exploitation rate provided early indications that fishery-induced evolution might result from overexploitation (e.g., Hutchings 2000). Law (2000) listed numerous examples of changing populations of various species, including Pacific salmon (*Oncorhynchus spp.*), and concluded that the primary question is not whether fishery-induced evolution is occurring, but rather how quickly.

With respect to Pacific salmon, investigations variously attribute observed changes in population characteristics to selective fisheries, climatic or oceanic conditions, and density-dependent effects. In an early paper, Vaughan (1947) speculated that fishing could have led to delayed run-timing in southeastern Alaskan pink salmon (*O. gorbuscha*) during the early 20th century. Hankin and Healey (1986) concluded that selective fisheries can decrease the mean age of Chinook salmon (*O. tshawytscha*) populations and increase the probability of significant population decline. Hamon et al. (2000) concluded that selectivity in gill net fisheries can be a strong selective force on the morphology (body shape as well as size) of sockeye salmon (*O. nerka*). Bigler et al. (1996) documented a decline in the size of Pacific salmon, including Yukon River Chinook salmon, but largely attributed the cause to ocean conditions and density-dependent effects on growth. Healey (1986) similarly concluded that observed declines in the size of Pacific salmon previously attributed to selective fisheries were at least partially attributable to climatic conditions and, like Riddell (1986), noted that fishery mortality accounts for only a fraction of total mortality. However, Quinn et al. (2002) found that fishery-induced selectivity was stronger than opposing selective pressures in determining the timing of Chinook and coho (*O. kisutch*) salmon spawning. Although investigations to date have been inconclusive with respect to cause, Hankin et al. (1993) and Hard (1995, 2004) found that age of maturation is heritable in Chinook salmon, which directly implies that some aspects of population structure are under partial genetic control and could respond to selection.

Implicating a single cause for change in a population characteristic as complex as life-history strategy is exceedingly difficult, particularly with observational data. A variety of environmental factors can produce changes in salmon characteristics, some of which might mistakenly be attributed to fishing. These factors include characteristics of the aquatic environment affected by climate, such as temperature, salinity, and the degree of upwelling in coastal waters; they also include biological phenomena such as density-dependent growth due to intra- and inter-specific interactions. An environmental change affecting growth could produce responses in phenotypic length at age similar to those produced by fishing selection (Morita et al. 2005). Similarly, Fukuwaka and Morita (2008) document an increase in the maturation size of chum salmon (*O. keta*) following cessation of high seas gill net fisheries, although temporally correlated environmental conditions could not be ruled out as causal factors.

Implicating fisheries as the cause of changes in life-history traits is premature without first evaluating both the genetic variability in these traits and the patterns of fishery selection required to precipitate such evolutionary changes. Two approaches that have shown some promise in

conducting such evaluations, by disentangling genetic effects of fishing from other factors, are analysis of phenotypic trends with general linear models and analysis of life history with reaction norm methodology. Both approaches have considerable appeal, but also limitations which arise from how they deal with genetic and environmental influences on phenotypic expression of growth, size, and maturation. In particular, the multivariate trend analyses employed in recent studies (e.g., Swain et al. 2007) offer a glimpse into potential genetic responses, but cannot definitively identify them as causal factors, although they may be highly correlated with estimates of selection differential.

Analyses of changes in the probability of maturation as influenced by size and age (e.g., Morita and Fukuwaka 2006, 2007) represent attempts to separate the influences of phenotypic plasticity from those of genetic variation in size and age using a probabilistic maturation reaction norm (PMRN). A PMRN is typically represented by a function describing the combination of size and age at first maturity along which the probability of maturation is 0.5. A frequent claim is that PMRNs can separate the influences of genetic variation from those of phenotypic plasticity on maturation, and thereby characterize the relationship between size and age and the likelihood of maturation under different levels of exploitation. Indeed, the PMRN approach allows removal of much of the effect of phenotypic plasticity from analyses of trends in size and maturation, which can leave patterns strongly suggestive of fisheries-induced evolution. However, the approach requires an assumption that the maturation reaction norm is genetically constrained while the growth trajectory is environmentally determined, a combination that seems biologically implausible. In other words, while the PRMN is an improvement over simple analyses of phenotypic trend, it cannot completely distinguish genetic from environmental influences or plastic responses, and it invokes questionable assumptions about the factors that influence the expression of growth and maturation. To improve this approach, investigators must better isolate the effects of these confounding factors, and coordinate the analyses with an enhanced understanding of the maturation process and its developmental indicators (e.g., Kraak 2007; Marshall and McAdam 2007; Wright 2007).

A recent review of the literature on salmon fishing (Hard et al. 2008) indicates that the opportunity for fishing selection is considerable, even though evidence for evolutionary response is not clearly documented. Hard et al. (2008) argued that there were three important, unanswered questions about fishing-induced evolution: whether trends in life history of exploited salmon are genetically based (Kuparinen and Merilä 2007), how quickly evolutionary response to fishing might occur, and whether such evolution is "reversible" through management responses. Developing management strategies that effectively incorporate evolutionary principles will require addressing these uncertainties, while being precautionary with regard to selectivity to limit opportunity for maladaptive evolutionary response to fishing. Careful, long-term monitoring of key demographic parameters and life-history traits such as size at age, spawn timing, and reproductive condition would be required to achieve this objective. The weight of evidence for appreciable heritability of size, age, and timing, and longer-term phenotypic trends in these traits (Hard et al. 2008) indicates that managers would benefit from incorporating evolutionary principles into the management of salmon fisheries. However, best practices for doing so in a consistent and practical way, beyond increasing escapement of larger and older fish (e.g., Policansky 1993a, b; Law 2007; Hutchings and Fraser 2008), have not yet been identified.

Concerns regarding the potential consequences of the continual removal of large Yukon River Chinook salmon in large-mesh gill net fisheries are being expressed with increasing frequency within regulatory processes and during other public meetings (Russ Holder, U. S. Fish and

Wildlife Service, personal communication). Yukon River Chinook salmon have been fished commercially for over a century, and sizeable catches are also taken in subsistence (U. S.) and aboriginal (Canada) fisheries. JTC (2006) provides a brief summary of the early years of the commercial fishery. Recorded catches began to increase in 1950, and commercial catches exceeding 100,000 fish were the norm from 1961 to 1997 (Vania et al. 2002). Buklis (1999) summarizes the changing economics of commercial fisheries in the Arctic-Yukon-Kuskokwim region from 1976-1997. Beginning in 1998, commercial catches of Yukon River Chinook salmon were drastically curtailed in response to declining abundance (Vania et al. 2002), and population productivity has remained low.

The Yukon River Chinook salmon fishery is currently managed with the primary objective of achieving escapement goals in selected locations where abundance is monitored (ADF&G 2004). Spawning aggregations occur throughout much of the 855,000 km^2 drainage (Brabets et al. 2000; Templin et al. 2005; Figure 1). Primary management methods include time and area closures and gear restrictions. In the Yukon River summer-season gill net fishery, gear is either restricted to no larger than 6.0-in mesh or is unrestricted. Catches during unrestricted openings are predominantly taken with 8.5-in gill nets and are therefore comprised of older, larger Chinook salmon, a high proportion of which are female, while catches during restricted openings take smaller fish and a greater proportion of males (Vania et al. 2002). Restricting mesh size to target smaller Chinook salmon could result in higher catches of chum salmon, for which the current commercial market is limited. Thus, the ability of fishery managers to restrict mesh size is limited to periods when chum salmon are absent or present in low numbers.

Selective fisheries such as the Yukon River summer-season gill net fishery have the potential to alter fundamental characteristics of its Chinook salmon population. However, the population dynamics of Chinook salmon are complex and adaptive mechanisms to moderate fishery-induced evolutionary pressures almost certainly exist. Hard (2004) concluded that the "intensity of stabilizing natural selection on size is critically important in determining response to fishing selection." Given this complexity, it is difficult to confidently predict the long-term effects of size-selective fisheries on Yukon River Chinook salmon. Nevertheless, an improved understanding of how such opposing selective pressures might interact to control population dynamics would be beneficial, both for inferring historic population characteristics and trends and for developing informed management strategies to maintain desirable population characteristics into the future.

Analysis of existing data on Yukon River Chinook salmon may be unlikely to provide meaningful insight into the occurrence of fishery-induced adaptation. No biological samples or abundance estimates are available from the earliest decades of the commercial fishery, a period during which moderate to substantial catches were taken, so no pre-fishery baseline is available. Any changes in the population prior to the 1960s occurred with little or no documentation. Basic biological data began to be collected in the 1960s, although each data set is subject to its own limitations. The longest time series of data are length, age, and sex samples from commercial and test fishery catches. Bigler et al. (1996) used this source of data to document a decline in mean weight and mean length at age, but also a slight increase in average ocean age, of Yukon River Chinook salmon. Hyer and Schleusner (2005) documented a widespread reduction in the prevalence of large Chinook salmon (length ≥ 900 mm) using much shorter time series of data obtained during escapement monitoring activities, although broad-scale trends in other metrics were not apparent.
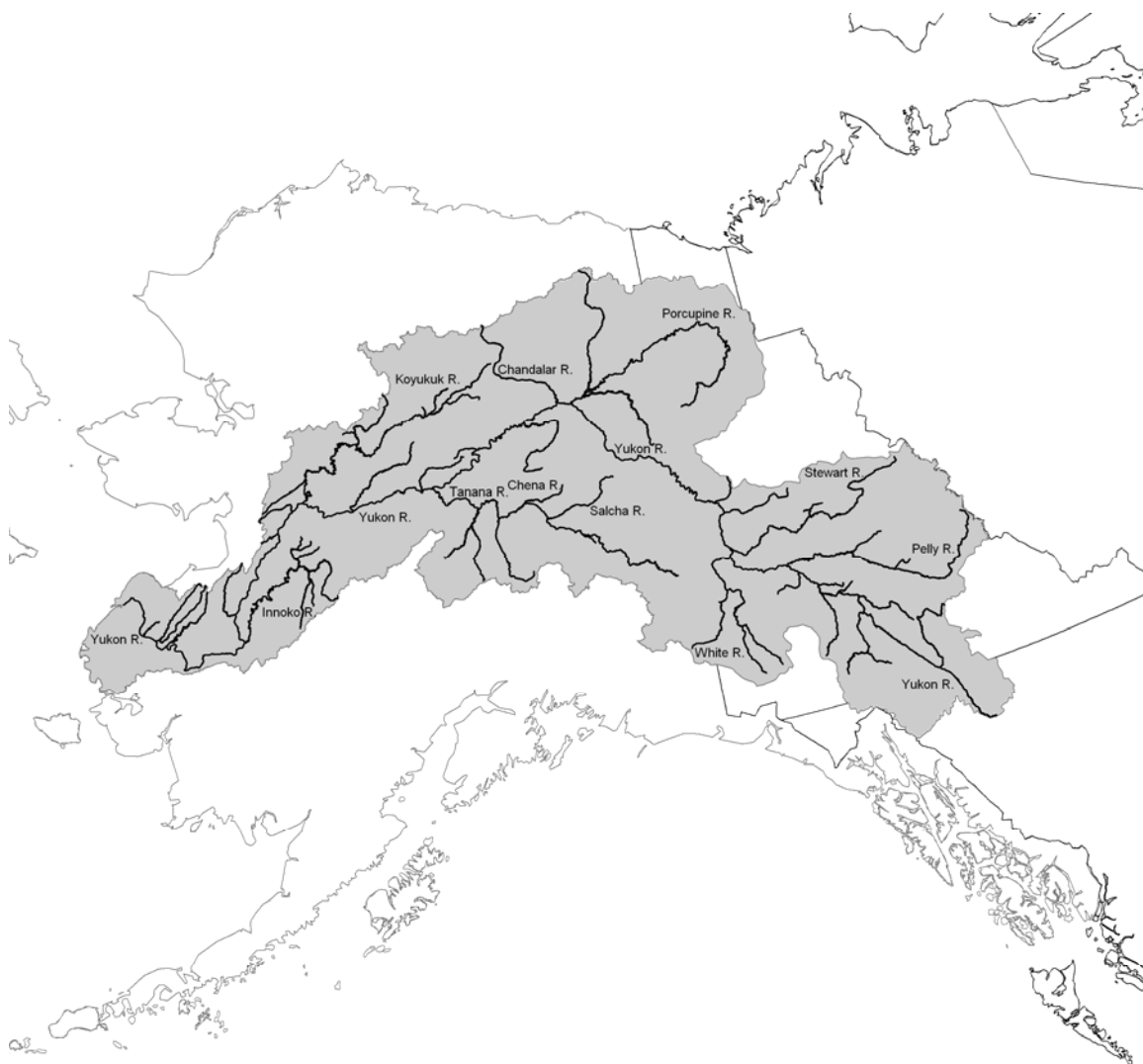
Figure 1. Map of the Yukon River drainage within Alaska and northwestern Canada.

To date, analyses of Yukon River Chinook salmon data have been inconclusive, although suggestive, with respect to trending population demographics. In addition to various data issues underlying each analysis, high levels of natural variation over evolutionarily short time scales might be expected to mask any trends that do exist. Perhaps more importantly, documentation of a trend is not sufficient to establish cause. For these reasons, we attempted to investigate the potential evolutionary consequences of size-selective fishing for Chinook salmon using computer simulation. We constructed a model integrating population dynamics and the heritability of traits. The model was parameterized with information from Yukon River Chinook salmon to the extent possible, although the model and the results should be generally applicable to stream-type Chinook salmon. Our primary goal was to investigate the interplay of fishery and natural selection for population demographics and productivity, with special attention to three central questions. First, is selective exploitation at rates plausible in Chinook salmon fisheries likely to induce adaptation? Second, if so, what aspects of salmon management are most strongly associated with fishery-induced adaptation? Finally, what recommendations can we offer fishery

managers: how hazardous might it be to ignore evolutionary considerations in salmon management, and can fisheries-induced evolution be reversed?

Methods

We approached model development by conceptualizing population dynamics as the result of a series of sequential stages within the life history of Chinook salmon (Figure 2). A sub-model for each stage was developed and parameterized using the best available information, which included professional literature, agency reports, available data or analyses, and best professional judgment.
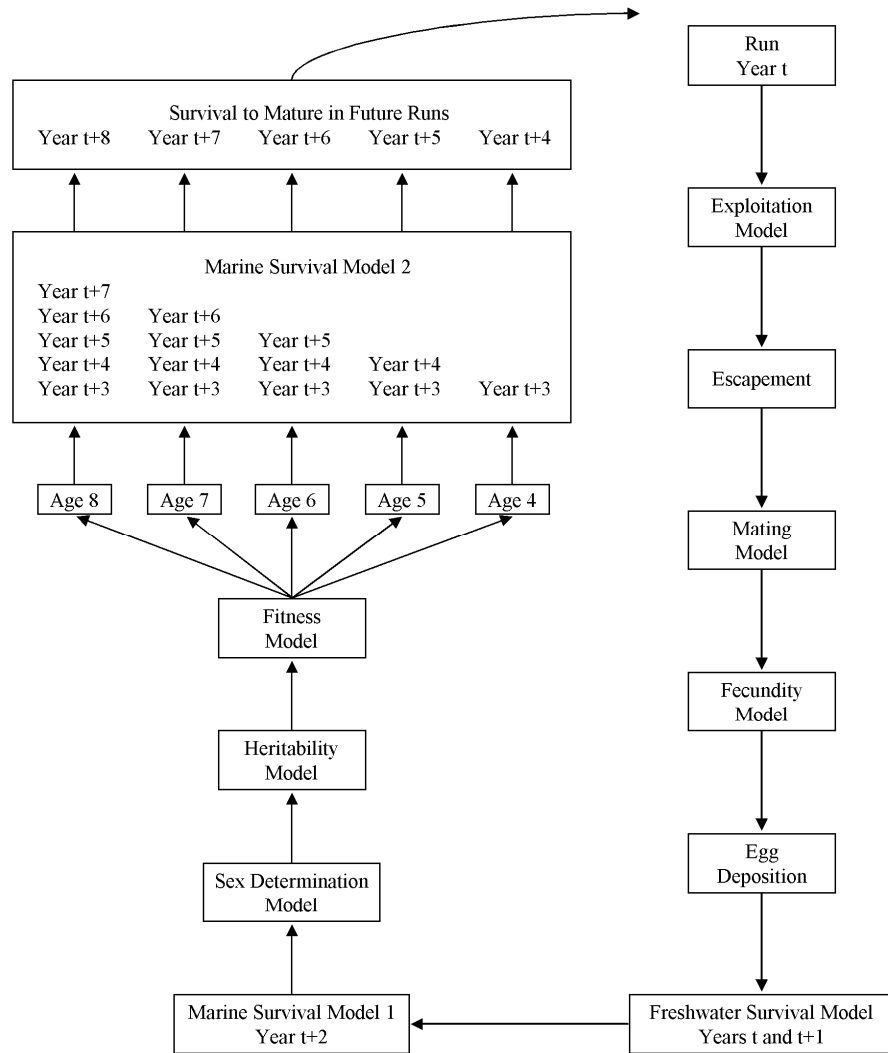
Figure 2. Schematic diagram showing the primary components of the Chinook salmon life history and population dynamics model.

The model consisted of all the sub-models operating in sequence. When independently developed sub-models are linked together in such a fashion, it is possible, perhaps even likely, for the sub-models to interact in unexpected ways and for model outputs to trend or otherwise perform unexpectedly. For that reason, the model was calibrated (e.g., Beaudouim et al. 2008) to be temporally stable in the absence of fishing by monitoring a subset of model outputs judged to be of greatest interest. Outputs that were most closely monitored during model calibration include the mean and variation of age at maturation for each sex, the mean and variation of length at maturation for each sex, age composition for each sex, and the mean and variation of annual run sizes.

Population dynamics were simulated, without fishing, and the average of these demographic characteristics were computed and compared with the target levels described earlier. When differences occurred, model parameters were changed slightly and the process was repeated. Many of the sub-models interact nonlinearly, and a change that moved one characteristic closer to its target value often moved a second characteristic further way from its target value. Model calibration was therefore a lengthy, iterative process, during which we strove to balance opposing tendencies of the model. In some cases, a seeming inability to attain desired properties caused us to reexamine sub-model structure. We were ultimately successful in modifying model parameters to reasonably approximate the desired population dynamics in the absence of fishing, and the sub-models described below are the end products of the calibration process.

The majority of the simulation code was written in R, version 2.60 (RDCT 2007). However, to increase execution speed, the mating sub-model (see *Mating Sub-model* below) was written in FORTRAN 95 (Metcalf et al. 2004) and compiled using the freeware G95 compiler available at http://www.g95.org/index.shtml.

Age, Sex, and Length Sub-model

Yukon River Chinook salmon are of the stream-type variety; most individuals spend one year in freshwater before smolting, although a small proportion currently reside in freshwater for two years. The total age of mature individuals ranges from 3 to 8, but the youngest and oldest age classes are currently rare. No unbiased sources of information on the demographic composition of Yukon River Chinook salmon exist. All sources of data on sex, size and age are biased to an unknown extent, either by gear selectivity or the potentially selective removal of a portion of the migrating adults in downriver fisheries.

The target average age composition of the un-fished population in the simulation was based on a combination of three run reconstructions (information on escapement and subsequent returns by age) available for Yukon River Chinook salmon; the Canadian main stem population for parent years 1979 to 1997 (JTC 2008), the Chena River population for parent years 1986 to 1994 (Evenson 2002), and the Salcha River population for parent years 1987 to 1994 (Evenson 2002). For each parent year, the estimated numbers of fish returning at age were summed across populations and the proportion by age was computed from the sum, after discarding the small number of age-3 fish (annual average of 0.2%). The proportions by age were then averaged across parent years and shifted slightly toward older-aged fish under the presumption that older fish may have been more prevalent in the past and in order to have a greater number of the oldest and largest fish in the simulated population (Table 1).

Table 1. Average age composition (proportion) of parent year
returns computed from run reconstructions of the Chena and Salcha
rivers and the Canadian Yukon River main stem populations, and
the target average age composition for the un-fished population in
the simulation.

Composition	Age				
	4	5	6	7	8
Run reconstruction average	0.057	0.260	0.557	0.121	0.003
Simulation target average	0.030	0.240	0.560	0.140	0.030

Sex composition by age was modeled using a combination of two data sources. The first source
consisted of records obtained from 1960 to 2005 during commercial fishery sampling in the
lower river fishing district Y1 by the Alaska Department of Fish and Game. These data were
sampled from fish caught using gill nets of various mesh sizes in both restricted and unrestricted
commercial openings, although the majority were likely caught in large-mesh gear and so might
be biased towards larger, older individuals. The second data set consisted of lower river test
fishery samples obtained from 1998 to 2005 (both data sets provided courtesy of Danielle
Evenson, Alaska Department of Fish and Game).

These two data sets were combined into a single data set and all records with missing sex, age, or
length data were discarded. Records of fish with length < 300 mm (presumed to be data
recording errors), total age of 3 (very rare), and fish of freshwater age 2 (also rare) were also
discarded. The mean and variance of length were then computed for each combination of sex
and total age. All records with length greater than 3.5 standard deviations from their mean were
identified as potentially erroneous outliers and discarded. The proportion of the individuals of
each total age that were females was computed using the resulting data set of 64,634 records
(Table 2). This data set is a complicated compilation of records obtained at various times using a
diversity of mesh sizes. Although the data are undoubtedly subject to gear selectivity bias, and
perhaps other biases, conditioning on age before computing the proportion of females should
partially nullify any biases. The resulting estimates of sex composition are expected to provide
reasonable approximations of sex composition by age.

Table 2. Proportion female by age
computed from the combined
commercial fishery and lower river
test fishery samples from fishing
district Y1.

Age				
4	5	6	7	8
0.05	0.29	0.61	0.63	0.67

The target average age composition (Table 1) and proportion female by age (Table 2) were multiplied and then scaled to sum to 1.0 for each sex to provide a model for average age composition by sex (Table 3).

Table 3. Age composition and the mean and standard deviation of age used as initial model parameters, by sex.

Sex	Age 4	5	6	7	8	Mean	Standard deviation
Female	0.003	0.134	0.656	0.169	0.039	6.1	0.82
Male	0.059	0.356	0.456	0.108	0.021	5.7	0.68

The mean and standard deviation of length, by sex, was estimated using data collected from 1995 to 2004 for species apportionment of sonar-derived estimates of total fish abundance near Pilot Station, Alaska (Pfisterer 2002; data provided courtesy of Toshihide Hamazaki, Alaska Department of Fish and Game). These fish were caught in gill nets of various mesh sizes, from 2.75 in to 8.5 in, and may therefore be less size-biased than other data sources, although a proportion of the commercial and subsistence catch occurs downriver from this location. However, reduced catches were taken in most of these years, in response to reduced run sizes, so the induced bias is not thought to be substantial. The net selectivity estimates of Bromaghin (2005) were used to derive a weight for each fish, based on its length and the mesh in which it was caught; the weight was taken as the inverse of the relative selectivity of each fish. The resulting weighted means and standard deviations were 808 mm and 91 mm for females, and 720 mm and 132 mm for males.

The correlation between age and length, which was estimated using the combined commercial and test fishery data set described earlier, was 0.82 and 0.58 for males and females, respectively.

The joint distribution of age and length was modeled using a bivariate normal probability density function (Kotz et al. 2000) for each sex. Although this is a continuous density, cut-points were established for each discrete age and a continuous value for age falling within the interval bounded by two cut-points was converted to the discrete age associated with that interval. Cut-points were established for each sex so that the resulting proportions by age approximated the proportions given in Table 3.

The means, standard deviations, and the correlations between age and length, as well as the cut-points, described above were used as initial parameters of the bivariate normal model. During model calibration, there was a tendency for mean lengths and ages to drift upward in the first few years and stabilize at means above the target values. To counteract this drift, the initial parameter values were adjusted, as necessary, to produce a stable model with the specified age, sex, and size composition in the absence of a fishery. The final values of the parameters used to initiate the model are presented in Table 4.

We attempted to use all available data in ways to minimize the effects of any biases they might contain, and therefore mimic the demographic composition of Yukon River Chinook salmon as closely as possible. However, the degree to which we were successful is unknown, and the

resulting age and size distributions are best viewed as representing a generic large-bodied, stream-type Chinook salmon population.

Table 4. Parameter values related to age and length developed during model calibration and used to initiate the simulation, by sex.

Parameter	Male	Female
Mean length	680	790
Standard deviation length	143	99
Mean age	5.6	6.0
Standard deviation age	0.902	0.715
Age-length correlation	0.82	0.58
Cut-point between age 4 and 5	4.32263	4.31170
Cut-point between age 5 and 6	5.44756	5.39983
Cut-point between age 6 and 7	6.58131	6.64326
Cut-point between age 7 and 8	7.31360	7.25576

Mating Sub-model

Males and females were paired for reproduction using a two-stage mating model. The first stage, which we term "proposal", was based on observations of the attractiveness of females to males (Figure 4 of Foote 1988). We used a range-restricted quadratic logistic function to model the probability that a male proposes to a female,

$$P(\text{Proposal}) \quad = \quad a + (b-a)\left\{1 + e^{-\beta_0 - \beta_1 x - \beta_2 x^2}\right\}^{-1}, \tag{1}$$

where $a = 0.05$, $b = 0.95$, $\beta_0 = -10$, $\beta_1 = 10$, $\beta_2 = 3$, and x was the ratio of female to male length (Figure 3). We evaluated a number of functions for the probability a female accepts a male (termed "acceptance") given proposal by a male. We were unable to find support for any particular function in the literature, and eventually selected Equation (1) to also represent the probability of acceptance given proposal, with the same parameter values but x redefined as the ratio of male to female length   Both males and females therefore had a strong preference for mates that were as large or larger than themselves.

This sub-model was implemented sequentially for each female in the escapement. For a given female, a male was selected at random from among all males in the escapement. The probability the two would mate was determined stochastically using the product of the probabilities of Proposal and Acceptance. If the pair did not mate, additional males were selected at random until mating was achieved. If the pair did mate, the next female was selected. This process was repeated until all females in the escapement had mated. Probabilities of mating therefore depended on the logistic functions, the length of a particular female, and the length distribution of all males available in an escapement.
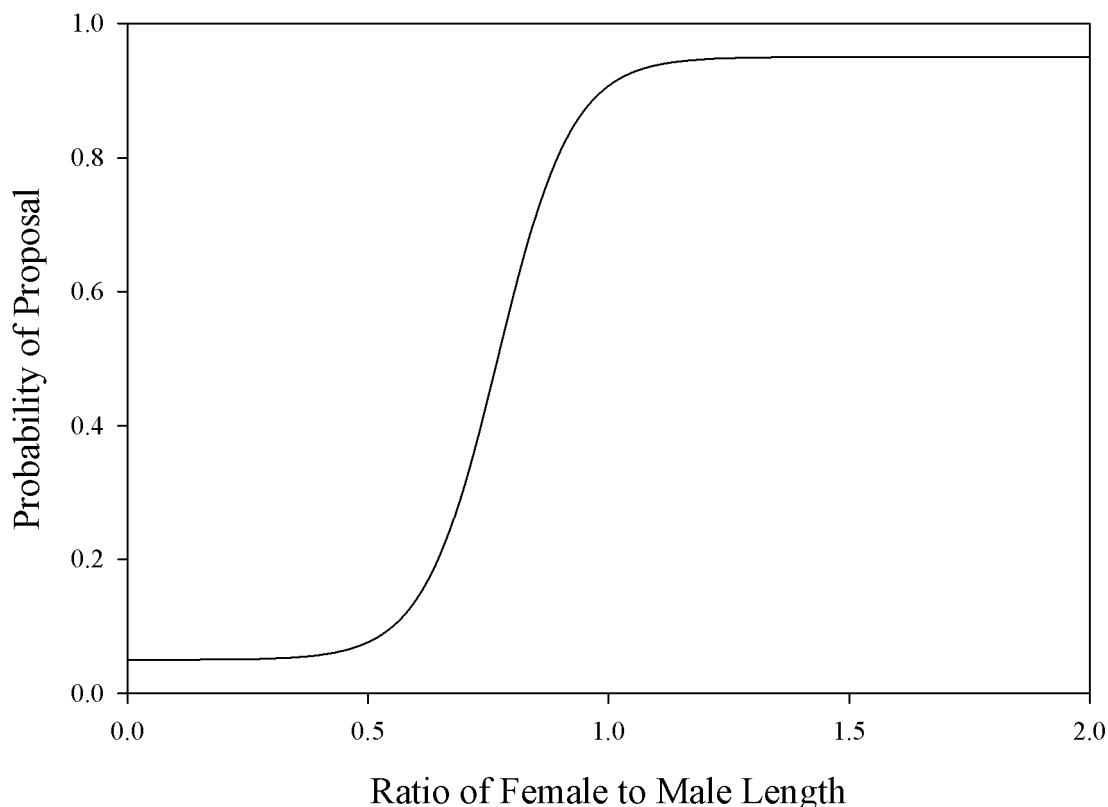
Figure 3. Probability a male proposes to a female as a function of the ratio of female to male length. The same function, with the horizontal axis redefined as the ratio of male to female length, was used for the probability of acceptance given proposal.

Characteristics of this sub-model include that females were monogamous, males were polygamous, and all males in the escapement did not necessarily mate. In our initial conceptualization of the mating sub-model, each female constructed multiple nests and probability models controlled the number of eggs to deposit in each nest and whether a female would pair with the same or a new male between nests. We eventually abandoned that concept because of the lack of data or prior models on which to base model structure and parameterization. The benchmark we were striving for was a small positive correlation (Kaitala and Getz 1995), of approximately 0.2, between the lengths of mated pairs, which this model produced in the un-fished population. A more realistic, and thus more complicated, model structure that produces a similar correlation between the lengths of mated pairs might be expected to produce similar simulation results, because the sizes and ages of a mated pair formed the input to the heritability model (see *Heritability and Fitness Sub-model* below) and thereby controlled the size and age of the subsequent generation.

Fecundity Sub-model

Data on the fecundity of Yukon River Chinook salmon are limited. Healey and Heard (1984) present an allometric model, estimated using a total of 15 average fecundity values computed from fish sampled in 1965 and 1981, but the individual observations were not available for our

inspection so this information was not used to parameterize this sub-model. Weidner (1972) and Skaugstad and McCracken (1991) reported data collected in the Tanana River and the Yukon River main stem in the general vicinity of the Tanana River confluence (Figure 1). Jasper and Evenson (2006), who describe fecundity data collected from the same area, found that fecundity had declined nearly 25% from the time period in which the data reported by Skaugstad and McCracken (1991) were collected. Whether this apparent trend represents a true decline, or is the result of a high level of natural variability or bias in the sampling or estimation of fecundity, is unknown. However, egg samples summarized in Jasper and Evenson (2006) were frozen for some time and the physical structure of some eggs was destroyed when the eggs were thawed for processing (James Jasper, Alaska Department of Fish and Game, personal communication). For that reason, we developed a fecundity sub-model using only the data reported by Weidner (1971) and Skaugstad and McCracken (1991).

The relationship between length and fecundity was explored using a variety of linear models. The most complex model was a six parameter model with a separate intercept, slope, and variance for each of the two data sources. Models were compared using the small sample version of the Akaike Information Criterion (AIC_C, Burnham and Anderson 2002). The model selected had three parameters: an intercept, slope, and variance common to both data sources (Figure 4).

Preliminary investigation of the linear model revealed that unrealistically low or high levels of fecundity were possible for females that were unusually small or large in length. We therefore adopted a Pearson model that closely approximated the linear model within the observed range of the data, but moderated the rate of change in fecundity for fish of unusually small or large length. The functional form of the Pearson model is

$$f(x) \quad = \quad a + b\left[1 + 4(x - c)^2\left(2^{\frac{1}{d}} - 1\right)\Big/ e^2\right]^{-d}. \tag{2}$$

Pearson model parameter values of $a = 4{,}515$, $b = 12{,}194$, $c = 1{,}304$, $d = 1{,}000{,}000$, and $e = 753$ were selected to approximate the linear model (Figure 4).

Residuals from the Pearson model appeared to be homogeneous for all lengths, with a standard deviation of approximately 1,630. A Kolmogorov test of the normality of model residuals (Conover 1999) was not rejected (p > 0.249). Therefore, fecundity was modeled as a normal random variable, with mean given by the Pearson model and a standard deviation of 1,630. As an additional precaution against unrealistically small fecundity values, a minimum fecundity of 2,000 eggs was used in the simulation.
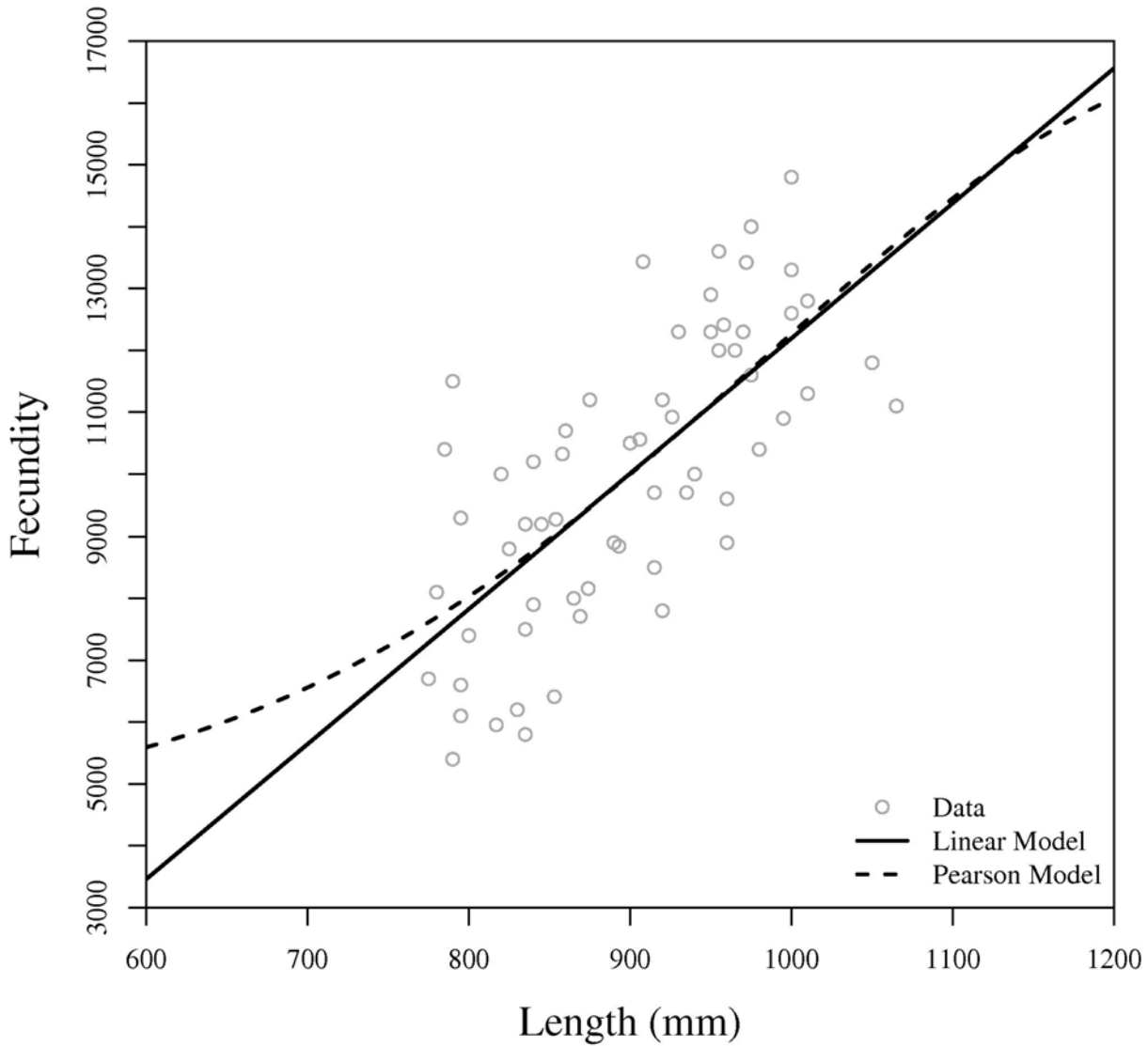
Figure 4. Fecundity data used to parameterize the fecundity sub-model, with the final linear model and the Pearson model of fecundity, as a function of female length. The Pearson model was used in the computer simulation, combined with a minimum fecundity of 2,000 eggs.

Survival Sub-models

We employed a Ricker stock-recruit model (Ricker 1975) as a conceptual base from which to develop survival rate sub-models. One parameterization of the Ricker model is

$$R = Se^{\alpha\left(1-\frac{S}{S_r}\right)},$$ (3)

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where

S = escapement in numbers of fish,
R = total return from S (over several years) in numbers of salmon,
α = parameter controlling shape (productivity), and
S_r = parameter controlling equilibrium abundance.

Two values of α were considered. A value of α = 2.25 was derived from the three run reconstructions of Yukon River Chinook salmon (see *Age, Sex, and Length Sub-model* above). This represents a comparatively high level of productivity for Chinook salmon. A reduced value of α = 1.5 was selected to represent a lower level of productivity.

We re-parameterized the model in Equation (3) to express production as a function of the total number of eggs deposited, E,

$$ R = E\left(e^{\frac{-\alpha E}{\mu_F S_r}}\right)\left(\frac{e^\alpha}{\mu_F}\right), \tag{4} $$

where μ_F is the mean number of eggs per spawner. A value of 3,700 was used for μ_F, which was obtained as the ratio of the expected fecundity relative to the length distribution females in an un-fished population (see *Age, Sex, and Length Sub-model* above) and an assumed sex composition of 50% females.

The second expression for R (Equation 4) can be viewed as the number of eggs deposited multiplied by density-dependent and density-independent survival rates. Average freshwater survival from the egg stage through year two in freshwater, λ_F, was taken as the density-dependent survival rate;

$$ \lambda_F = e^{\frac{-\alpha E}{\mu_F S_r}}. \tag{5} $$

The density-independent component of Equation 4 is the product of survival rates in years 3 through 8 and probabilities of maturation at a particular age (see *Heritability and Fitness Sub-model* below). Conceptually, if λ_i is the probability of surviving from age i-1 to i and M_a is the probability of maturing at age a,

$$ \left(\frac{e^\alpha}{\mu_F}\right) = \lambda_3\lambda_4\prod_{i=4}^{7}(1-M_i)\lambda_{i+1}. \tag{6} $$

We implemented constant sex-specific annual marine survival from age 3 until maturation, denoted λ_{MF} and λ_{MM} for females and males, respectively. Therefore, Equation 6 was approximated by

$$\left(\frac{e^{\alpha}}{\mu_F}\right) \approx \lambda_{M1}\left(\frac{\lambda_{MF} + \lambda_{MM}}{2}\right)^{\left(\frac{\mu_{AF} + \mu_{AM}}{2} - 3\right)}, \tag{7}$$

where λ_{M1} is the mean survival in the first year of marine residence and μ_{AF} and μ_{AM} denote the mean target age at maturation for females and males, respectively, in an un-fished population (see *Age, Sex, and Length Sub-model* above). The portion of Equation 7 in parentheses following λ_{M1} therefore represents average annual marine survival after age 3 multiplied by the average number of years an individual would be subject to that mortality. A model for λ_{M1} was therefore obtained from a re-expression of Equation 7;

$$\lambda_{M1} = \left(\frac{e^{\alpha}}{\mu_F}\right)\left(\frac{\lambda_{MF} + \lambda_{MM}}{2}\right)^{-\left(\frac{\mu_{AF} + \mu_{AM}}{2} - 3\right)}. \tag{8}$$

Survival during freshwater residence and the first year of marine residence was equal for both sexes. An individual of sex G maturing at age A (see *Heritability and Fitness Sub-model* below) was therefore subject to a mean lifetime survival rate, λ, of

$$\lambda = \lambda_F \lambda_{M1} \left(\lambda_{MG}\right)^{A-3}, \tag{9}$$

where G equals either F for females or M for males. Using this survival rate construction, a deposition of E eggs produced an average total return that approximated Equation 4.

The survival rates sub-models were implemented by first multiplying the number of eggs deposited by a lognormal random variable with mean equal to $\ln(S_2 S_3)$ and a standard deviation of $(0.8)(0.425)$. The total standard deviation of 0.425 was based on the level of variation in return-per-spawner estimates from the run reconstructions described above (see *Age, Sex, and Length Sub-model* above), while the multiple of 0.8 was based on Bradford's (1995) partitioning of survival rate variance. The result was the number of salmon surviving from egg deposition through their first year in the marine environment. Sex composition was then established for the survivors with a single draw from a normal probability distribution with mean 0.50 and standard

deviation 0.05, values which were derived from the run reconstructions described earlier (see *Age, Sex, and Length Sub-model* above) and Table 3. The age and size at maturation were established after the first year in the marine environment (see *Heritability and Fitness Sub-model* below). Annual sex-specific marine survival rates for age 3 to maturation were also randomized as lognormal deviates, with means ln(0.82) and ln(0.77) for females and males, respectively, and a common standard deviation of 1.05. These values were derived from a combination of the literature, professional judgment, and initial model calibration.

Heritability and Fitness Sub-model

We used a modification of an approach developed by Ronningen (1974), Olausson and Ronningen (1975), and Réale and Roff (2001) to characterize phenotypic changes in correlated life history traits (here, length and age at maturation). The advantage of this approach was that genetic and environmental sources of variation in the phenotype were quantified and could be tracked, and phenotypic evolution could be predicted without tracking individual genes, which have not been identified for these traits. These authors showed that a phenotype expressed in an individual, X_i, in terms of genetic and environmental components of variance could be characterized by:

$$X_i = m\sqrt{\frac{1}{2}h^2} + E_i\sqrt{1 - \frac{1}{2}h^2} \;,$$

(10)

where m was the genotypic mean, h^2 was the trait heritability, and E_i was the environmental deviation. E_i was assumed to be normally distributed with mean 0 and variance V_E (i.e., $E_i \sim N(0,V_E)$); the latter term that includes E_i was then normally distributed with mean 0 and variance equal to

$$V_E\left(1 - \frac{1}{2}h^2\right).$$

(11)

Assuming a full-sib pedigree structure, two trait phenotypes, $X_{i,j}$ and $Y_{i,j}$, depended on their heritabilities, and genetic and environmental correlations, according to the equations

$$X_{i,j} = a_{x,i}\sqrt{\frac{1}{2}h_x^2} + b_{x,i,j}\sqrt{1 - \frac{1}{2}h_x^2} \;,$$

(12)

and

$$Y_{i,j} = r_A a_{x,i} \sqrt{\frac{1}{2}h_x^2} + a_{y,i}\sqrt{\frac{1}{2}\left(1-r_A^2\right)h_y^2} + r_E b_{x,i,j}\sqrt{1-\frac{1}{2}h_x^2} + b_{y,i,j}\sqrt{\left(1-\frac{1}{2}h_y^2\right)\left(1-r_E^2\right)}, \tag{13}$$

where $X_{i,j}$ and $Y_{i,j}$ were the trait values for the jth individual in family i; $a_{x,i}$ and $a_{y,i}$ were random standard normal values common to the ith family; $b_{x,i,j}$ and $b_{y,i,j}$ were random standard normal values of the jth individual from the ith family; h_x^2 and h_y^2 were the heritabilities of each trait; r_A was the genetic correlation between the two traits; and r_E was the "environmental" correlation between the traits, calculated from the phenotypic correlation, r_P, as

$$r_E = \left(r_P - \frac{1}{2}h_x h_y\right)\Big/ \sqrt{\left(1-\frac{1}{2}h_x^2\right)\left(1-\frac{1}{2}h_y^2\right)}. \tag{14}$$

Model outputs were $X_{i,j}$ and $Y_{i,j}$. Model inputs included $a_{x,i}$ and $a_{y,i}$; $b_{x,i,j}$ and $b_{y,i,j}$; h_x^2 and h_y^2; r_A; r_E; and r_P (as well as the number of phenotypes in each family desired). For more detail see Simons and Roff (1994), Roff and Preziosi (1994), and Roff (2006).

We modified this approach as follows; let

X_R = a bivariate vector of the age and length phenotype of reproducing individuals,

X_O = a bivariate vector of the age and length phenotype of an offspring,

μ_R = the expectation $E[X_R]$,

Σ_R = the dispersion matrix $V[X_R]$,

Σ_T = the initial dispersion matrix of age and length (see *Age, Sex, and Length Sub-model* above),

ε_{MP} = the bivariate standardized average mid-parent deviation from μ_R, a constant bias term within each family,

ε_G = a bivariate random genetic error term common to all offspring within each family, $\varepsilon_G \sim N(0, D(1/\sqrt{2}, 1/\sqrt{2})\Sigma_R)$, where $D(v)$ is a diagonal matrix with the vector v along the diagonal,

ε_E = a random environmental error term for individual offspring, $\varepsilon_E \sim N(0, \Sigma_T)$,

h_A^2 = the heritability of age, and

h_L^2 = the heritability of length.

The bivariate phenotypes of offspring surviving to age 3 (see *Survival Sub-models* above) were then modeled as

$$X_O = \mu_R + D\left(\sqrt{h_A^2}, \sqrt{h_L^2}\right)(\varepsilon_{MP} + \varepsilon_G) + D\left(\sqrt{1-h_A^2}, \sqrt{1-h_L^2}\right)\varepsilon_E. \tag{15}$$

Heritability values of 0.35 and 0.34 were used for age and length, respectively; these parameter values were obtained by restricted maximum likelihood estimation from a Chinook salmon population in Washington State (Hard 2004). We did not generate an age-structured genetic covariance matrix directly because of the lack of available information on genetic covariation among lengths expressed at different ages; instead, the genetic covariation of length and age was modeled by adjusting the phenotypic variances and covariances of ages and lengths at age by the empirically derived heritability estimates (Hard et al. in press). The overall phenotypic correlation between length and age was 0.48. This approach may overestimate the responses in lengths expressed at younger ages to selection on large fish, but it is unlikely to misconstrue the direction of the responses to selection over the relatively short term because the estimate of genetic correlation between the traits was also positive. The direction of selection on fish of particular ages is primarily dependent on the threshold sizes of fish exposed to selection and the form of the selection (e.g., disruptive versus directional).

The heritability sub-model (Equation 15) was then implemented separately for male and female offspring surviving to age 3. In order to maintain the distinction between the age and length distributions of each sex, the mid-parent error ε_{MP} for each family was computed after first transforming the bivariate age-length distribution of the reproducing individuals of one sex to that of the other sex using spectral and Cholesky decompositions of the variance matrices (Seber 1977). All error terms were randomly drawn from sex-specific bivariate normal distributions. A single random genetic error term ε_G was drawn for all offspring of a given sex within each family. A random environmental error term was then drawn for each individual offspring, and its phenotype (maturation age and length) thereby established.

Application of the heritability sub-model was followed by what we term a fitness sub-model. This sub-model was conceptualized as a selective force that would tend to disfavor individuals whose phenotypes deviated greatly from the un-fished mean age and length (Law 1991; Hard 2004; see *Age, Sex, and Length Sub-model* above). It therefore represented stabilizing selection toward a naturally optimum length and age, i.e., a force in opposition to fishery-induced selection which might reflect natural and/or sexual selection on size and age in the population. The fitness sub-model, f(A,L), was constructed as a bivariate normal density (Hogg and Craig 1978) scaled to have a maximum of 1.0, with means equal to the un-fished means and variances equal to seven times the un-fished variances, i.e.,

$$f(A,L) = \exp\left\{-\frac{1}{7(2)\left(1-\rho^2\right)}\left[\left(\frac{A-\mu_A}{\sigma_A}\right)^2 - 2\rho\left(\frac{A-\mu_A}{\sigma_A}\right)\left(\frac{L-\mu_L}{\sigma_L}\right) + \left(\frac{L-\mu_L}{\sigma_L}\right)^2\right]\right\}. \tag{16}$$

The variance multiplier of seven was established during preliminary model calibration as the value which stabilized the un-fished population without reducing variances below the desired levels previously described. The effect is a selection function whose value is high over much of the natural range of length and age, but declines more steeply as deviations from the un-fished mean increase. The fitness sub-model is difficult to visualize in three dimensions, so we provide a two-dimensional hypothetical example for length alone to illustrate its use and the magnitude of its effect (Figure 5). In this example, the fitness sub-model transforms the hypothetical length density of the population to one slightly more similar to the mode of the fitness function and the length density of the un-fished population.
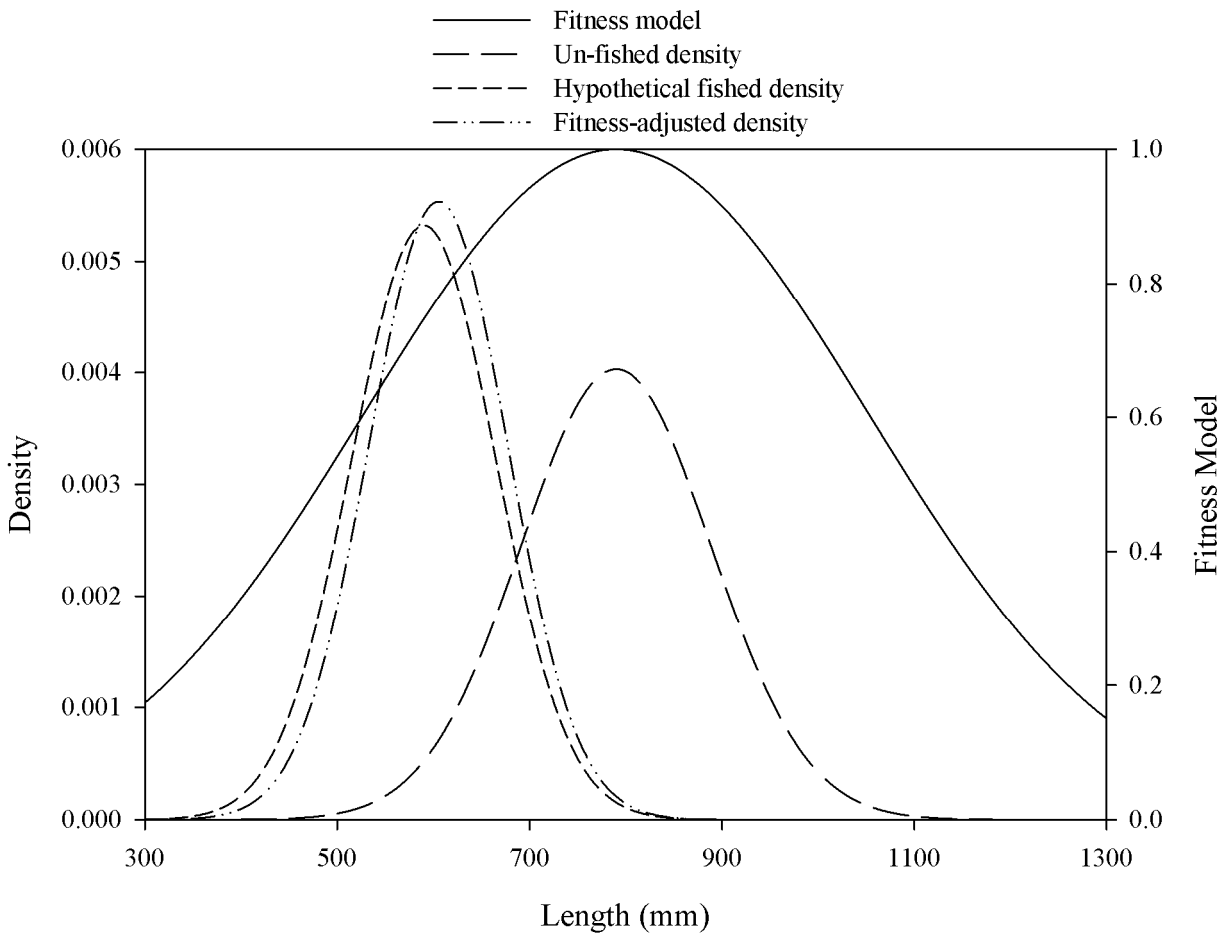
Figure 5. A hypothetical example in two dimensions of the effect of the fitness sub-model.

The fitness model was implemented by drawing a sample of offspring, equivalent in size to the number of individuals surviving to age 3, from the output of the heritability sub-model, with replacement, using the values of the fitness function as probabilities of selection. The result of this sampling process was a collection of individuals whose lengths and ages at maturation were established, although subject to additional marine mortality until maturation (λ_{MF} and λ_{MF}, see *Survival Sub-models* above), resulting in a parent year return apportioned to year of maturation. Surviving offspring maturing in a common year were aggregated to form annual runs.

Exploitation Sub-model

The exploitation sub-model was constructed from three components, an escapement goal (desired number of reproducing salmon), a level of management precision, and an exploitation rate. A target escapement goal, S_G, was established as a multiple, k, of the escapement that maximizes sustainable average yield, S_{MSY} (Ricker 1975; see *Planned Simulations* below); 0.5, 1.0, and 1.5 were used as values to k to represent a range from under-escapement to over-escapement relative to S_{MSY}. Given a target escapement goal $S_G = kS_{MSY}$, an escapement goal range of $0.8S_G$ to $1.6S_G$ was established (Eggers 1993). The management objective was to manage toward the lower end of the range in years of small runs and toward the upper end of the range in years of large runs, which approximates the approach of Yukon River fishery managers (Gene Sandone, Alaska Department of Fish and Game, personal communication).

The ability of management to assess run size and manage accordingly was modeled as a uniform random variable (Johnson et al. 1995) centered on the true run size. Two levels of management precision were utilized. Under more precise management, managers were able to assess the size of a run within 15% of the true run size, while run size was assessed within 30% of the true run size under less precise management.

Given a simulated (true) run size, a randomly generated assessment of the run size (N) within the bounds of management precision, and an escapement goal, we constructed an exploitation rate model to establish a catch level. If a run was assessed to be less than $0.8S_G$, no fish were taken. If a run was assessed to exceed $0.8S_G$, a constant exploitation rate γ was applied to the portion of the assessed run in excess of $0.8S_G$. The escapement goal therefore increased linearly, between $0.8S_G$ and the maximum of $1.6S_G$, with the assessed run size. Two values of γ were employed, with $\gamma = 0.85$ representing a more aggressive fishery than $\gamma = 0.5$. The exploitation rates on the entire run that would occur without error in run assessment are presented in Figure 6.

The assessed run abundance and the resulting exploitation rate were used to establish a catch level. Each fish in the run was assigned a probability of capture, using the length-based relative net selectivity estimates of Bromaghin (2005) as sampling probabilities. A catch of the determined size was then removed from the run using unequal probability sampling without replacement. Catch levels were always achieved, with realized escapements varying commensurate with error in assessing run size. However, realized exploitation rates on the entire run were capped at 0.95 to prevent all fish from being caught, which could occur in years of very large runs that were over-estimated by an error greater than the escapement goal. Fish that were not caught comprised the reproductive population for that year and were used to generate offspring to return in subsequent years.

Planned Simulations

We conducted a preliminary ("burn-in") simulation to randomize the starting point for all subsequent simulations; this was done independently for the low-productivity ($\alpha = 1.50$; Equation 3) and high-productivity ($\alpha = 2.25$) simulations. The population was initialized with a generation of escapements equal to the equilibrium abundance level of $S_r = 10,000$, and population dynamics were simulated for 2,200 years. Results from the first 200 years were discarded, to disassociate results from the constant starting point of 10,000 spawners, and the results from the remaining 2,000 years were randomized into 250 blocks of data containing 8 years. Each block was randomly assigned to initialize one of the 250 replications comprising each simulation. In addition, the last 2,000 years of data for each productivity level were used to
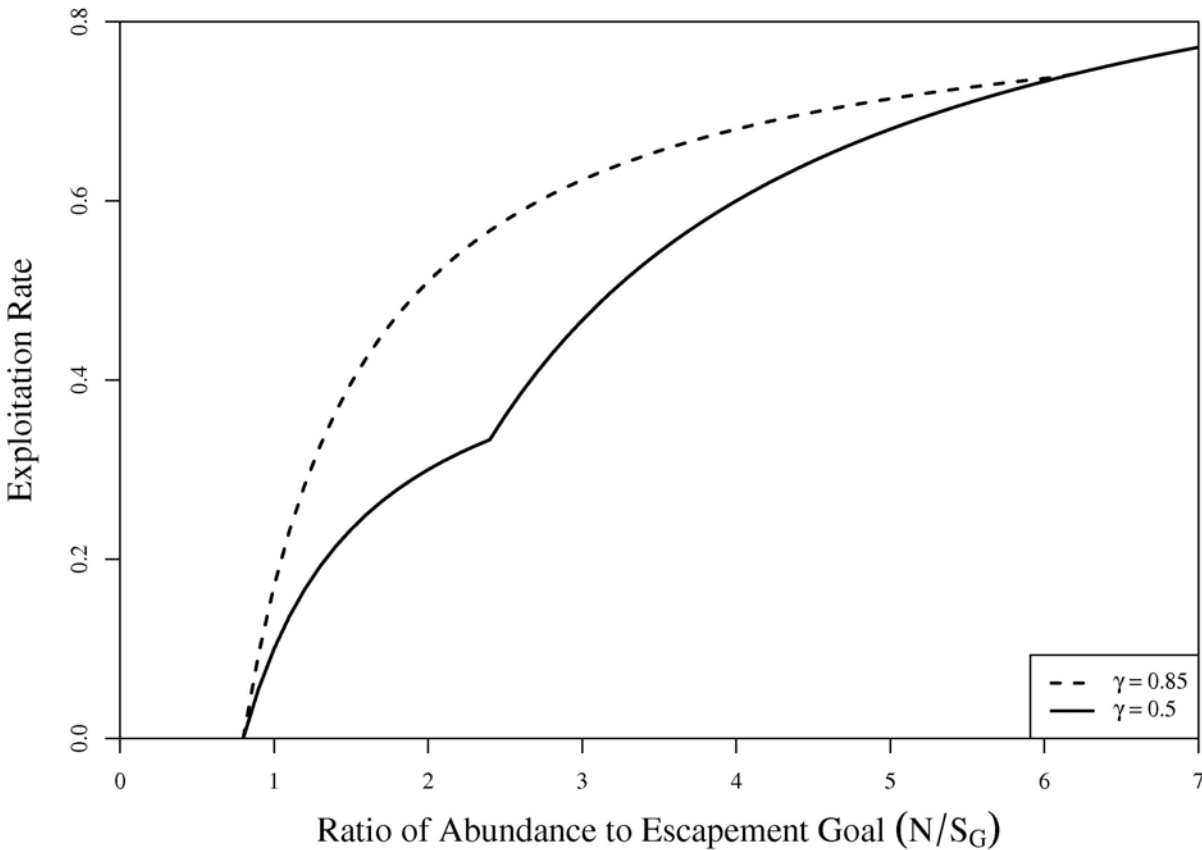
Figure 6. The rate at which the total run was exploited, in the absence of management error in assessing run abundance, under each of the two exploitation rate (γ) models.

estimate the level of escapement maximizing sustained yield (S_{MSY}) using the approximation of Hilborn (1985) that incorporates the expectation of lognormally distributed quantities. S_{MSY} was estimated to be 3,505 in the high-productivity case (Figure 7), and 4,014 in the low-productivity case (Figure 8); these values were used to establish escapement goals (see *Exploitation Sub-model* above).

We planned to conduct an initial set of 24 simulations, formed by the combinations of a productivity level (2 levels) and the management controls of an exploitation rate λ (2 levels), a level of management precision (2 levels), and an escapement goal (3 levels). In all of these simulations, catches were taken using the selectivity function for an 8.5-in gill net (Bromaghin 2005). In addition, a no-fishing control simulation was conducted for each of the two levels of productivity (Table 5).

Each simulation consisted of 250 replications of modeling population dynamics for 200 years, or 25 complete generations based on a maximum age of 8 years. Information from the last 8 years of each replication was saved so that the simulation could be continued for additional years, perhaps under different management conditions. Additional simulations were anticipated, with specifics being dependent upon an analysis of the results of this initial collection of simulations.
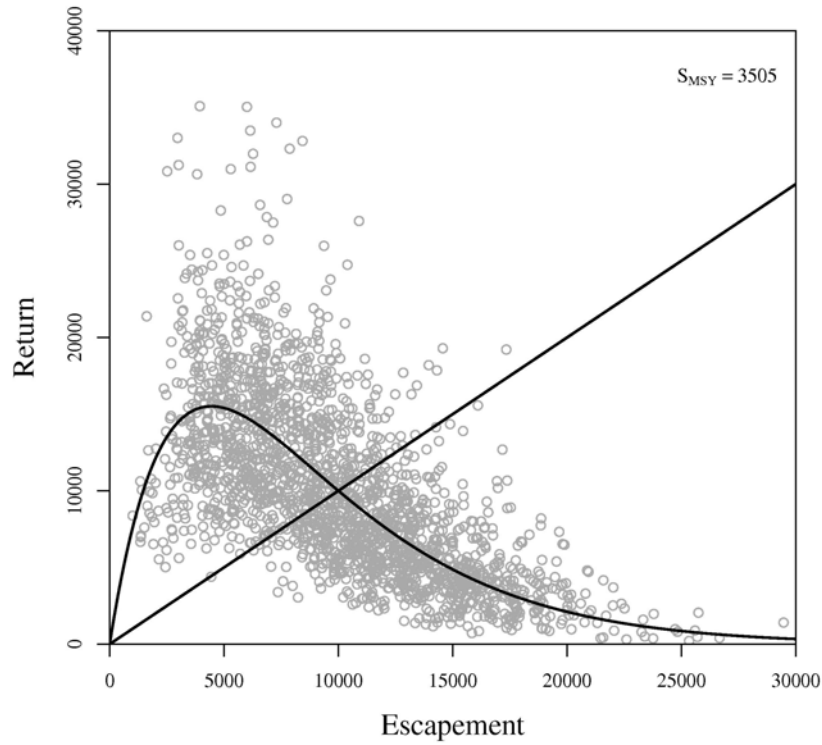
Figure 7. Escapements and subsequent returns observed during the high productivity burn-in simulation. These data were used to initialize high productivity simulations, and to estimate the escapement that maximized average yield (S_{MSY}) for high productivity simulations.
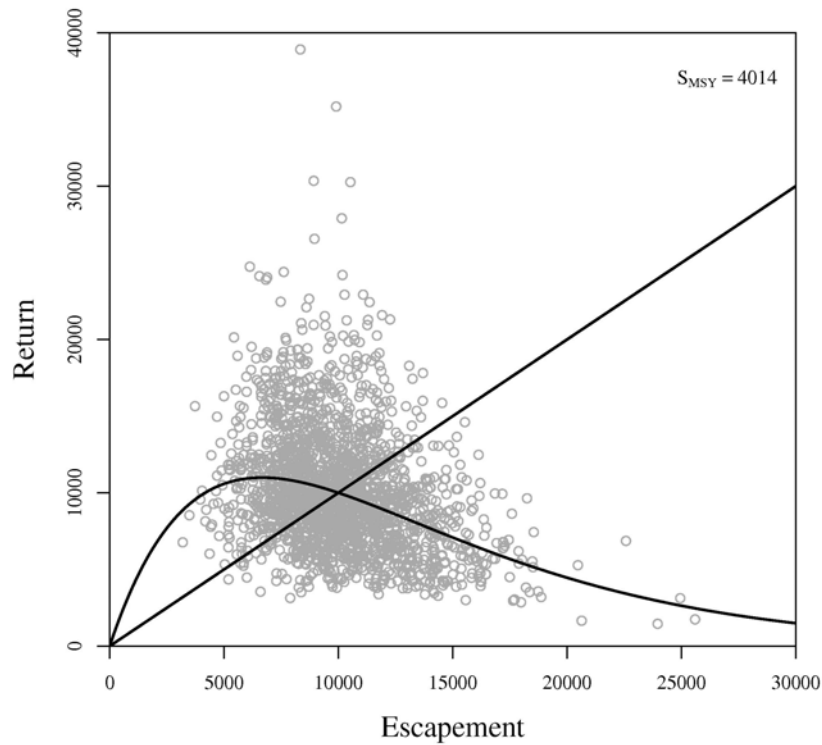
Figure 8. Escapements and subsequent returns observed during the low productivity burn-in simulation. These data were used to initialize low productivity simulations, and to estimate the escapement that maximized average yield (S_{MSY}) for low productivity simulations.

Table 5. Parameter values that varied among the 26 planned simulations. The value listed for the escapement goal is a multiple of the escapement that maximizes sustained yield, S_{MSY}. In all cases, except the two no-fishing control simulations, catches were taken with 8.5-in mesh gill nets.

Simulation	Productivity	Exploitation	Management precision	Escapement goal
1	2.25		No harvest control	
2	2.25	0.85	± 30%	0.50
3	2.25	0.85	± 30%	1.00
4	2.25	0.85	± 30%	1.50
5	2.25	0.50	± 30%	0.50
6	2.25	0.50	± 30%	1.00
7	2.25	0.50	± 30%	1.50
8	2.25	0.85	± 15%	0.50
9	2.25	0.85	± 15%	1.00
10	2.25	0.85	± 15%	1.50
11	2.25	0.50	± 15%	0.50
12	2.25	0.50	± 15%	1.00
13	2.25	0.50	± 15%	1.50
14	1.50		No harvest control	
15	1.50	0.85	± 30%	0.50
16	1.50	0.85	± 30%	1.00
17	1.50	0.85	± 30%	1.50
18	1.50	0.50	± 30%	0.50
19	1.50	0.50	± 30%	1.00
20	1.50	0.50	± 30%	1.50
21	1.50	0.85	± 15%	0.50
22	1.50	0.85	± 15%	1.00
23	1.50	0.85	± 15%	1.50
24	1.50	0.50	± 15%	0.50
25	1.50	0.50	± 15%	1.00
26	1.50	0.50	± 15%	1.50

Results

Planned Simulations

In the two control simulations with no fishing (Simulations 1 and 14), population demographics showed no signs of trending, providing evidence of model stability in the absence of fishing; it was such stability that we were seeking during model calibration. Conversely, population demographics showed trends under all fishing scenarios considered in the planned simulations, with the population shifting toward smaller, younger fish in response to the selective removal of large fish.

We selected the mean length and age of all fish in the run to illustrate the temporal patterns observed in the population demographics in response to size-selective exploitation. Mean length and age were computed for each year in each of the 250 replications within a simulation, and then averaged across replications for each year. In nearly all fishing scenarios considered, mean

length displayed a consistent rate of decline for approximately 50 years, after which the rate of decline tended to moderate (Figures 9 and 10). In most cases, mean length was approximately stable by Year 100. Mean length decreased by approximately one third in the high-productivity simulations (Figure 9), while the decline was somewhat less, approximately one quarter, in the low-productivity simulations (Figure 10). Mean age responded similarly (Figures 11 and 12).

There were two exceptions to this general pattern, the low-productivity simulations 21 and 27 (Table 5; Figures 10 and 12). The fishery in these simulations had the lowest exploitation rate among all scenarios considered, with an escapement goal of $1.5(S_{MSY})$ and an exploitation rate of 50% within the escapement goal range. In these cases, mean length and age declined throughout the 200 years of the simulation and did not stabilize. Given the consistent downward trend, we presume that both characteristics would have eventually stabilized had the simulation been conducted for a greater number of years. In the corresponding simulations with high productivity (Simulations 7 and 13), mean length and age also declined more slowly than in the other high-productivity fishing scenarios (Figures 9 and 11). However, in these cases, mean length eventually stabilized at a level somewhat greater than that observed in the other fishing scenarios.

The modeled population was stable prior to initiation of the fishery, experienced a period of change in response to the initiation of selective exploitation, and, in most cases, reached a new equilibrium (Figures 9 to 12). To compare the relative influence of the parameters controlling fishing (exploitation rate, management precision, and escapement goal), we constructed box-plot figures for a selected subset of model outputs using the 250 replications in year 200 of each simulation:

- the size of the run and the escapement (run – catch) are presented in Figures 13 and 14;
- the catch and the exploitation rate are presented in Figures 15 and 16;
- the mean length of all females and males in the run are presented in Figures 17 and 18;
- the mean length of all females and males in the run, by age, are presented in Figures 19-28;
- the mean age of all females and males in the run are presented in Figures 29 and 30;
- the proportion of all fish in the run that are of a particular age, by sex, are presented in Figures 31-40; and
- the average fecundity (number of eggs per female) and the total number of eggs among all females in the escapement are presented in Figures 41 and 42.

With respect to an individual box-plot, the box represents the central 50% of the values. The lower error bar, or "whisker," represents the smallest data value greater than the 1st quartile – 1.5 times the interquartile range (IQR; IQR = 3rd quartile – 1st quartile), and the upper error bar represents the largest data value less than the 3rd quartile + 1.5(IQR). The circles denote extreme observations.
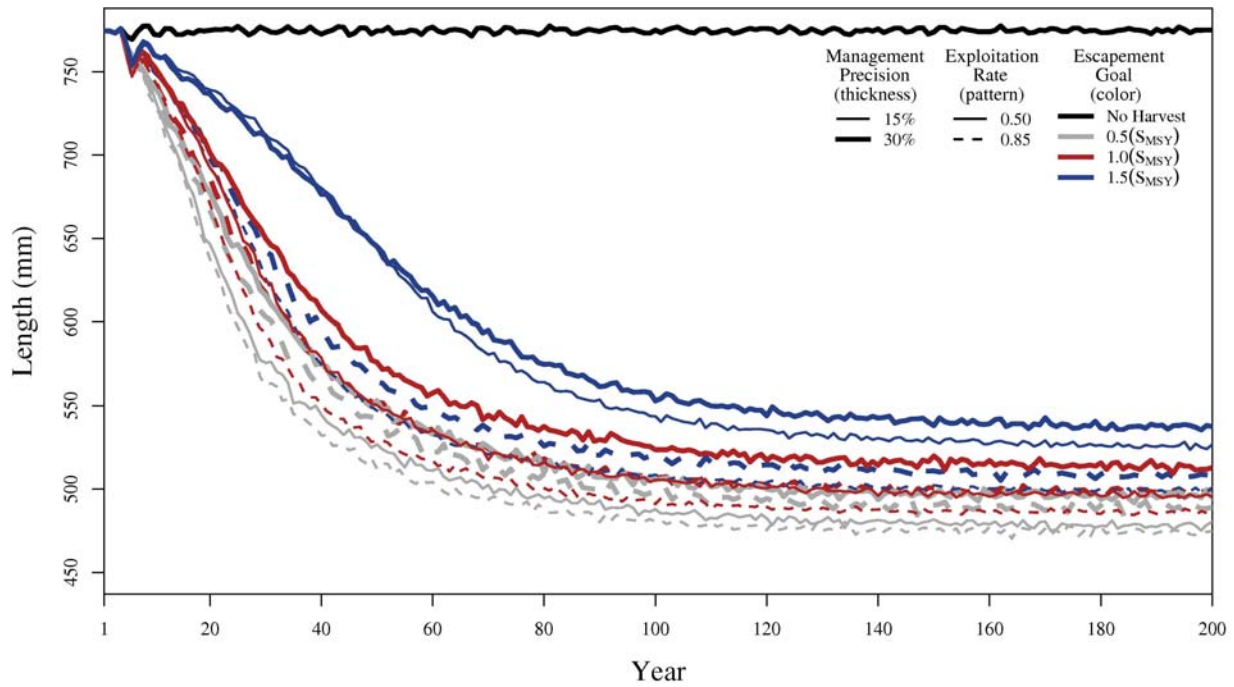
Figure 9. Mean length (mm) of all fish in a run observed during high-productivity simulations (1 – 13). Fishing scenarios consisted of a no-fishing control and 12 combinations of an exploitation rate, management precision, and escapement goal. All catches were taken with the selectivity of an 8.5 in gill net.
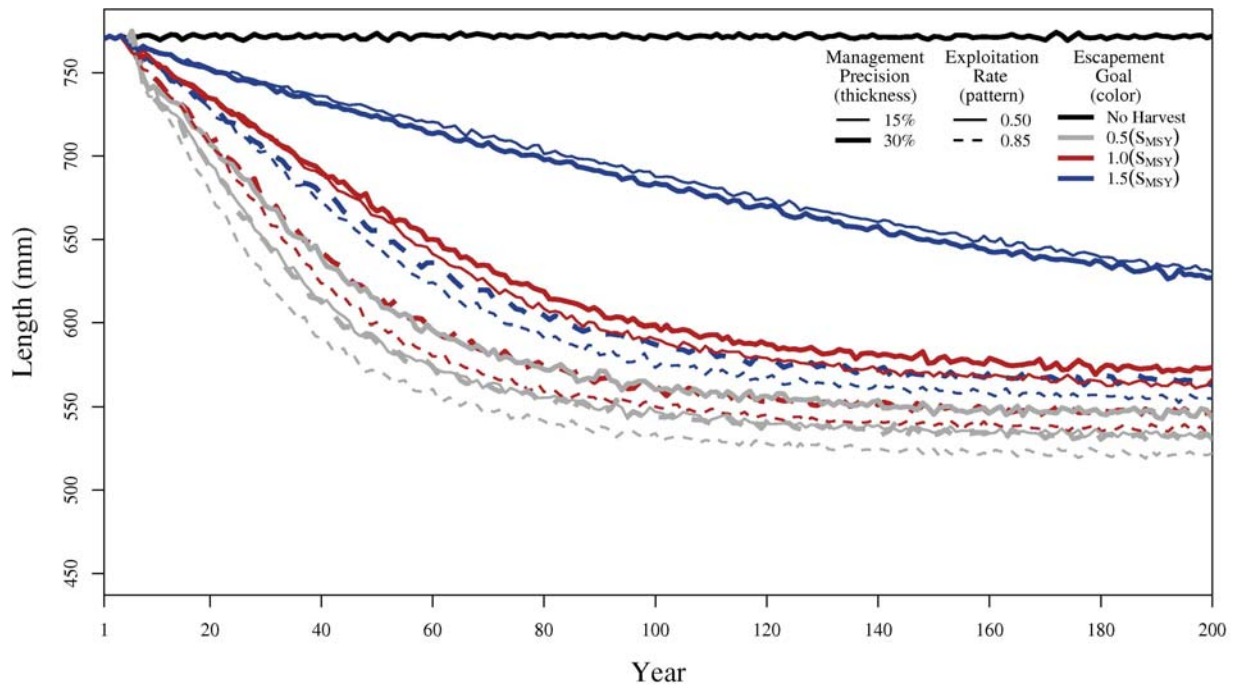
Figure 10. Mean length (mm) of all fish in a run observed during low-productivity simulations (14 – 26). Fishing scenarios consisted of a no-fishing control and 12 combinations of an exploitation rate, management precision, and escapement goal. All catches were taken with the selectivity of an 8.5 in gill net.
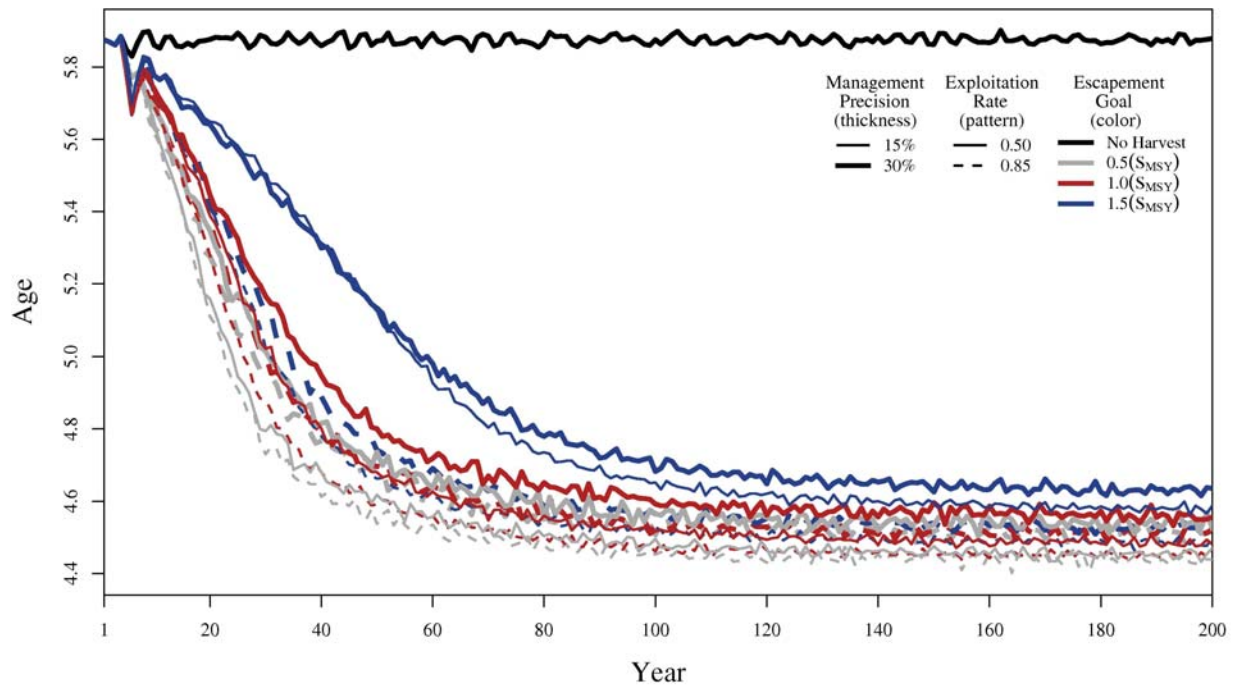
Figure 11. Mean age (yr) of all fish in a run observed during high-productivity simulations (1 – 13). Fishing scenarios consisted of a no-fishing control and 12 combinations of an exploitation rate, management precision, and escapement goal. All catches were taken with the selectivity of an 8.5 in gill net.
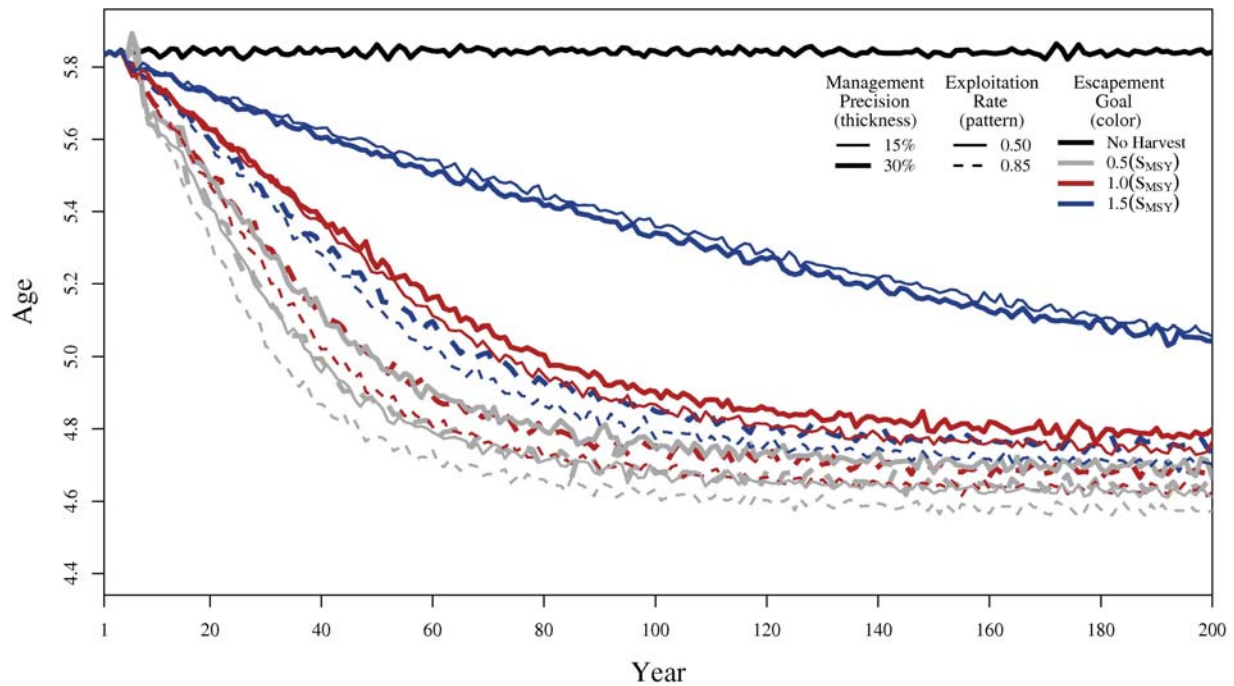
Figure 12. Mean age (yr) of all fish in a run observed during low-productivity simulations (14 – 26). Fishing scenarios consisted of a no-fishing control and 12 combinations of an exploitation rate, management precision, and escapement goal. All catches were taken with the selectivity of an 8.5 in gill net.

Fishery Metrics—Fishing tended to increase the run size, compared to the no-fishing control, in the high-productivity simulations (Figure 13). Initiation of the fishery resulted in escapements (Figure 14) being shifted from the equilibrium point, where the Ricker model crosses the replacement line, to the lower values on the ascending limb of the Ricker curve (Figure 7), thereby resulting in greater run sizes. Results from the low-productivity simulations displayed this pattern more weakly, as the expected production at the reduced escapement levels was approximately equal to that at the equilibrium point because of the reduced productivity.

Not surprisingly, the magnitude of the escapement goal had the greatest effect on both run size (Figure 13) and escapement (Figure 14), in both high- and low-productivity simulations. In all cases, the magnitude of the escapement goal was positively associated with the magnitude of the resulting run sizes. Holding other factors constant, an exploitation rate of 0.50 tended to produce somewhat larger escapements and run sizes than an exploitation rate of 0.85. Similarly, a management precision of 15% led to a slight reduction in the variability of the escapements (Figure 14) and, consequently, slightly greater run sizes (Figure 13).

As catch and exploitation rate are directly related to run size and escapement, the above summarization of the results for run size and escapement are largely mirrored in the results for catch (Figure 15) and exploitation rate (Figure 16). An escapement goal of $0.5(S_{MSY})$ led to reduced run sizes and catches compared to the other levels of escapement. As one would expect, the high-productivity simulations tended to have substantially greater catches than was observed in the low-productivity simulations. Exploitation rates were negatively correlated with the escapement goal level in all cases (Figure 16).

Population Demographics—As previously noted, 200 years of selective fishing for large individuals led to dramatic reductions in the mean length and size of the modeled population. The average length of females (Figure 17) and males (Figure 18) declined by approximately 20% (Figure 17, Simulation 26) to over 40% (Figure 18, Simulation 7) across the range of fishing scenarios considered. The patterns observed across fishing scenarios differed somewhat from the patterns observed in the fishery. As would be expected, mean length in Year 200 was positively associated with the magnitude of the escapement goal. However, increased management precision led to slightly greater reductions in mean length, and less variation in mean length, presumably because the selective fishery was implemented more effectively and selection was therefore more efficient. Perhaps most noticeably, mean length declined more severely in the high-productivity simulations than in the low-productivity simulations. We attribute this result to the lower escapement goals warranted by the higher productivity, resulting in higher selection differentials (see *Planned Simulations* above).

The patterns observed in mean length of an entire run were also observed in the mean length at age of both males and females (Figures 19-28). The patterns are somewhat muted, or even distorted, for the older age classes, primarily because few old fish remained in the population after 200 years and the box-plots are based on very small sample sizes. For example, a box-plot could not be constructed for age-8 males in Simulation 8 because there were no males of that age in any of the replications (Figure 28).
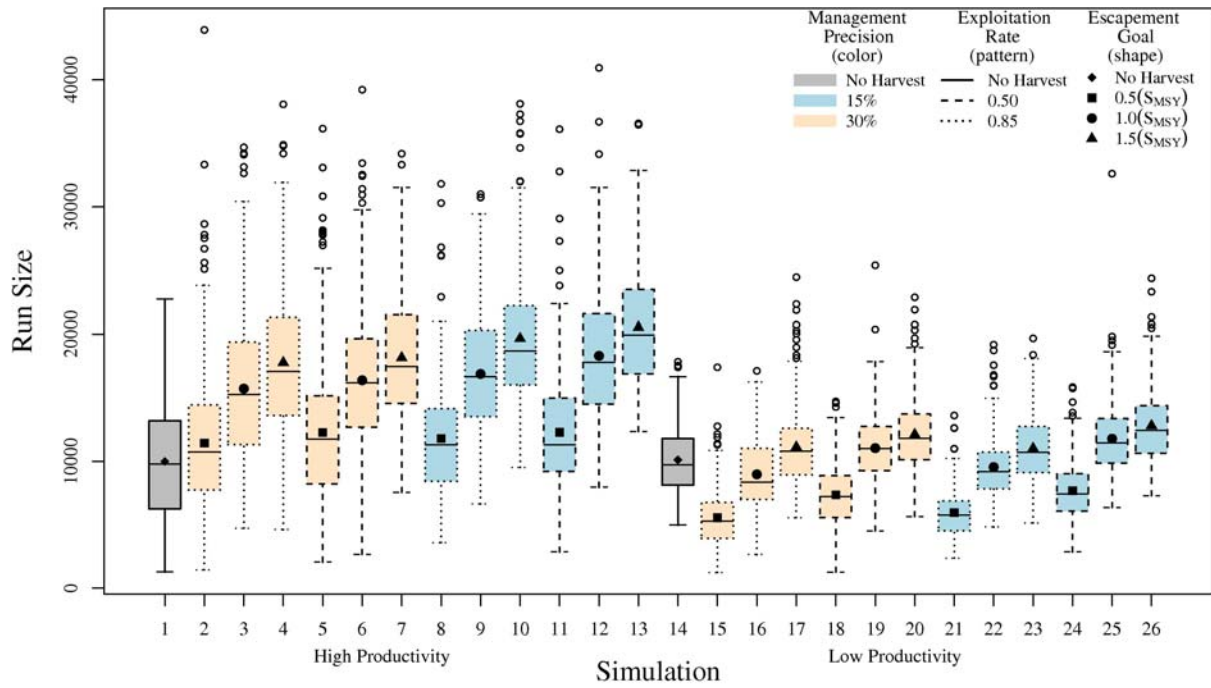
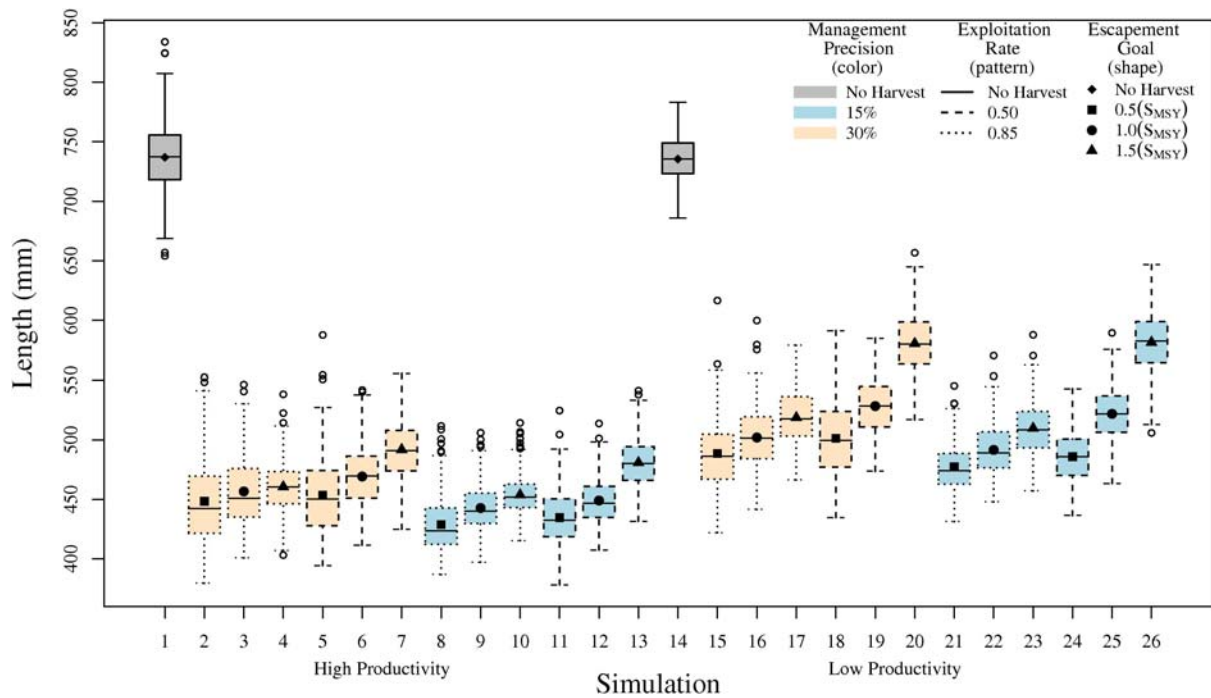**Figure 13. Box-plots of the run size in Year 200, constructed from the 250 replications within each of the 26 planned simulations.**
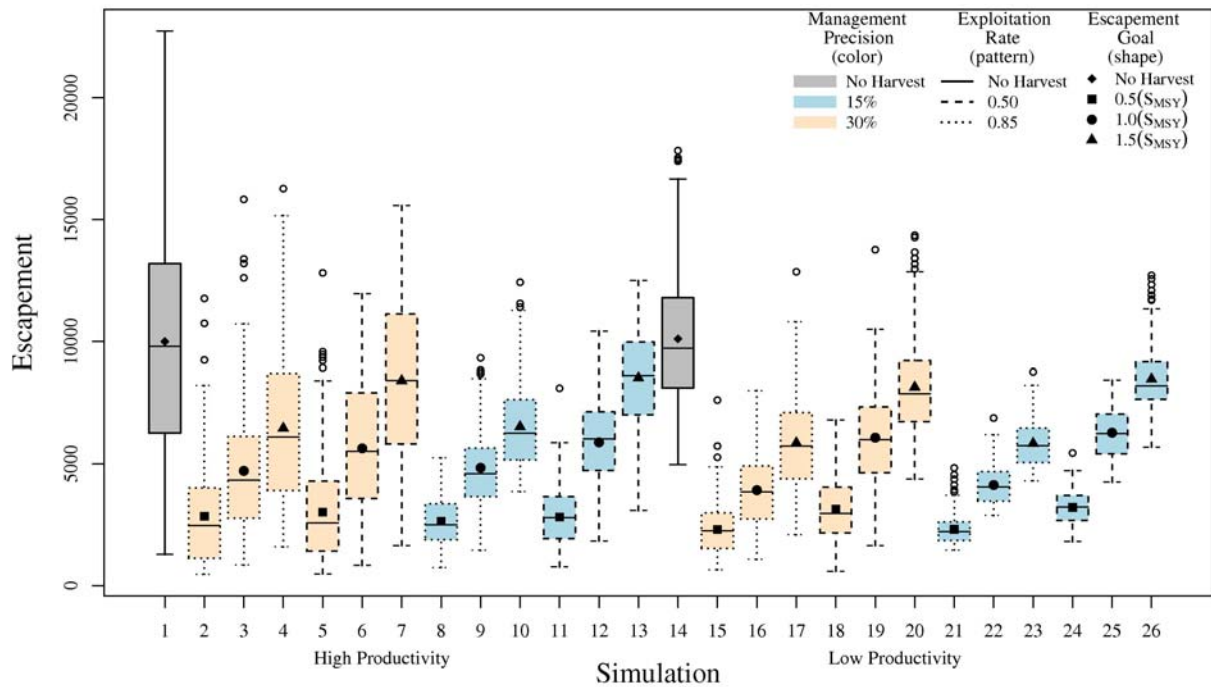
Figure 14. Box-plots of the escapement in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

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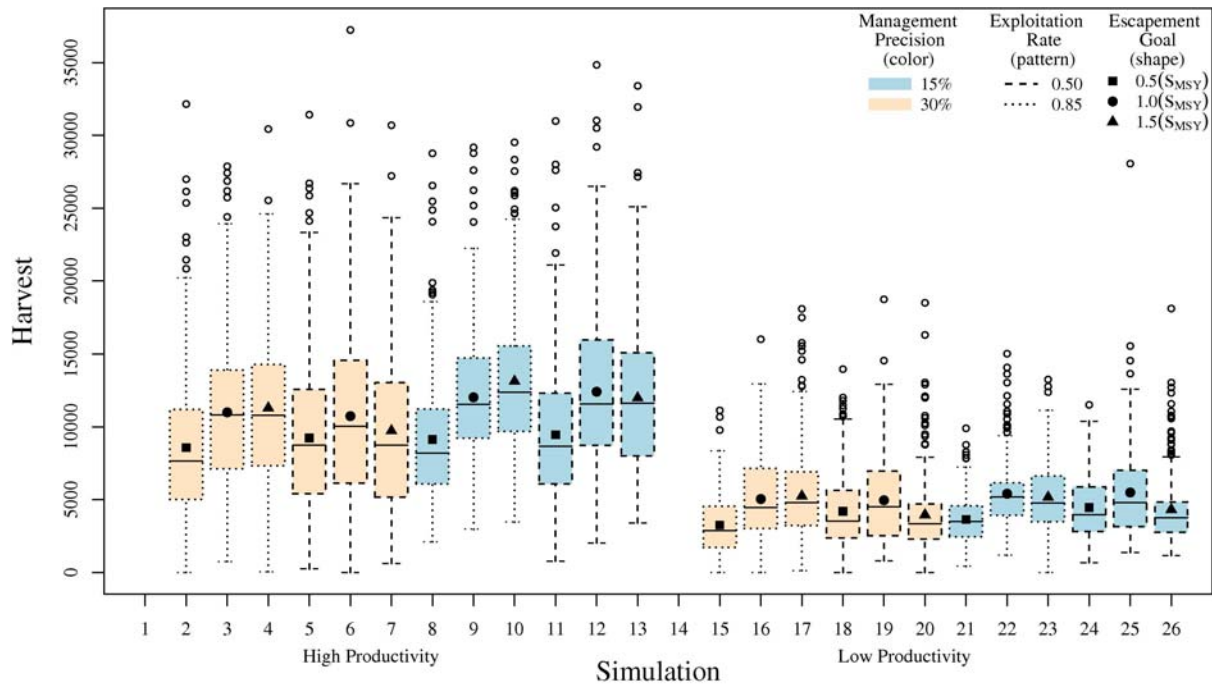
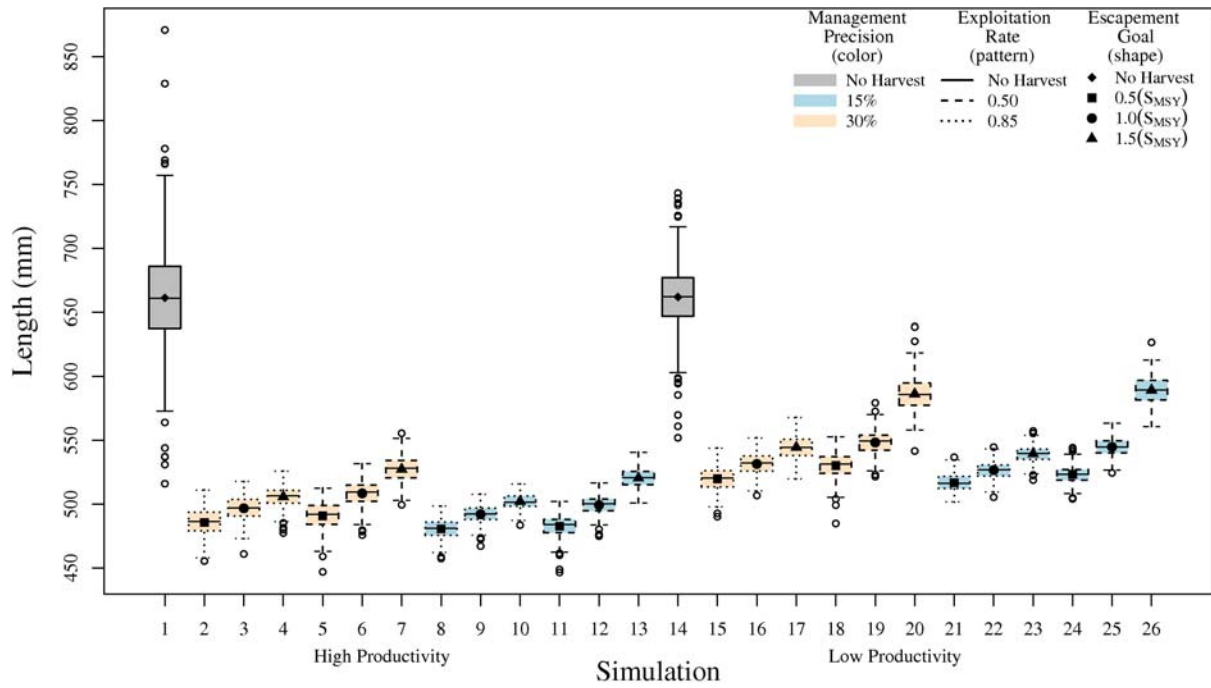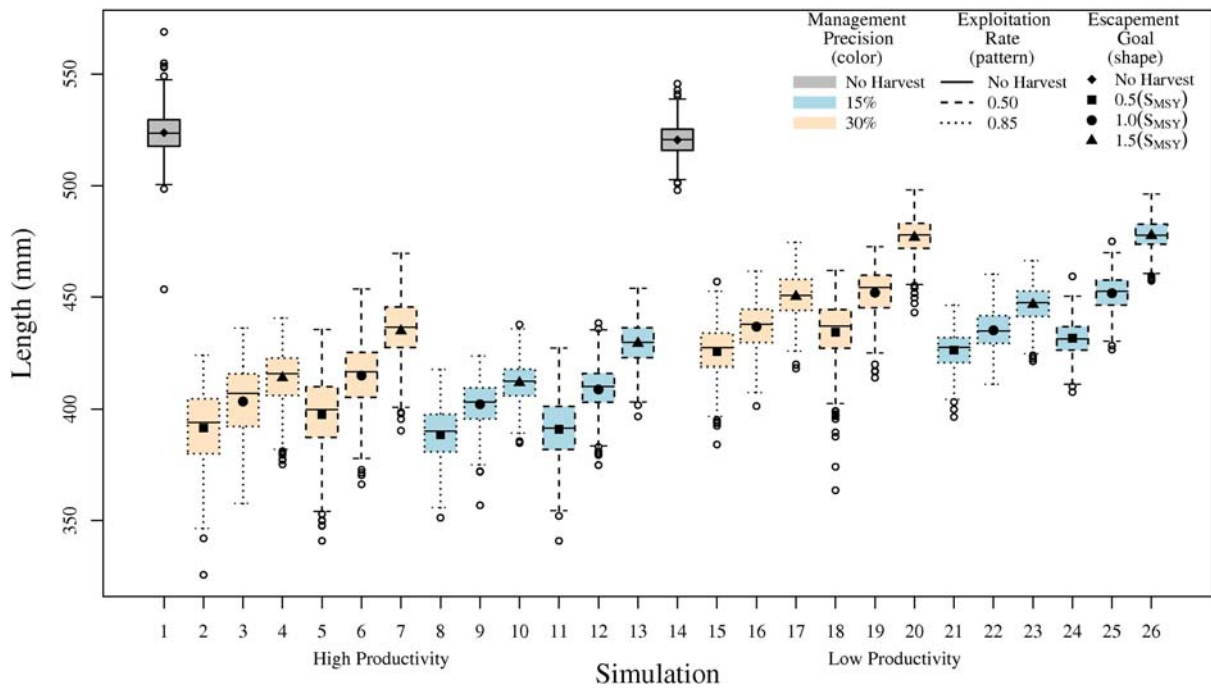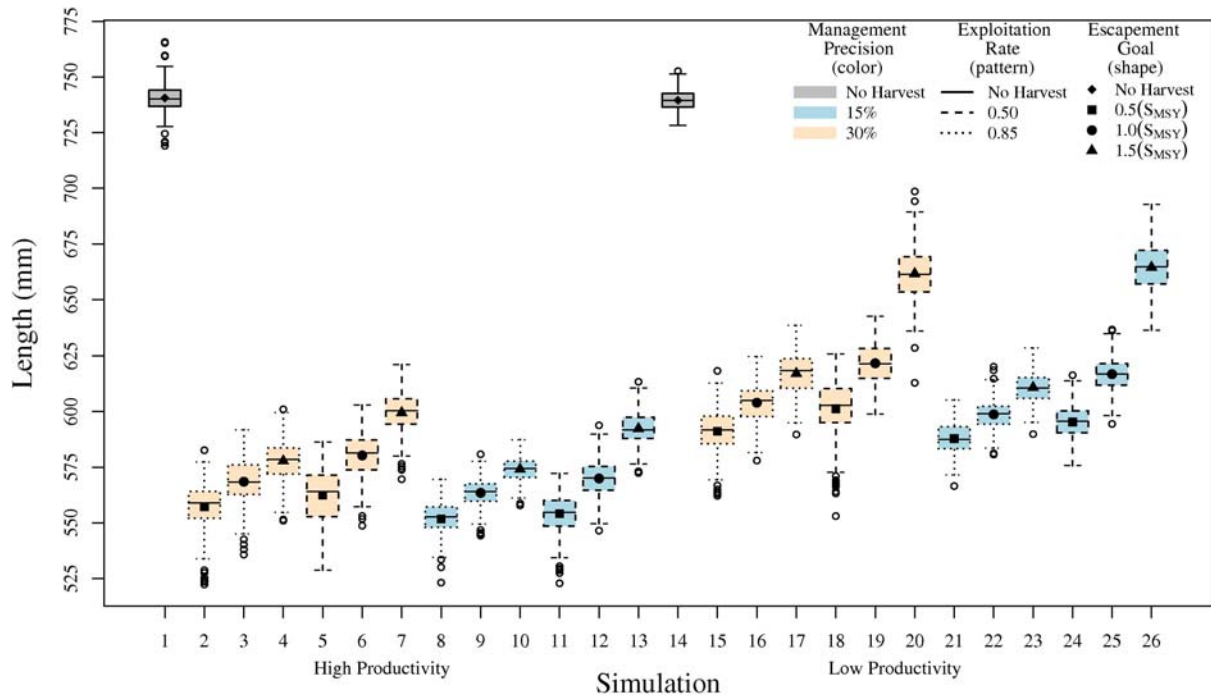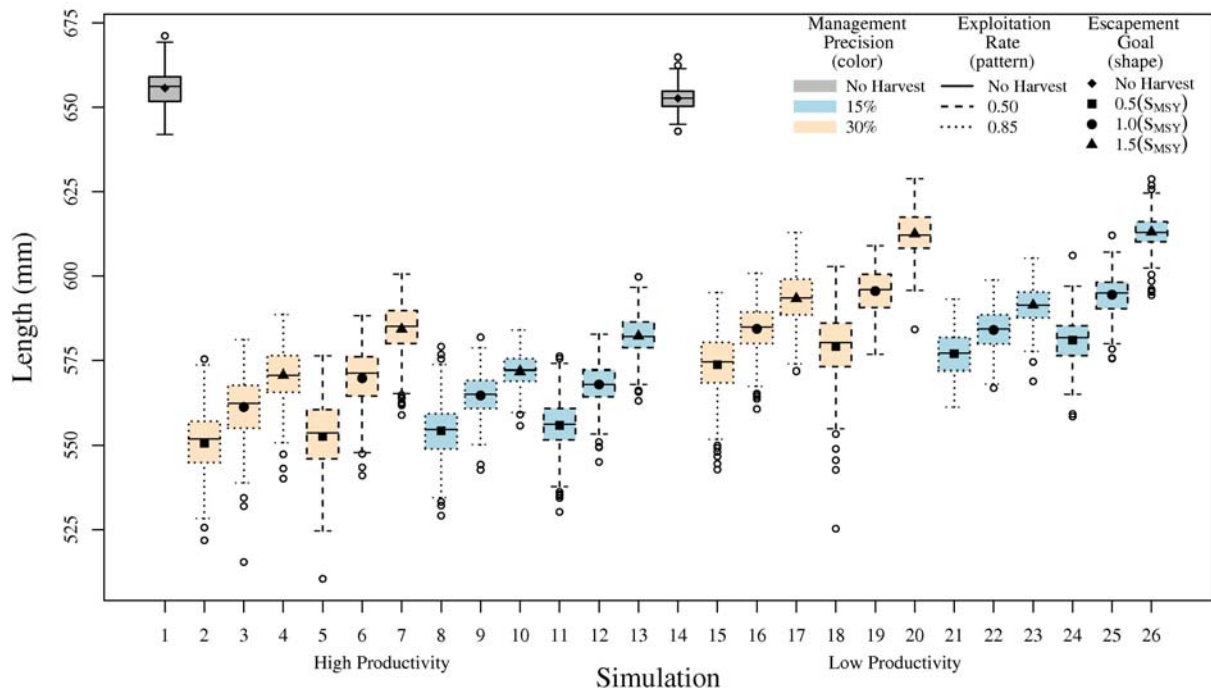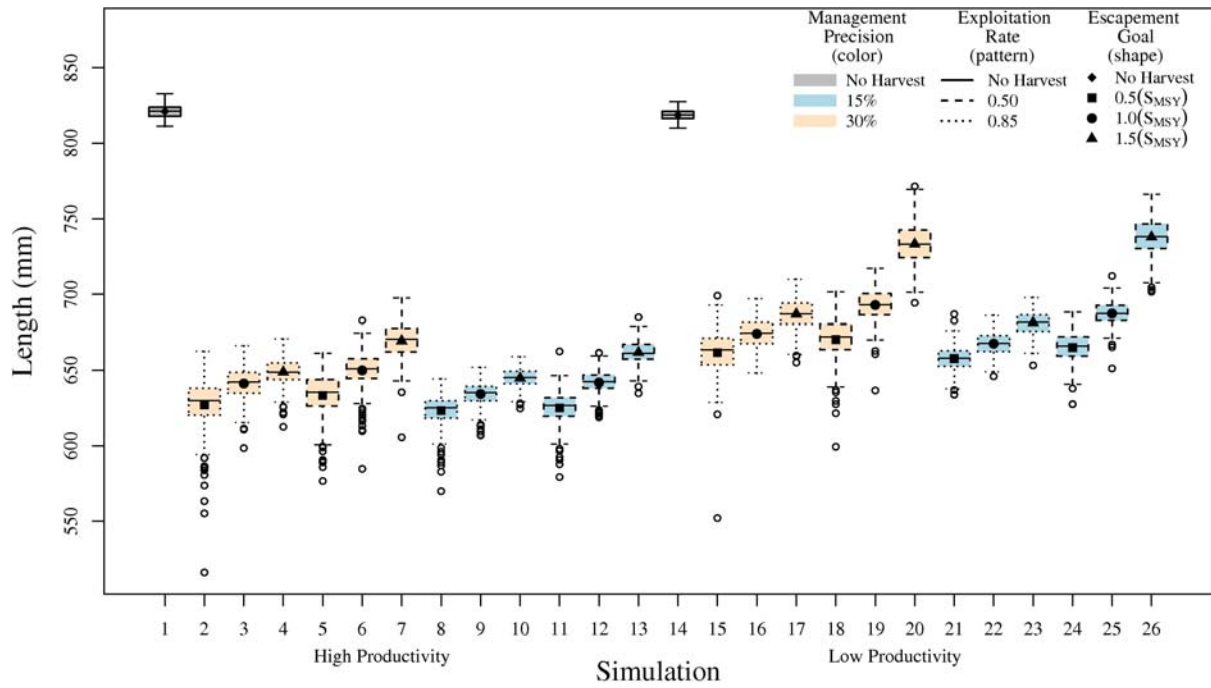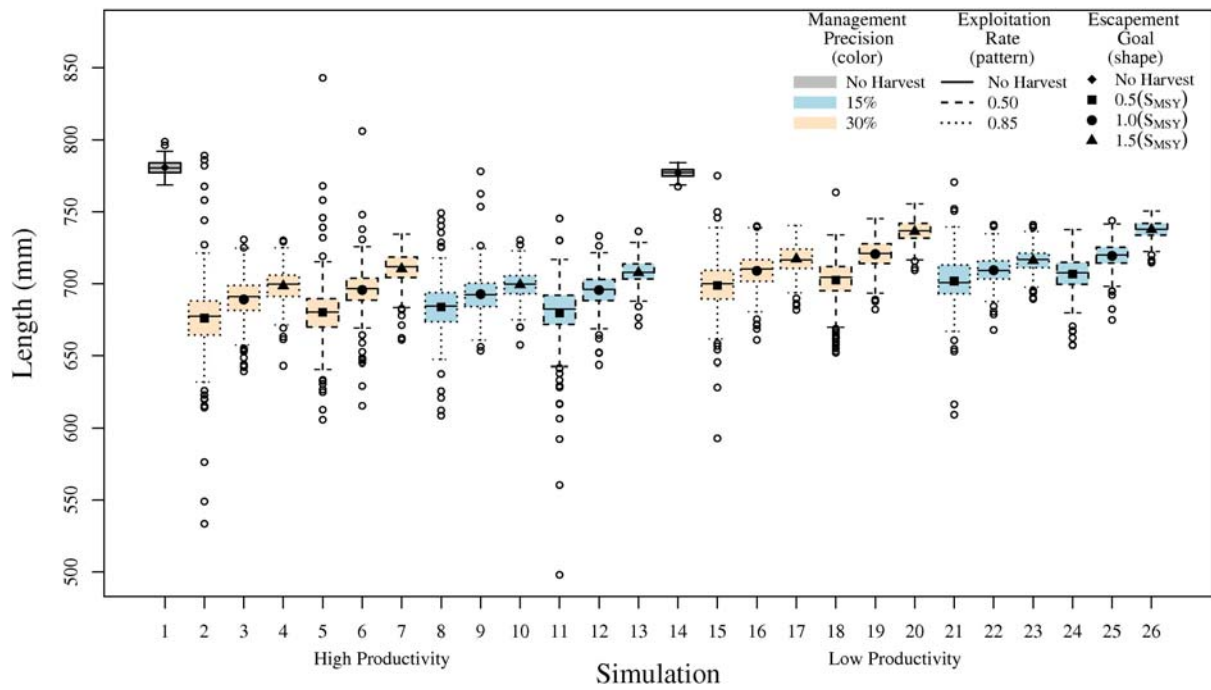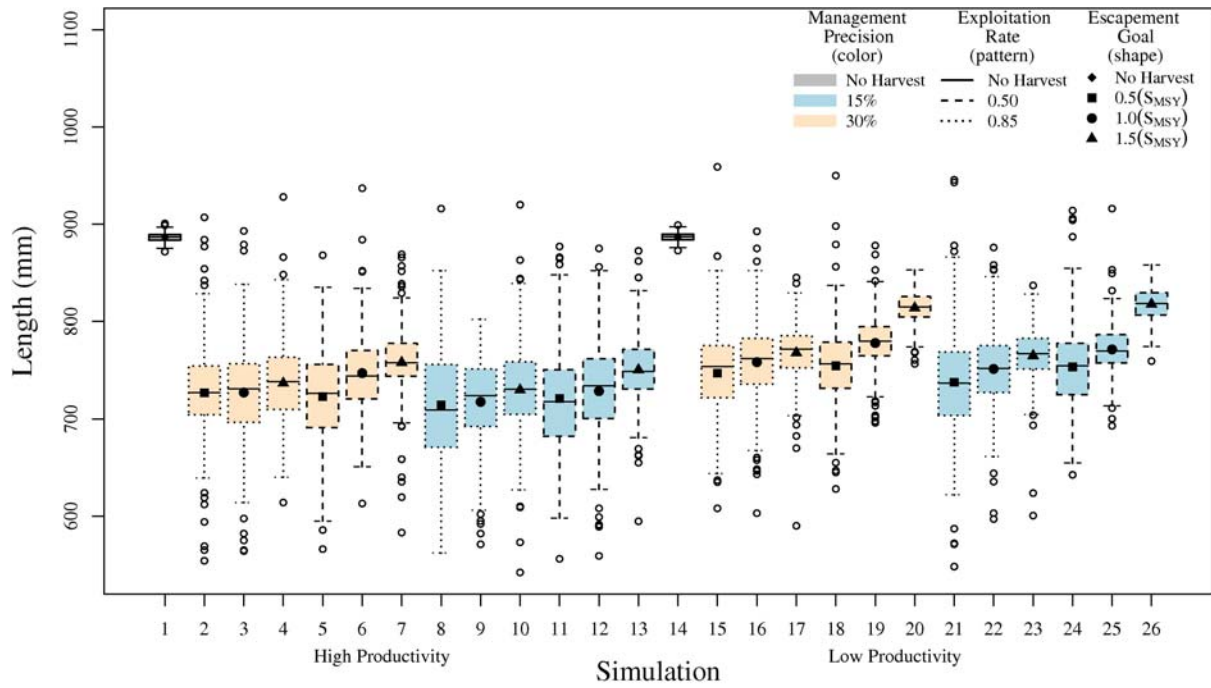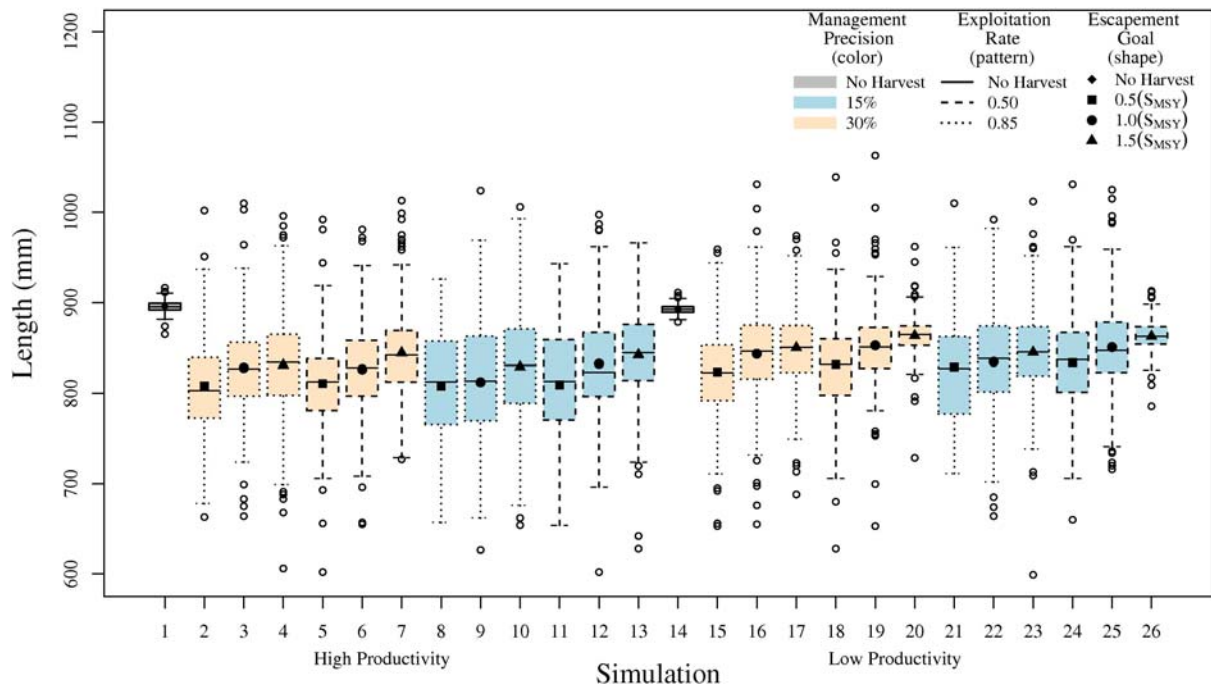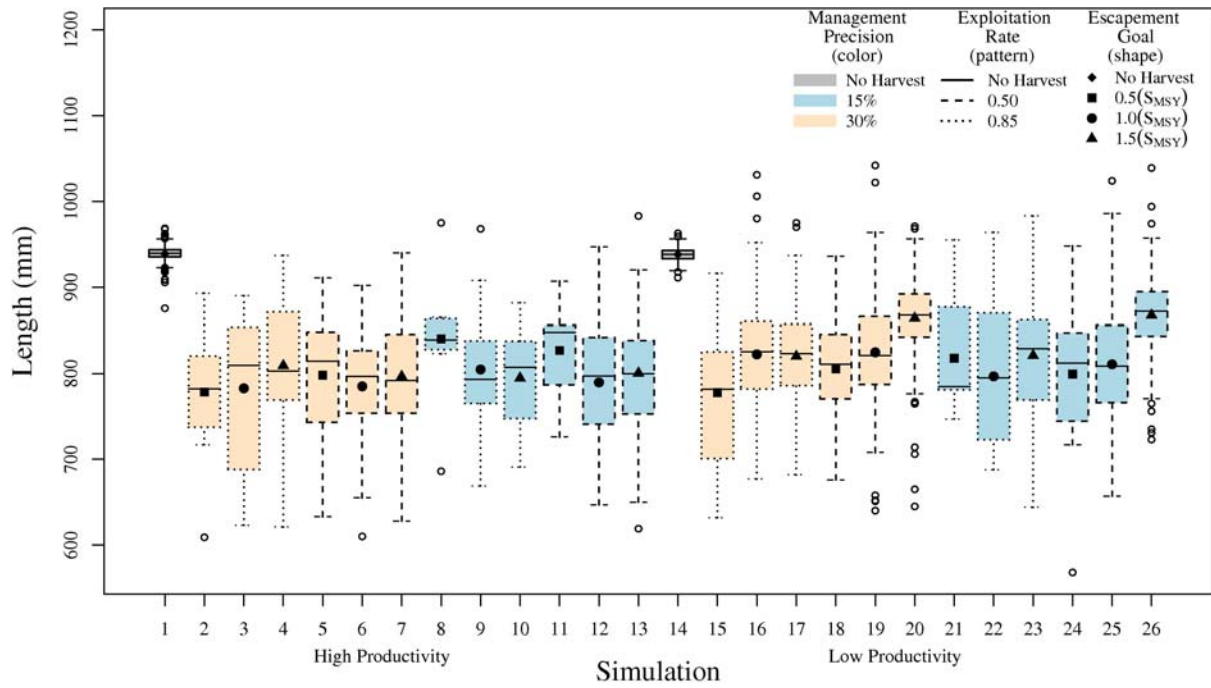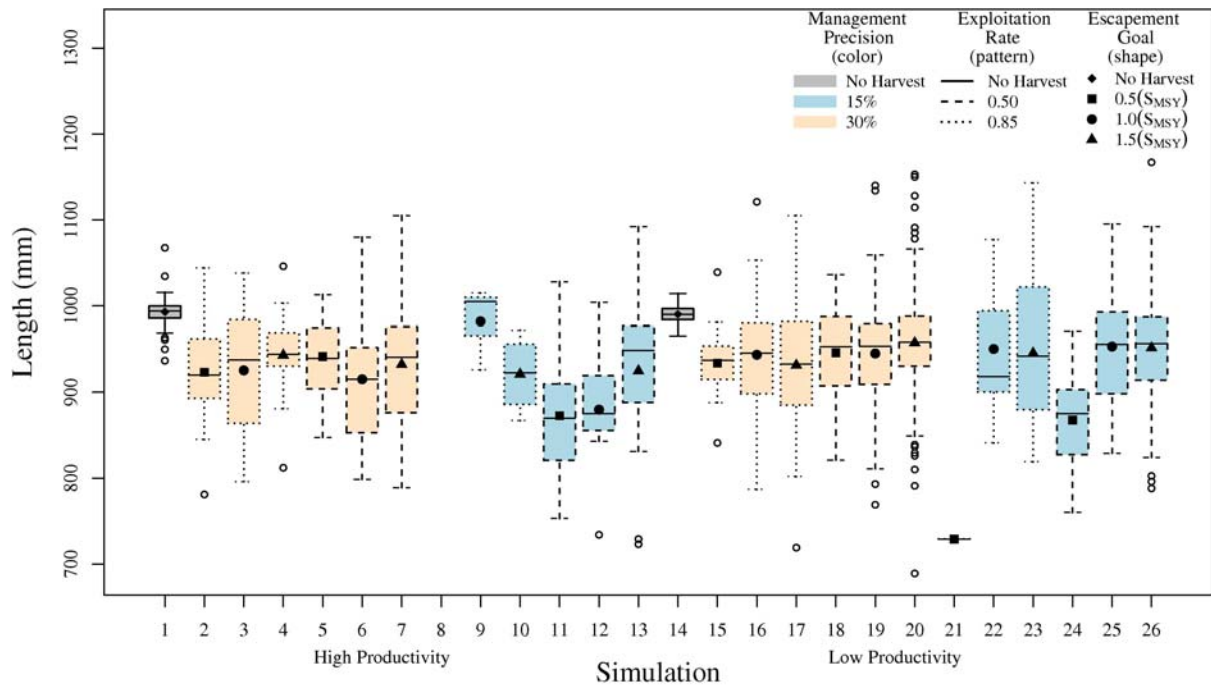**Figure 15. Box-plots of the catch in Year 200, constructed from the 250 replications within each of the 26 planned simulations.**
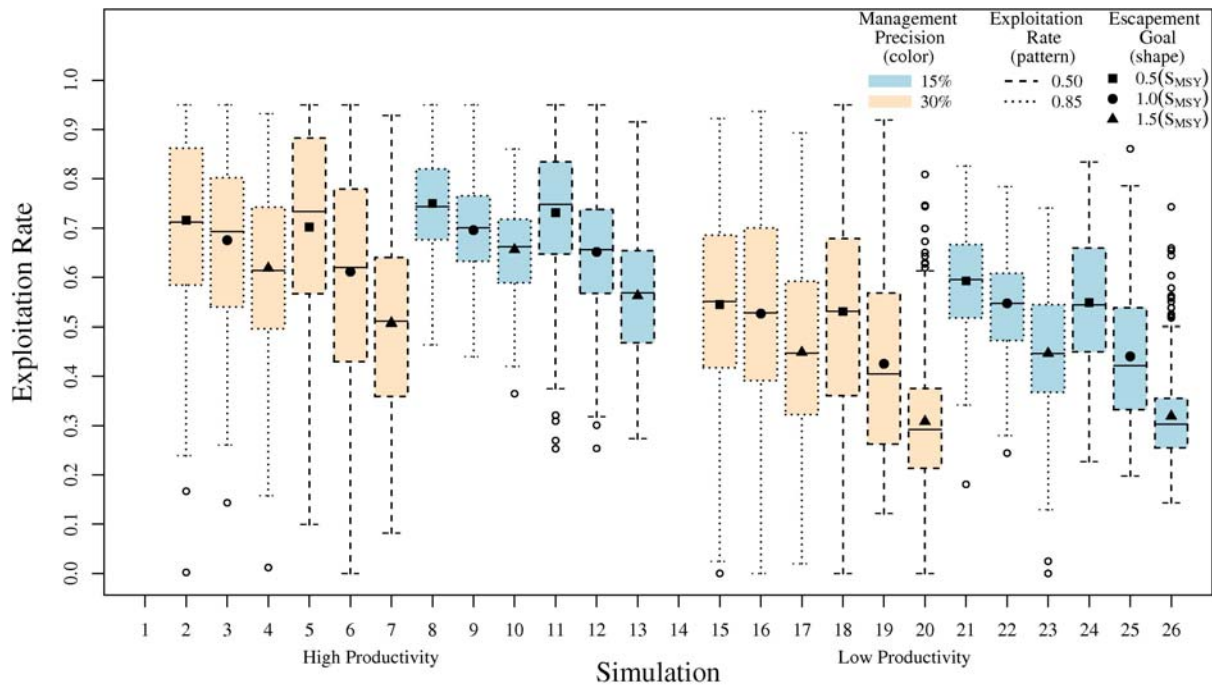
Figure 16. Box-plots of the exploitation rate, constructed from the 250 replications within each of the 26 planned simulations.
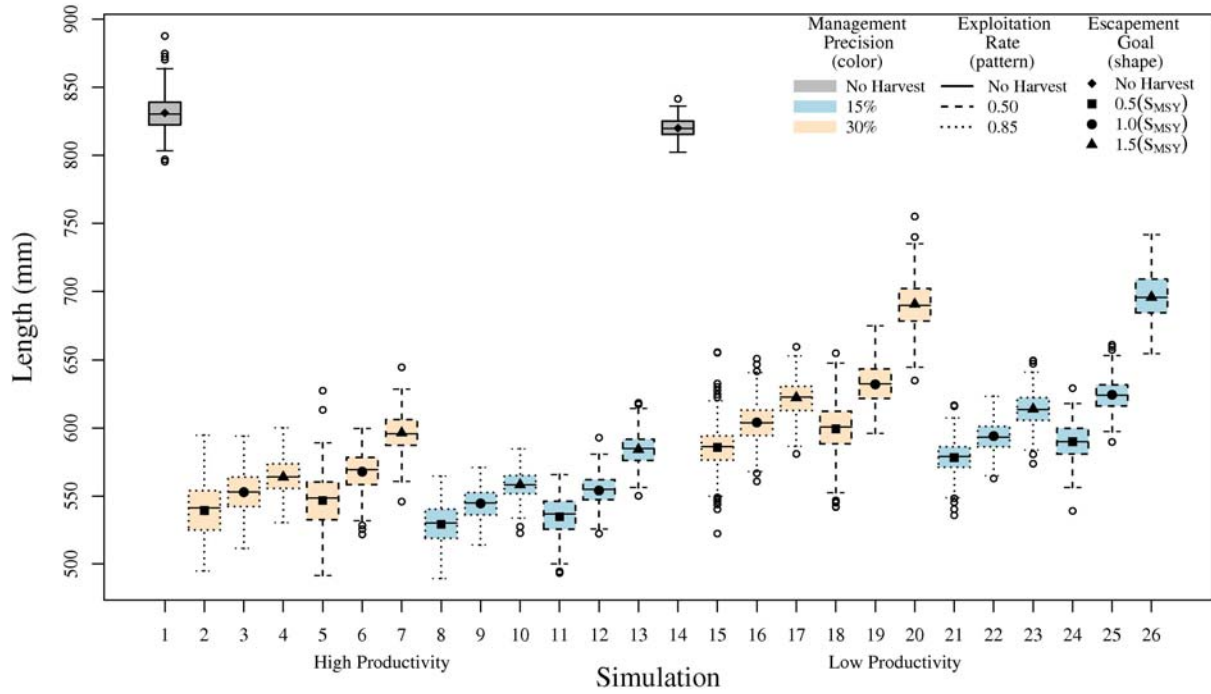
Figure 17. Box-plots of the mean length of females in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 18. Box-plots of the mean length of males in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

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Figure 19. Box-plots of the mean length of age-4 females in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 20. Box-plots of the mean length of age-4 males in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 21. Box-plots of the mean length of age-5 females in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 22. Box-plots of the mean length of age-5 males in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 23. Box-plots of the mean length of age-6 females in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 24. Box-plots of the mean length of age-6 males in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 25. Box-plots of the mean length of age-7 females in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 26. Box-plots of the mean length of age-7 males in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

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Figure 27. Box-plots of the mean length of age-8 females in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

Figure 28. Box-plots of the mean length of age-8 males in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.

As noted previously, mean age responded in a nearly identical fashion (Figures 29 and 30). Changes in the mean age are reflected in the age class composition of each sex. For both males and females, the proportion of the run comprised of age-4 (Figures 31 and 32) and age-5 (Figures 33 and 34) fish increased substantially in comparison with the no-fishing control, while the proportion of the run comprised of age-6 (Figures 35 and 36), age-7 (Figures 37 and 38), and age-8 (Figures 39 and 40) fish declined commensurately. By Year 200, the modeled runs contained almost no fish older than age-6 (Figures 37-40), with the notable exception of a remnant number of age-7 individuals in Simulations 20 and 26 (Figure 39), the simulations with the lowest exploitation rates (Figure 14).

Population Productivity—The reduced size of females (Figure 17) led to commensurate reductions in mean fecundity (Figure 41) and the total number of eggs deposited (Figure 42). The reduction in egg deposition was largely counterbalanced by a density-dependent increase in freshwater survival (Equation 5) to maintain run sizes, although reduced run sizes were observed in some of the low-productivity simulations with the smallest escapement goals (Figure 13, Simulations 15 and 21).

Data from the last 100 years of each simulation, during which the population had stabilized under most fishing scenarios, were used to investigate the utility of post-fishery data for estimating of the potential productivity of the un-fished population. For each replication within a simulation, the total returns from the last 100 escapements were computed and the productivity parameter α of a Ricker model (Ricker 1975; Equation 3) was estimated using linear regression and the lognormal error adjustment of Hilborn (1985). The estimates obtained for each simulation were plotted using box-plots to summarize the distribution of the estimates obtained (Figure 43). Estimates of the productivity parameter under all fishing scenarios tended to be substantially less than estimates obtained from an un-fished population, reflecting a reduction in apparent productivity, i.e., a larger number of small females were needed to produce a fixed number of eggs because of the decline in average fecundity.

Fishery Selection—The effects of fishery selection over time were explored via mean selection differentials (Law 1991; Swain et al. 2007). A selection differential is computed by subtracting the value of a measure, such as mean length, that characterizes the component of the population that escapes fishing selection (but before reproduction) from the corresponding measure for the entire run before selection. Negative values of the selection differential therefore reflect the case where the measure is greater in the catch than in the run. Selection differentials were computed for each year in each replication, and mean selection differentials were then computed by averaging over all replications within a simulation.

Mean selection differentials for length observed in the high- and low-productivity simulations are presented in Figures 44 and 45 for females and in Figures 46 and 47 for males. The pattern through time is consistent across all simulations for both sexes. In the initial years of the fishery, the length of fish in the run declines in response to selective removal of large fish. The mean length of fish in the catch also declines, but less sharply as the fishery continues to be selective for the large fish remaining in the runs. The result is an initial decline in the mean selection differential. As large fish becoming increasingly rare in the population, the mean selection differential tends to increase and stabilize as the modeled population reaches a new size equilibrium. The strength of this pattern is more pronounced in the high-productivity simulations, as well as for males in comparison to females. A nearly identical pattern was observed in the mean selection differentials for age (Figures 48-51). The one exception is
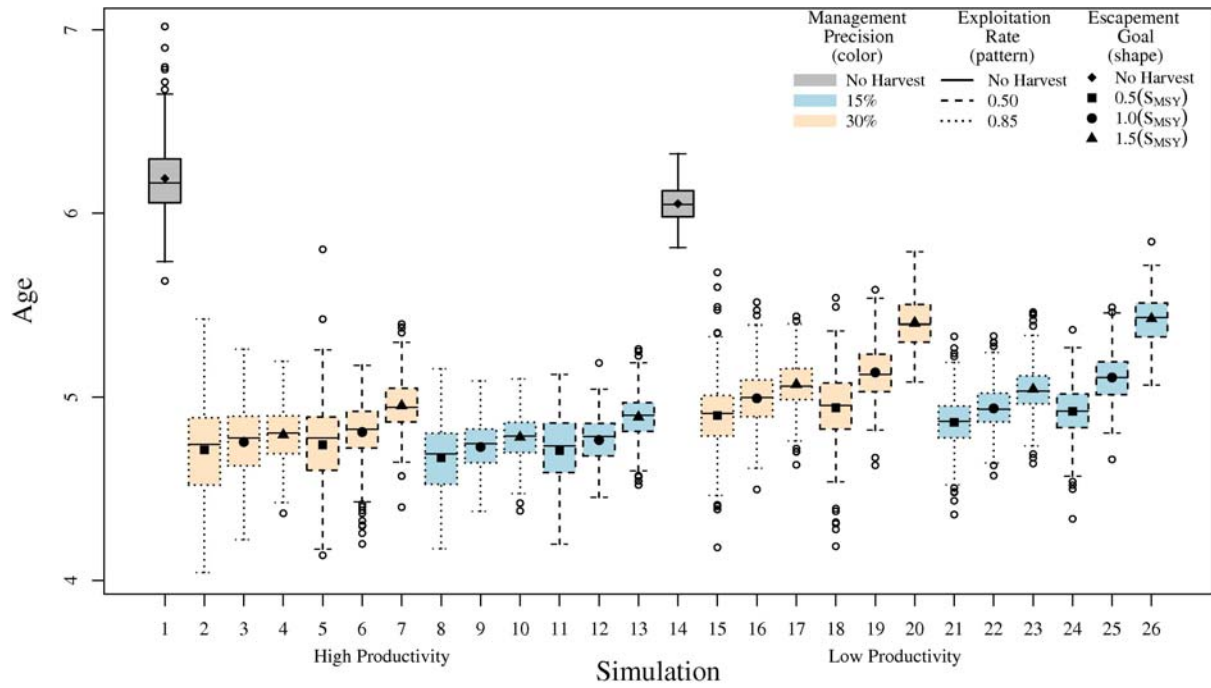
Figure 29. Box-plots of the mean age of females in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.
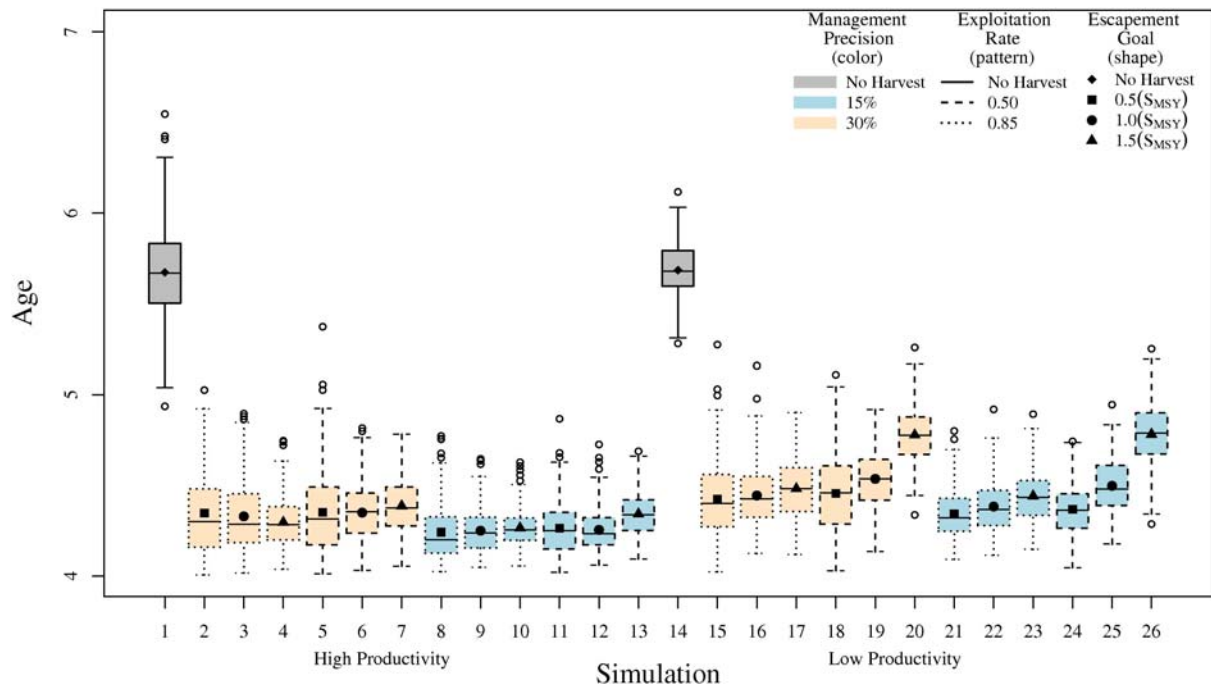

Figure 30. Box-plots of the mean age of males in the run in Year 200, constructed from the 250 replications within each of the 26 planned simulations.
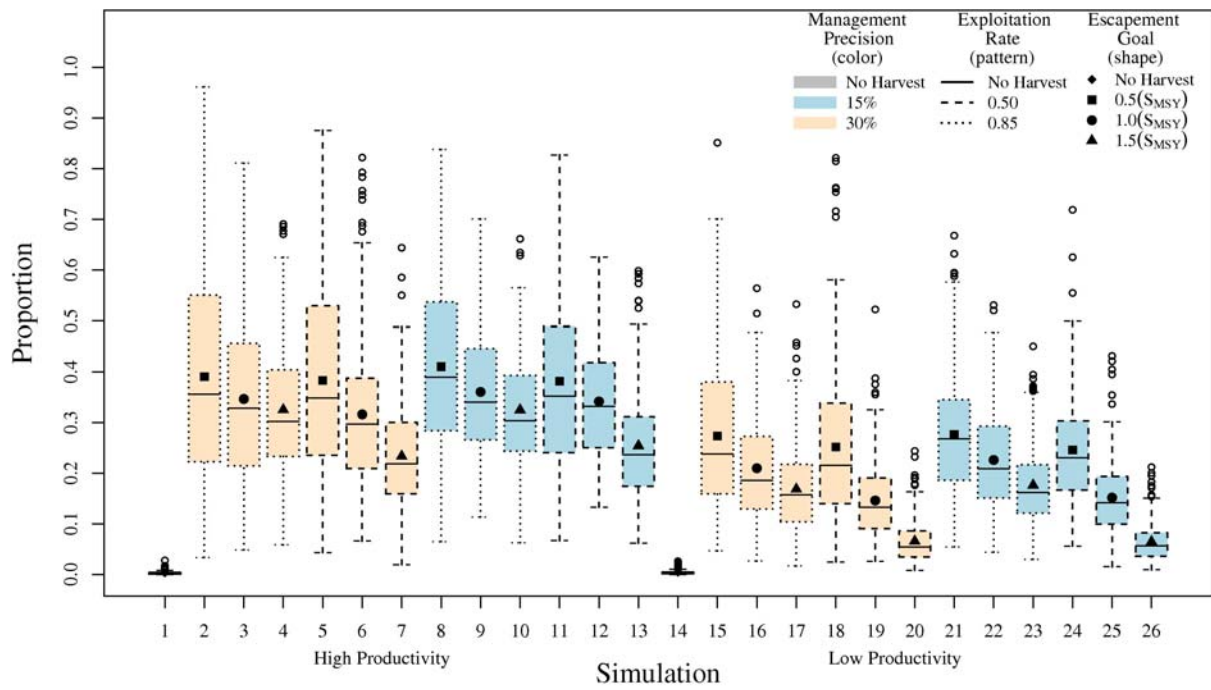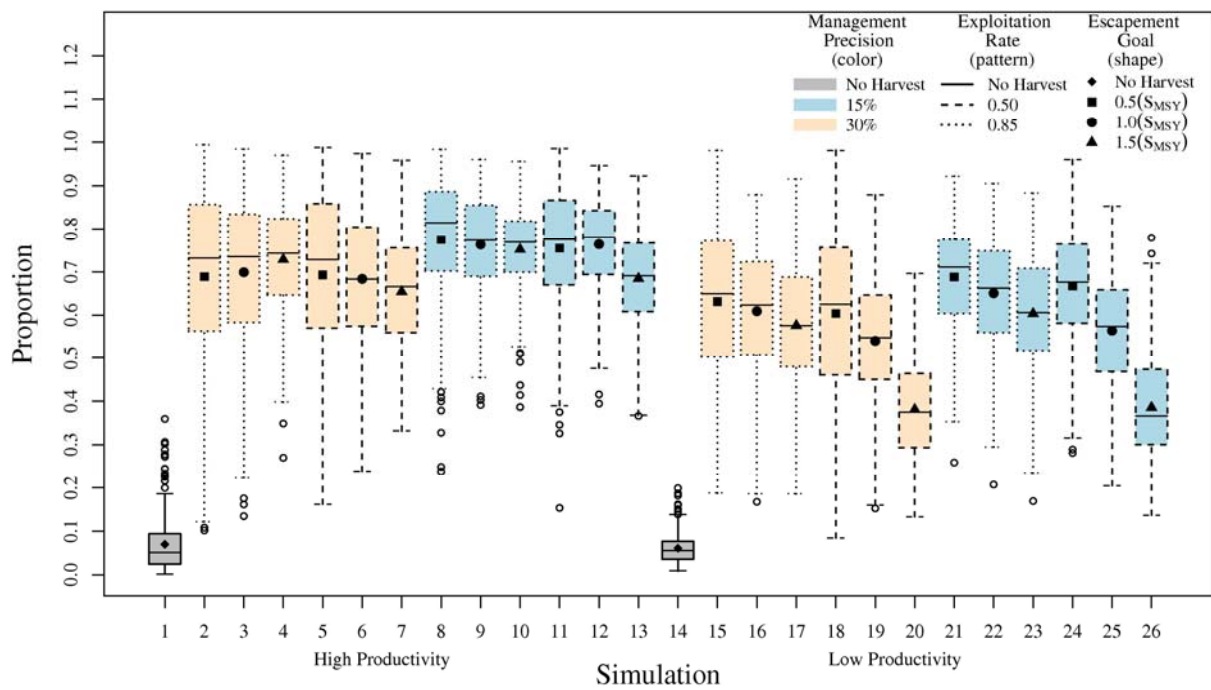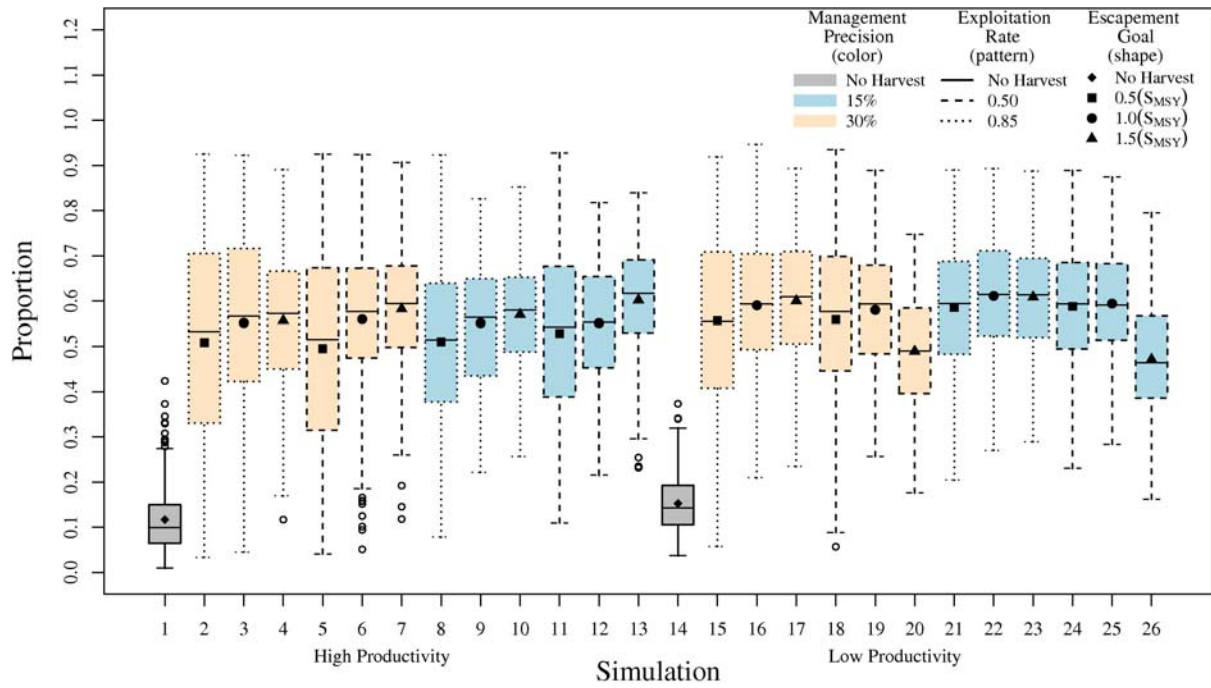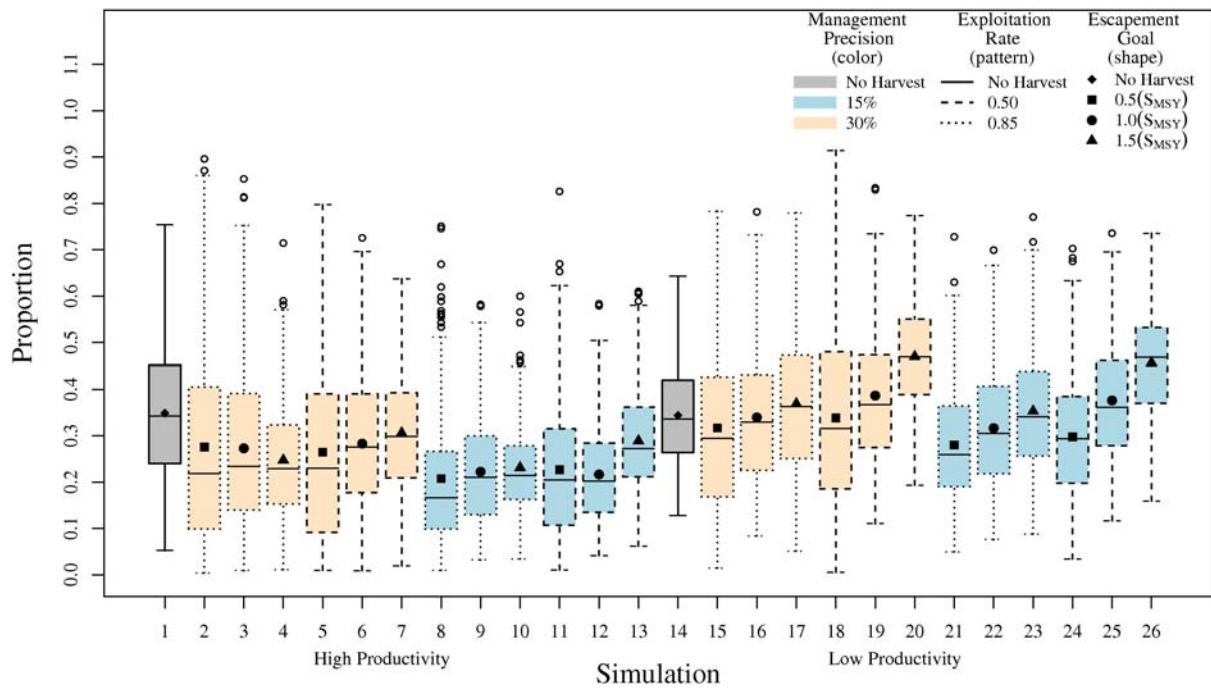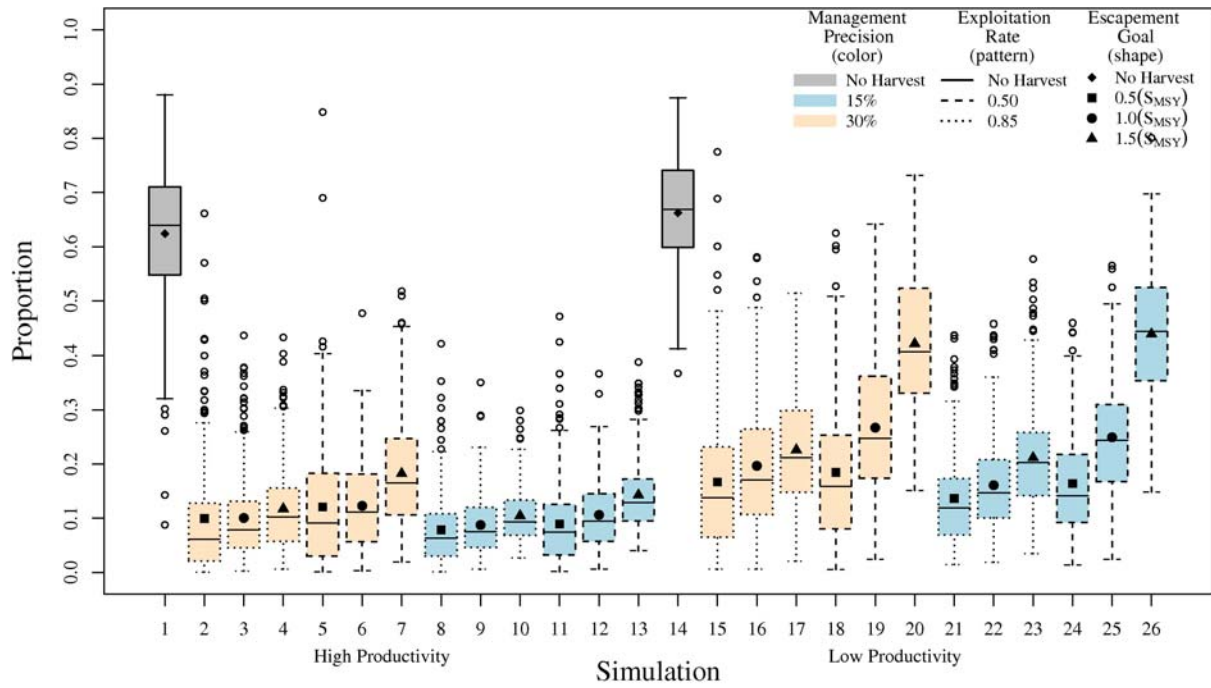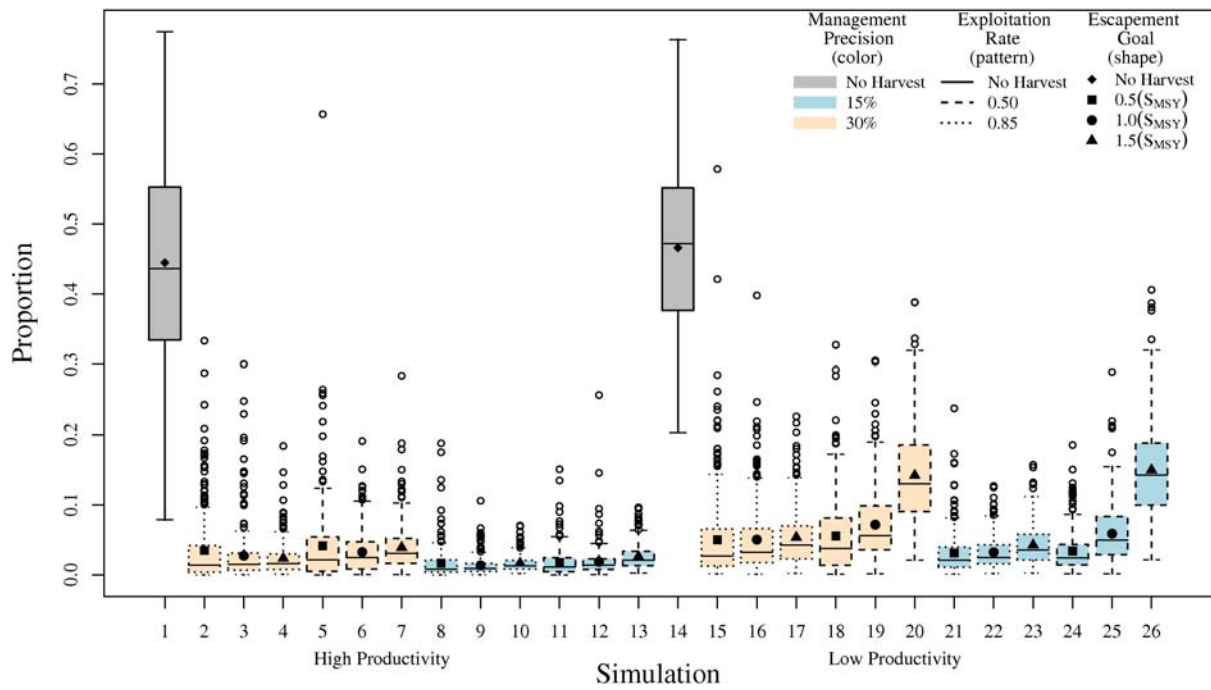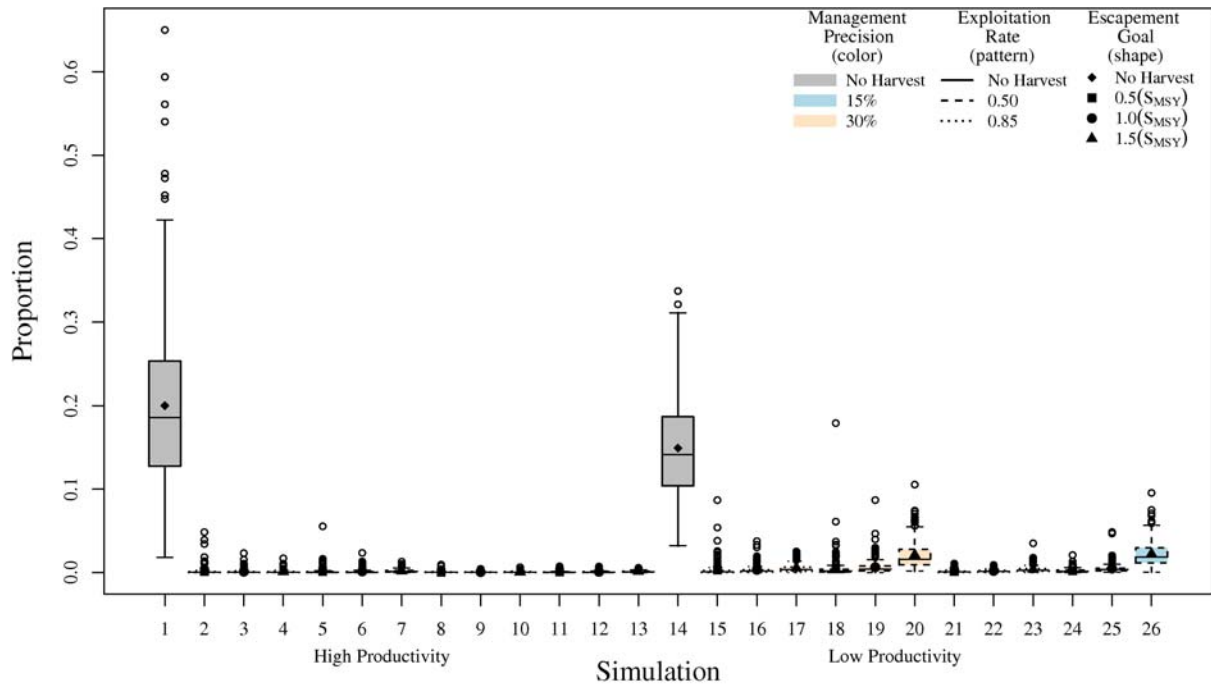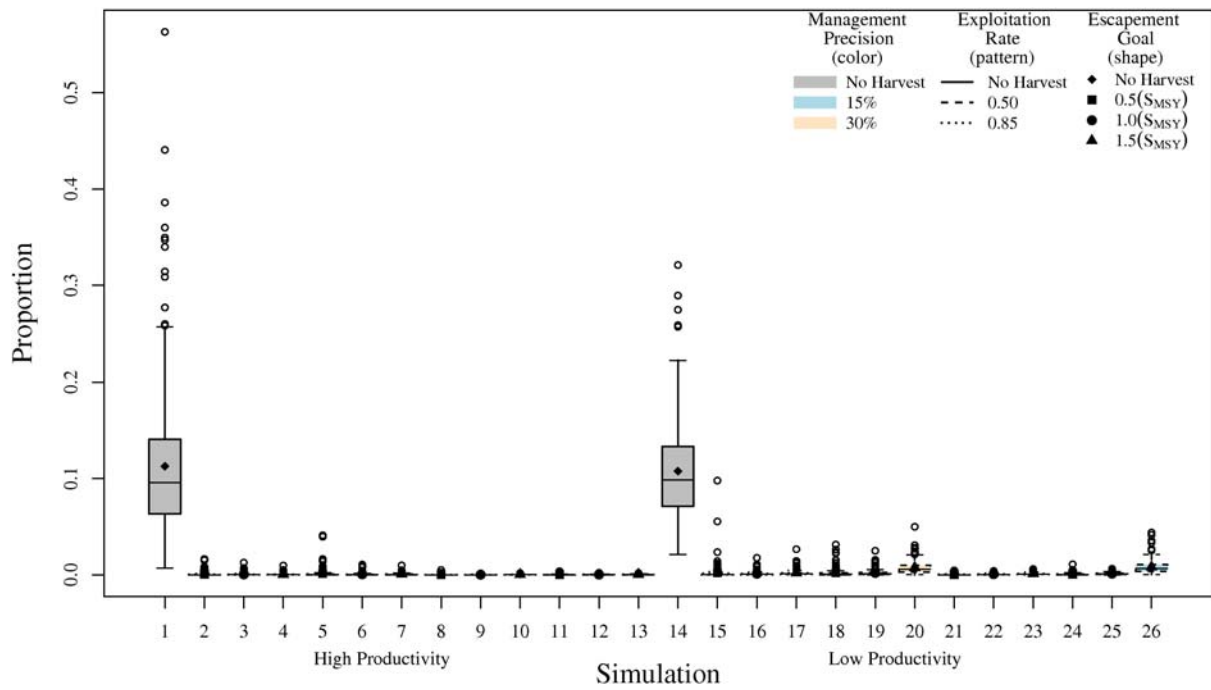
Figure 31. Box-plots of the proportion of females in the run in Year 200 that are age-4, constructed from the 250 replications within each of the 26 planned simulations.

Figure 32. Box-plots of the proportion of males in the run in Year 200 that are age-4, constructed from the 250 replications within each of the 26 planned simulations.
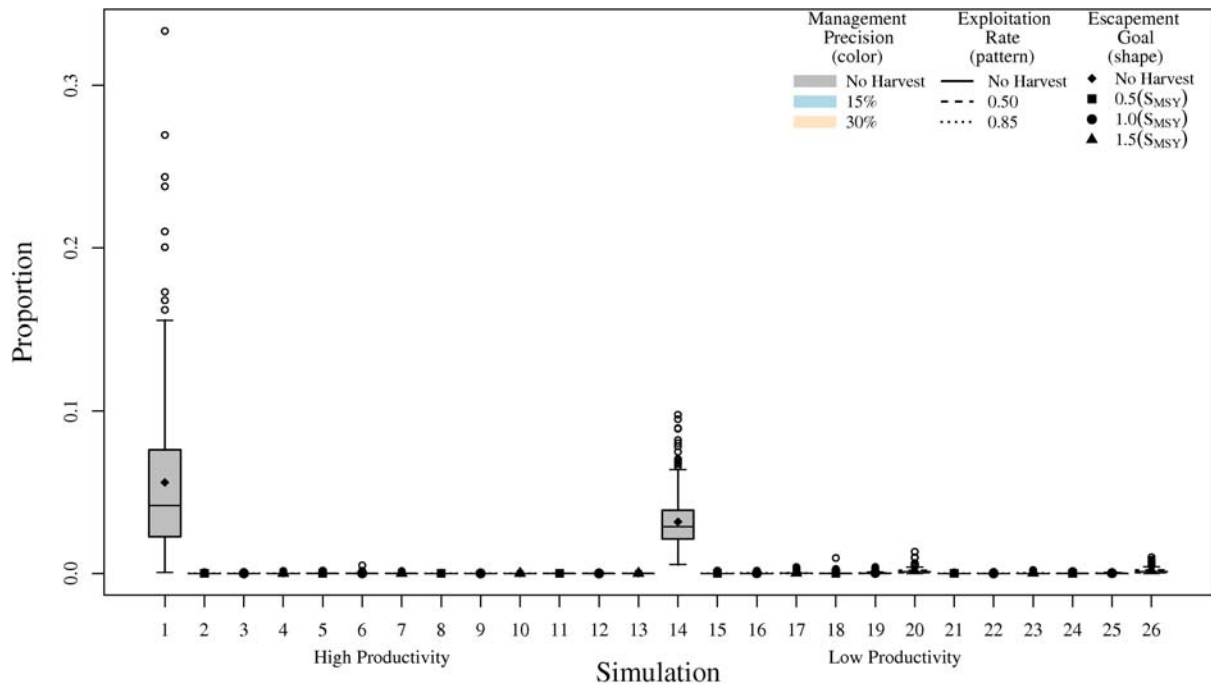
Figure 33. Box-plots of the proportion of females in the run in Year 200 that are age-5, constructed from the 250 replications within each of the 26 planned simulations.
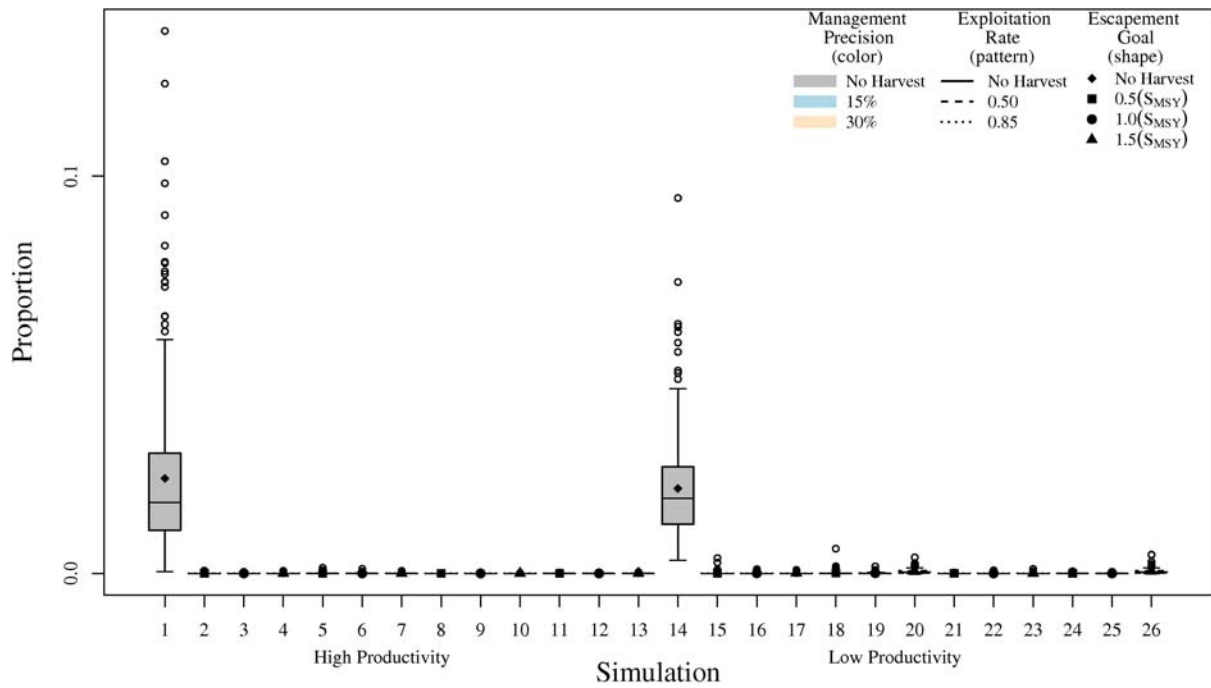

Figure 34. Box-plots of the proportion of males in the run in Year 200 that are age-5, constructed from the 250 replications within each of the 26 planned simulations.
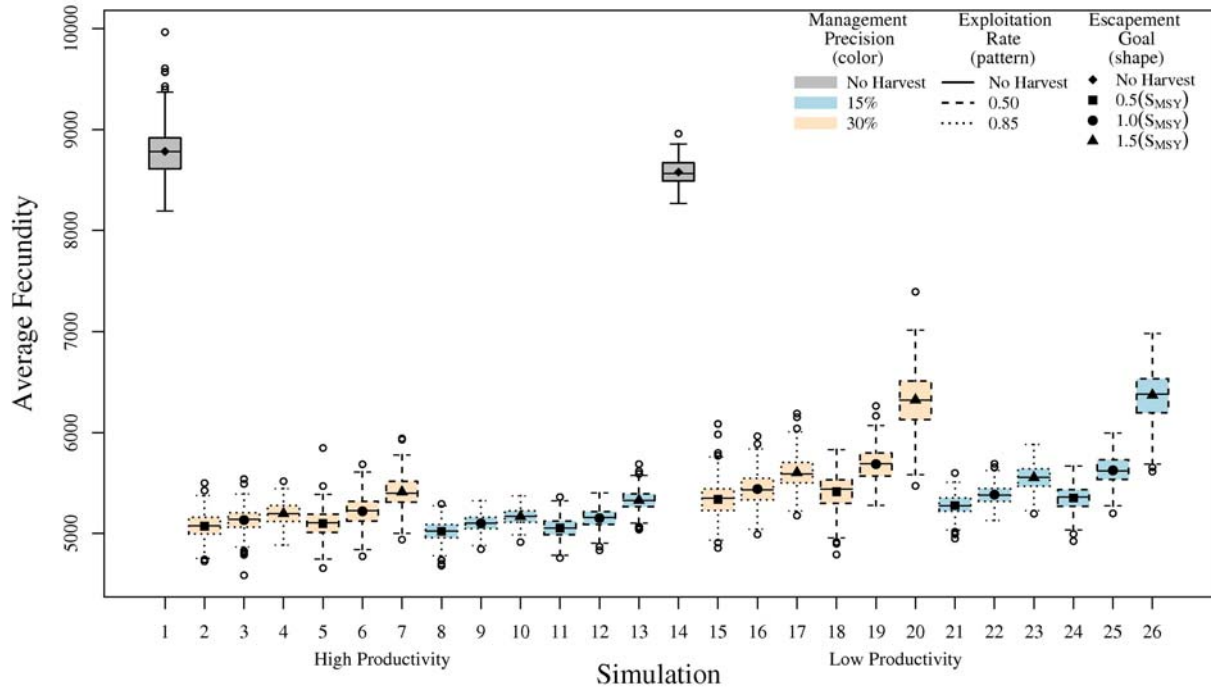
Figure 35. Box-plots of the proportion of females in the run in Year 200 that are age-6, constructed from the 250 replications within each of the 26 planned simulations.

Figure 36. Box-plots of the proportion of males in the run in Year 200 that are age-6, constructed from the 250 replications within each of the 26 planned simulations.

Figure 37. Box-plots of the proportion of females in the run in Year 200 that are age-7, constructed from the 250 replications within each of the 26 planned simulations.

Figure 38. Box-plots of the proportion of males in the run in Year 200 that are age-7, constructed from the 250 replications within each of the 26 planned simulations.

Figure 39. Box-plots of the proportion of females in the run in Year 200 that are age-8, constructed from the 250 replications within each of the 26 planned simulations.

Figure 40. Box-plots of the proportion of males in the run in Year 200 that are age-8, constructed from the 250 replications within each of the 26 planned simulations.

Figure 41. Box-plots of the mean number of eggs per female (fecundity) in Year 200, constructed from the 250 replications within each of the 26 planned simulations.
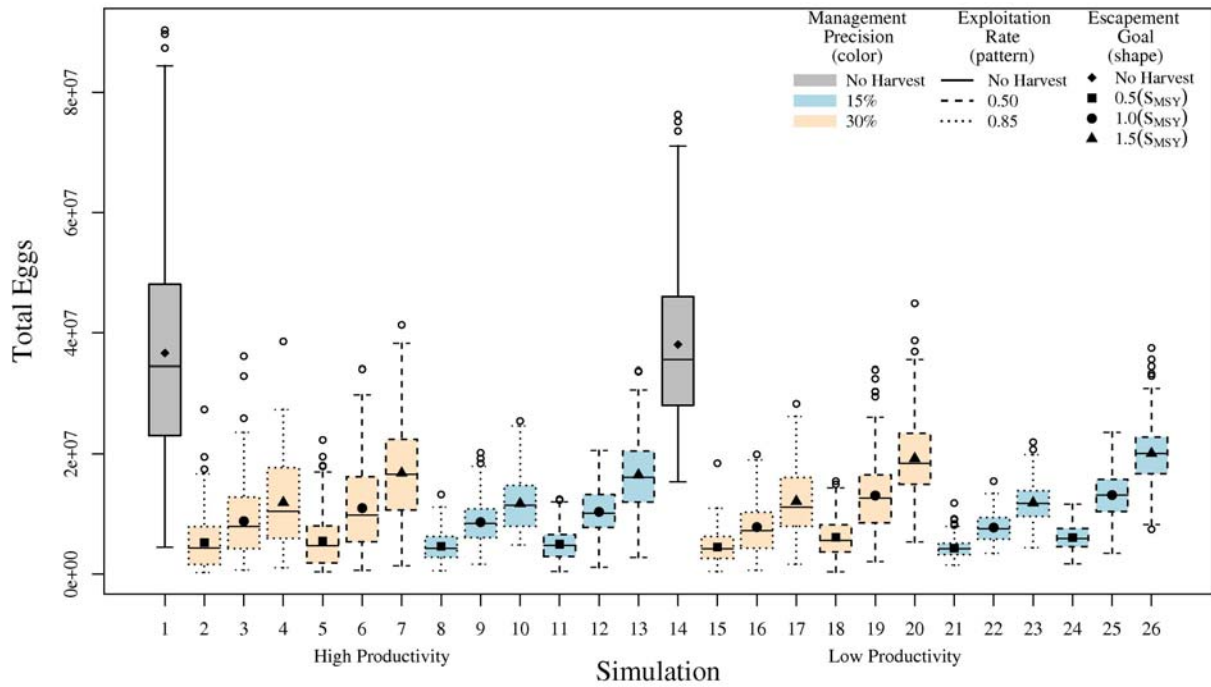
Figure 42. Box-plots of the total number of eggs deposited by all females in the escapement in Year 200, constructed from the 250 replications within each of the 26 planned simulations.
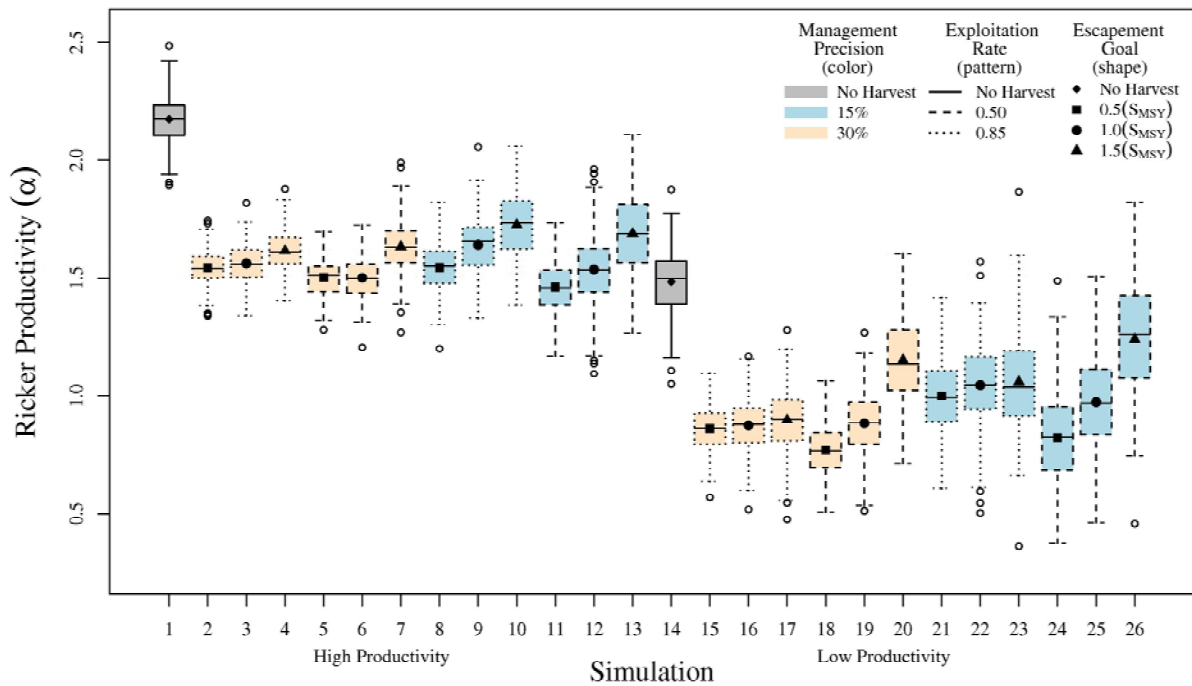
Figure 43. Box-plots of realized estimates of the productivity parameter, α, of a Ricker production model obtained using the last 100 years of escapement-return data from each replication, constructed from the 250 replications within each simulation.

Simulation 26 (Table 5), in which the modeled population had not stabilized by Year 200. In this case, mean selection differentials for females declined throughout the 200 years of the simulation (Figures 45 and 49). The mean selection differentials for males stabilized and began to increase much later in Simulation 26 than in the other simulations (Figures 47 and 51).

Alternative Fishing Simulations

A subset of the planned simulations was selected to investigate the response of the modeled population to alternative fishing scenarios, intended to represent potential management responses to a perceived decline in fish length or age. Because of the similarity of the results obtained under the two levels of management precision, only simulations with a management precision of 15% were selected. For each of the high- and low-productivity scenarios, we selected one simulation in which the population response had been among the greatest (Simulations 8 and 21; Table 5) and a second in which the response had been among the least (Simulations 13 and 26; Table 5).

Each of these four original simulations was extended an additional 200 years, for a total of 400 years, under a variety of alternative fishing scenarios. In one suite of scenarios, the exploitation rate was held at its original value, while the mesh size was reduced from 8.5 in to 7.5 in. In a second suite of scenarios for Simulations 8 and 21 only, for which the original exploitation rate had been 0.85, the mesh size was reduced to 7.5 in and the exploitation rate was reduced to 0.50. In both suites of scenarios, each simulation was extended with the original escapement goal and with increased escapement goals, in increments of 0.5(S_{MSY}) up to a maximum of 3.5(S_{MSY}),
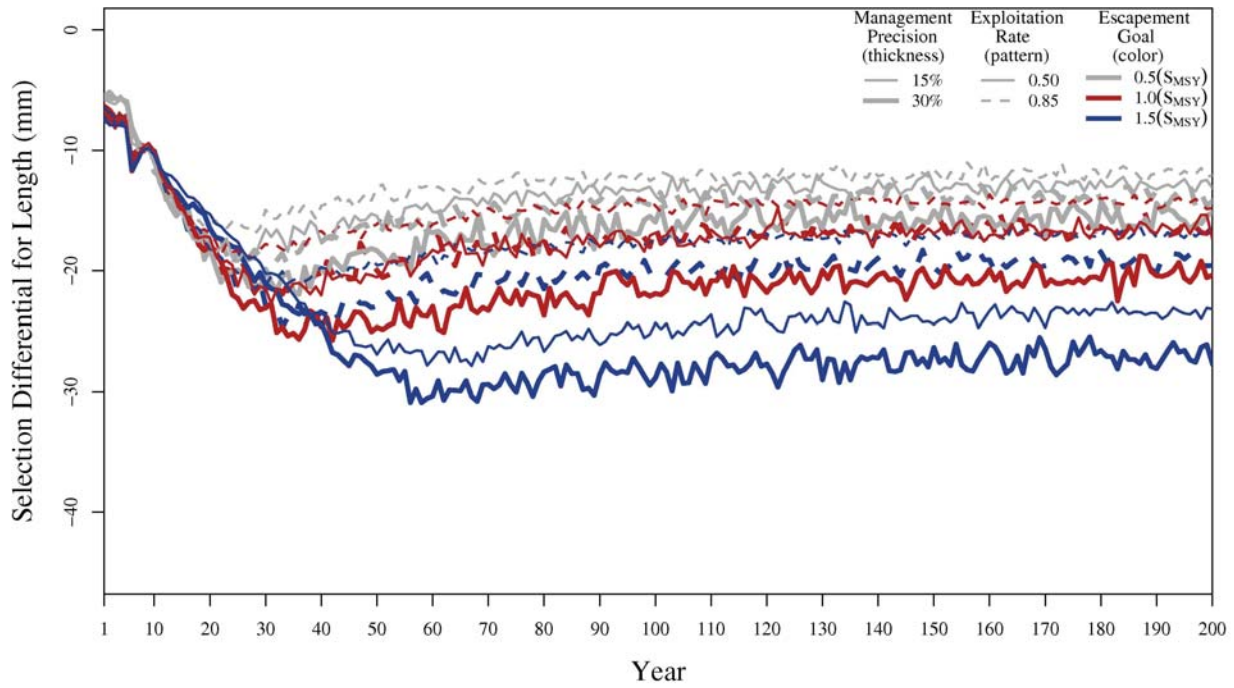
Figure 44. Mean selection differential, computed across replications within each simulation, for length of females in the high-productivity simulations.
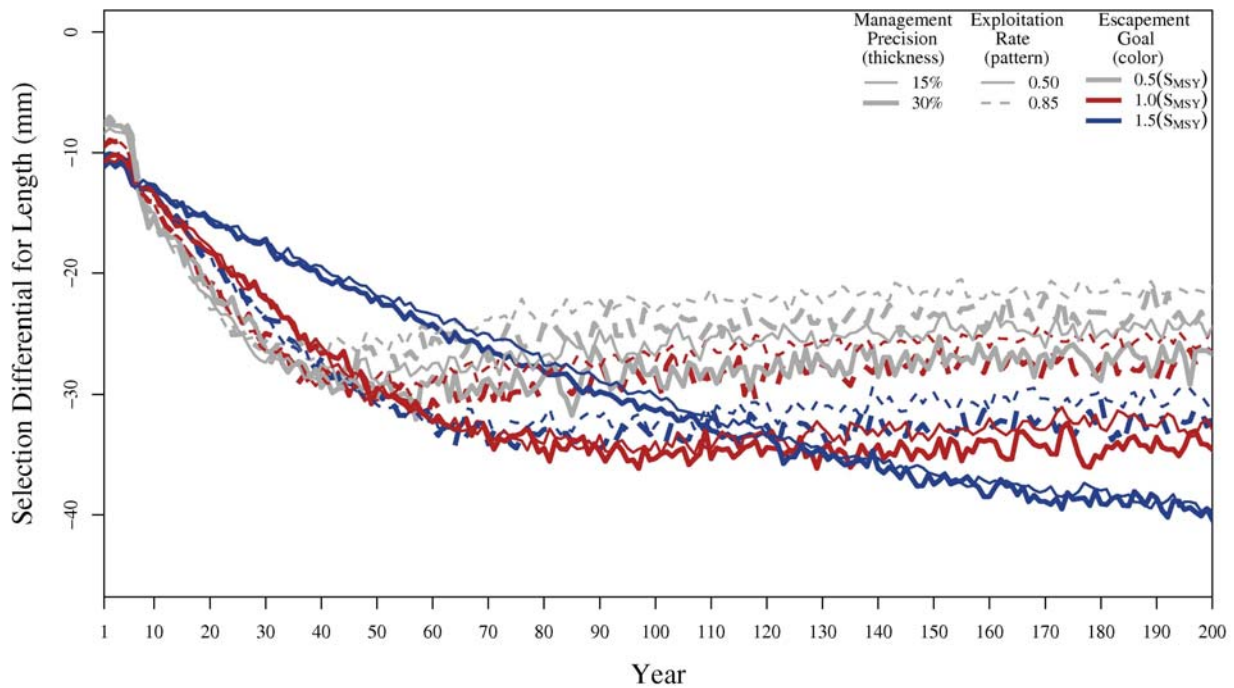

Figure 45. Mean selection differential, computed across replications within each simulation, for length of females in the low-productivity simulations.
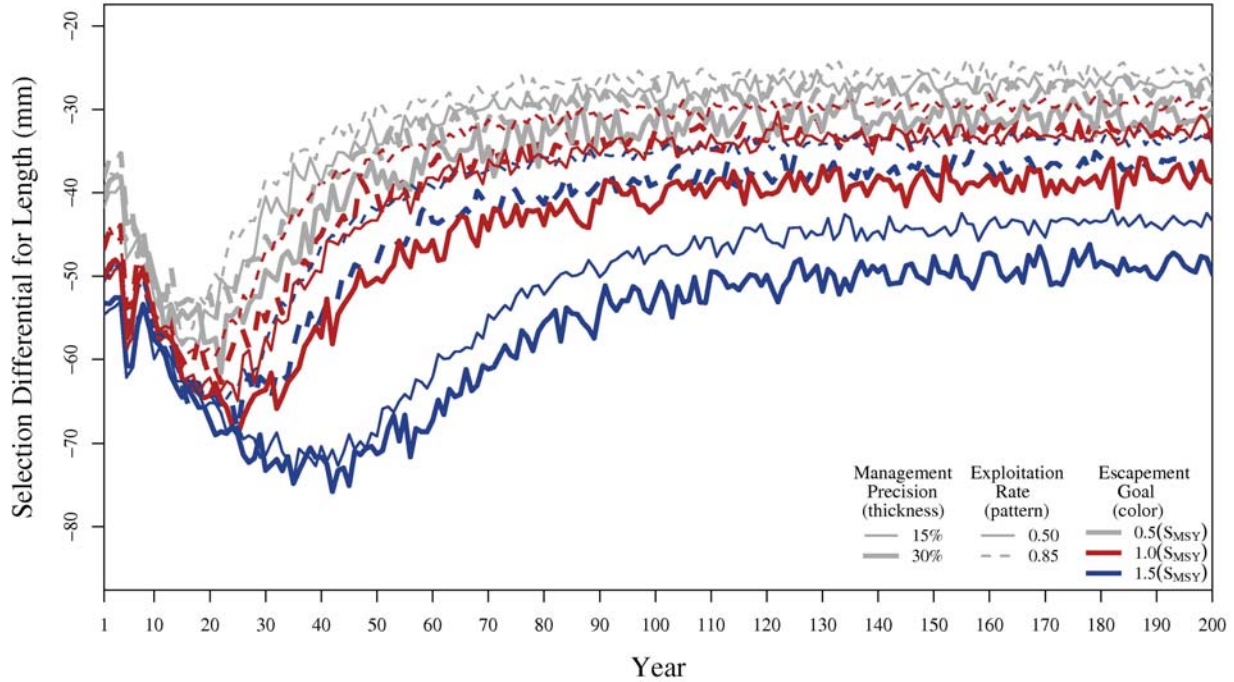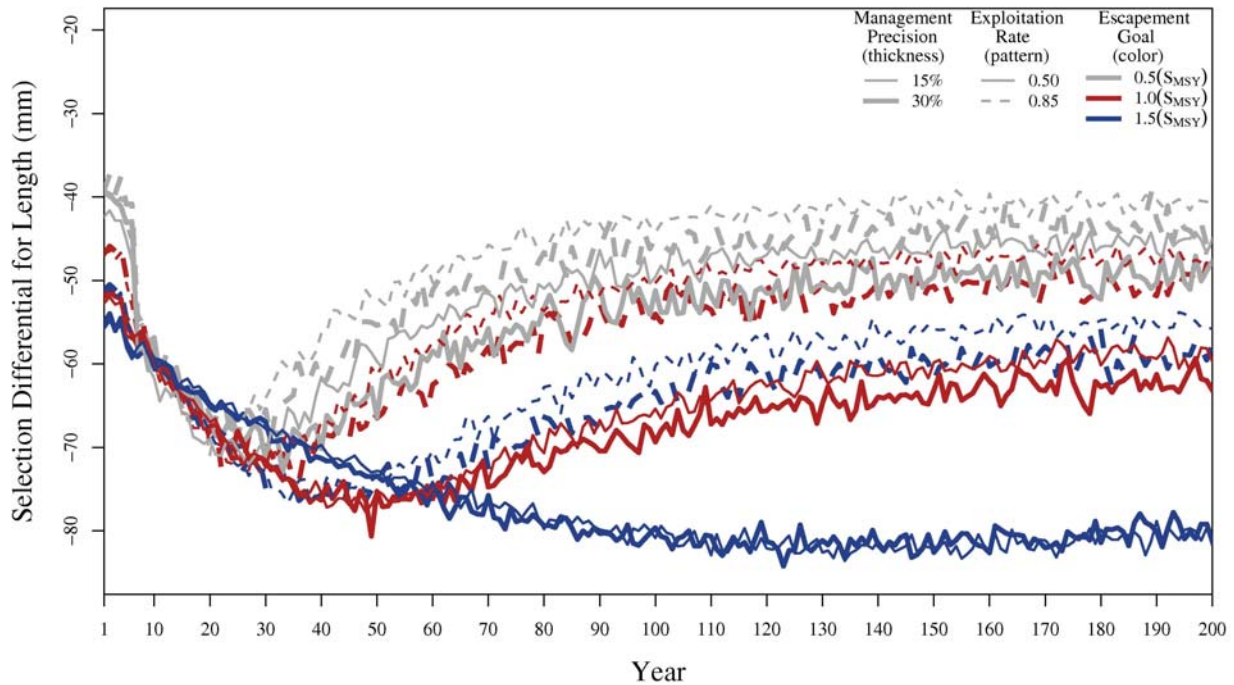
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Figure 46. Mean selection differential, computed across replications within each simulation, for length of males in the high-productivity simulations.

Figure 47. Mean selection differential, computed across replications within each simulation, for length of males in the low-productivity simulations.
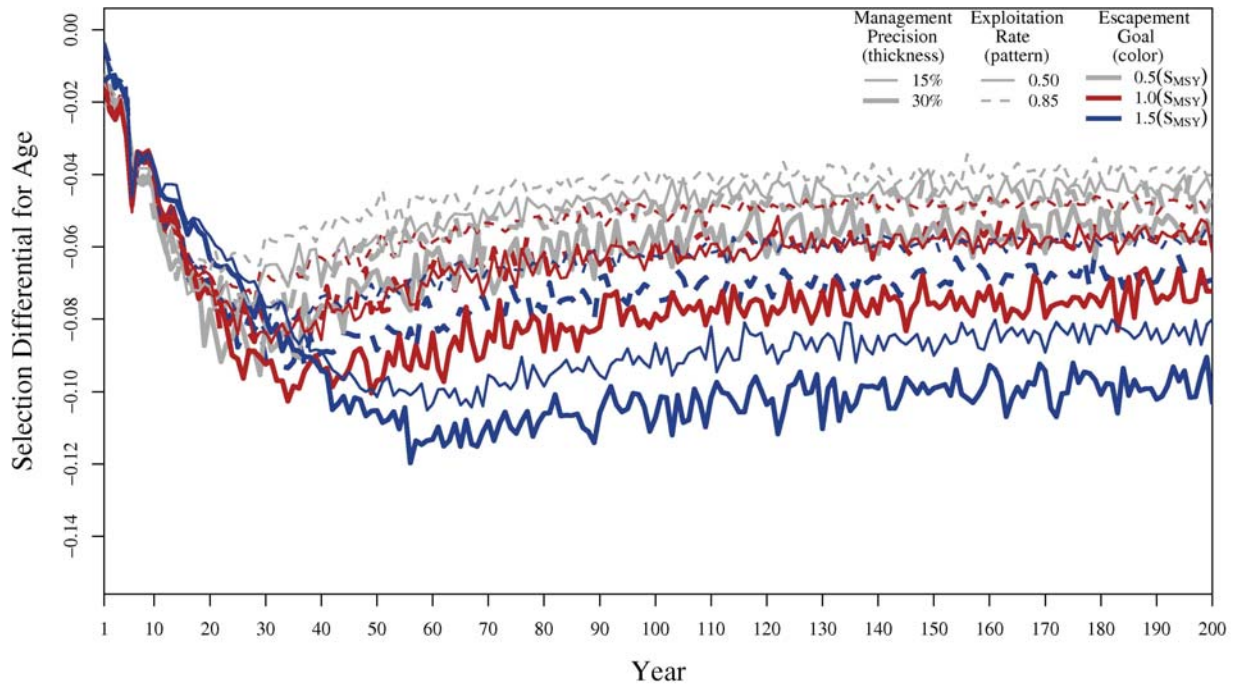
Figure 48. Mean selection differential, computed across replications within each simulation, for age of females in the high-productivity simulations.
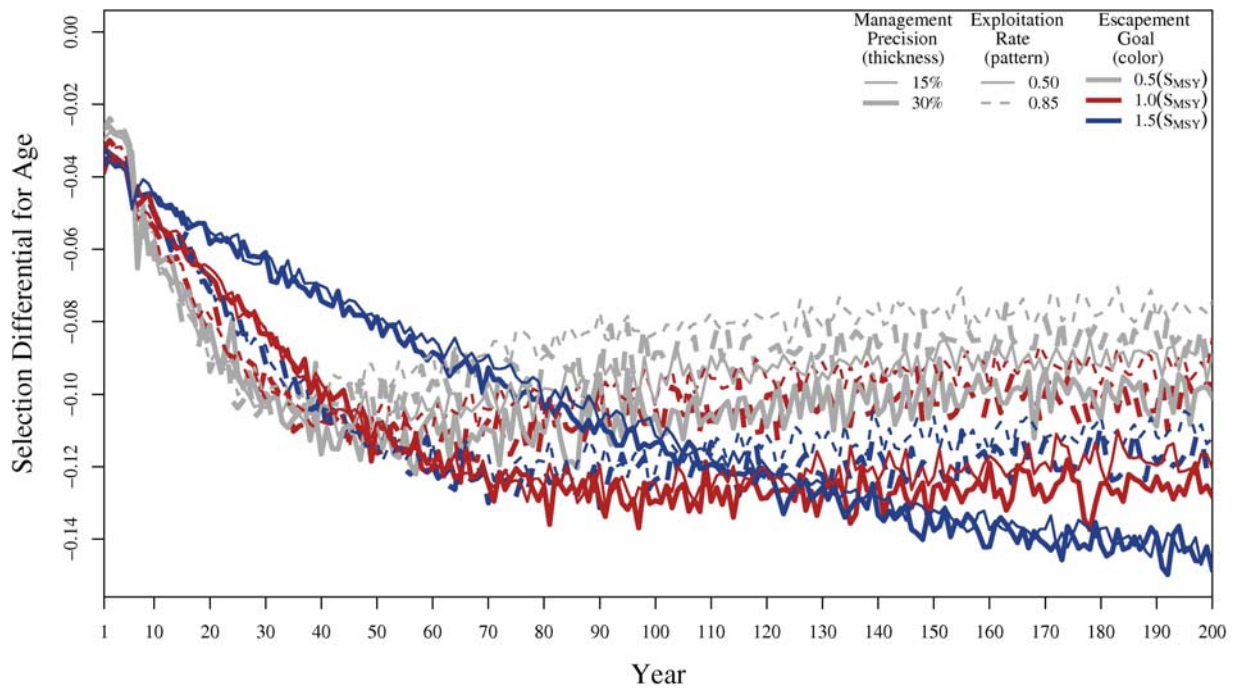

Figure 49. Mean selection differential, computed across replications within each simulation, for age of females in the low-productivity simulations.
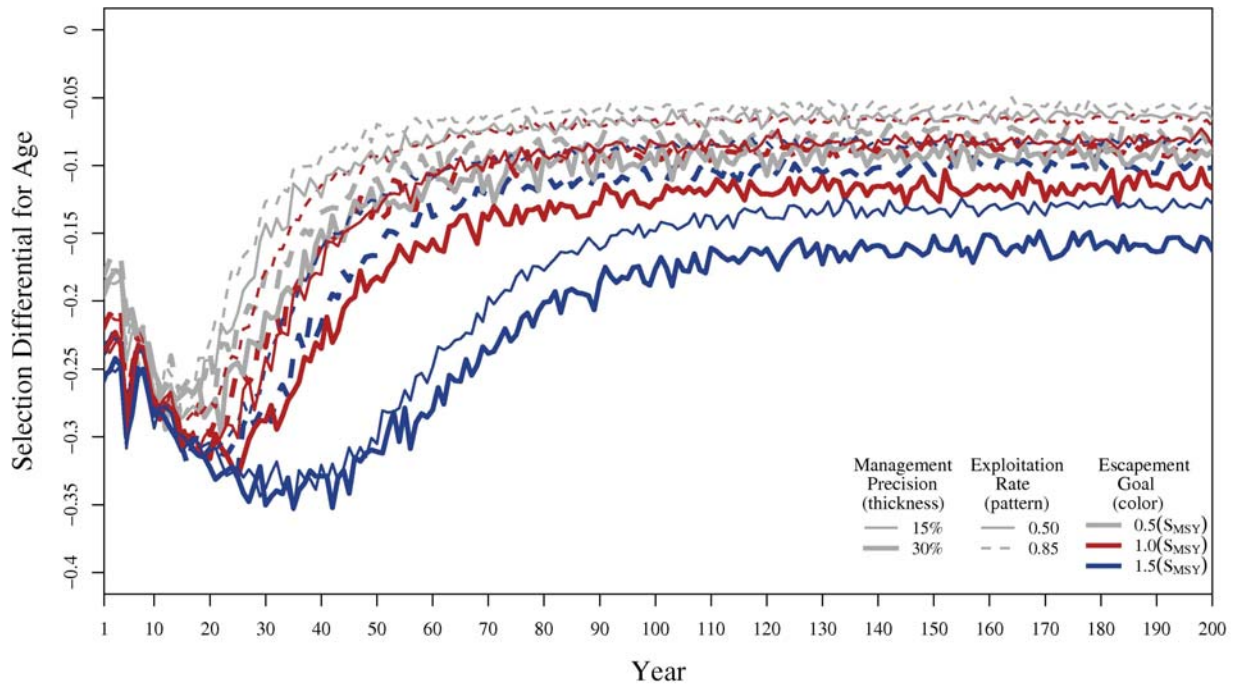
Figure 50. Mean selection differential, computed across replications within each simulation, for age of males in the high-productivity simulations.
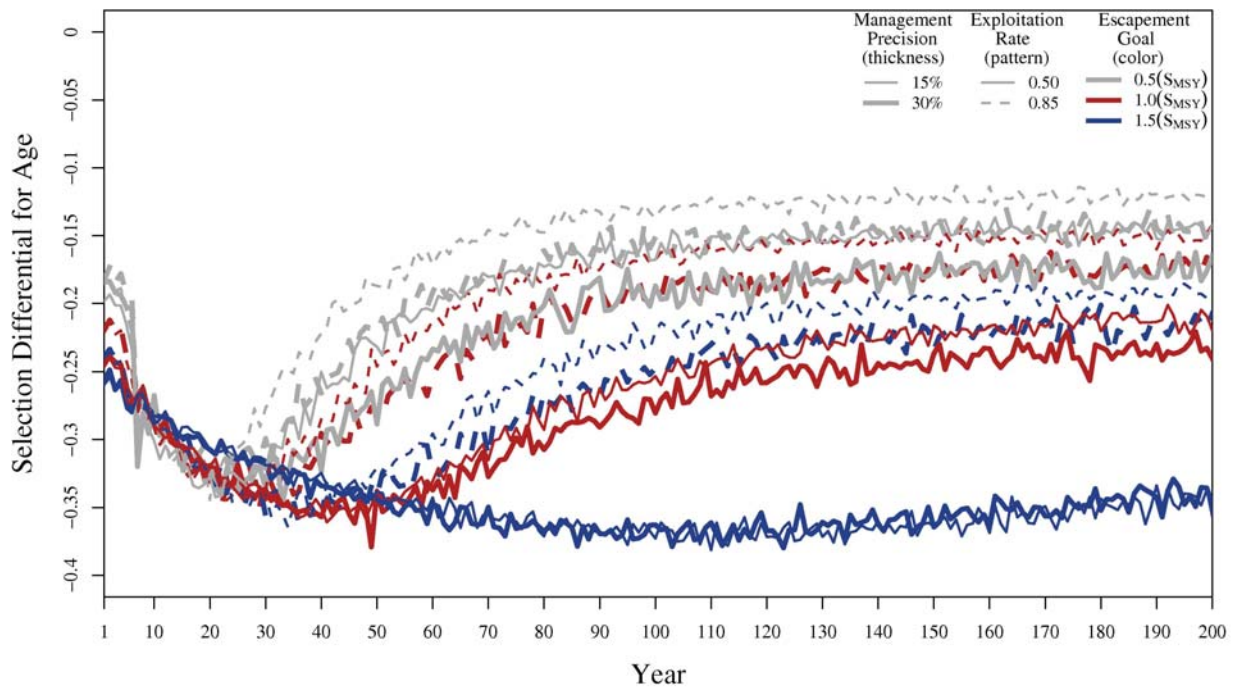

Figure 51. Mean selection differential, computed across replications within each simulation, for age of males in the low-productivity simulations.

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until the modeled population was observed to make substantial movement in the direction of the original no-fishing equilibrium. Fishing was stopped completely in a third scenario.

Mean length and age were again selected to represent the results of the alternative fishing simulations. For each of the four original simulations, box-plots of mean length and age were constructed at 50-year intervals using the results of the 250 replications of the original simulation and each alternative fishing simulation.

Simulation 8 was a high-productivity simulation conducted with a mesh size of 8.5 in, an exploitation rate of $\gamma = 0.85$, and an escapement goal of $0.5(S_{MSY})$ (Table 5). Alternative fishing simulations were conducted for an additional 200 years using a reduced mesh size of 7.5 in and the original exploitation rate of $\gamma = 0.85$. A simulation was conducted at the original escapement goal of $0.5(S_{MSY})$ and at each increment of $0.5(S_{MSY})$. However, a substantial response in mean length and age was not obtained at even the largest escapement goal considered, $3.5(S_{MSY})$, a level of escapement well above the equilibrium value of 10,000. A no-fishing simulation was also conducted. Box-plots of mean length and age for the original simulation, the no-fishing simulation, and the alternative fishing simulations with escapement goals of $3.0(S_{MSY})$ and $3.5(S_{MSY})$ are presented in Figures 52 and 53, respectively. When the exploitation rate was also reduced from $\gamma = 0.85$ to $\gamma = 0.50$, a substantial response in mean length and age was observed at an escapement goal of $2.5(S_{MSY})$ (Figures 54 and 55).

Simulation 13 was a high-productivity simulation conducted with a mesh size of 8.5 in, an exploitation rate of $\gamma = 0.50$, and an escapement goal of $1.5(S_{MSY})$ (Table 5). Alternative fishing simulations were conducted for an additional 200 years using a reduced mesh size of 7.5 in and the original exploitation rate of $\gamma = 0.50$. A simulation was conducted at the original escapement goal of $1.5(S_{MSY})$ and at each increment of $0.5(S_{MSY})$. A substantial response in mean length and age was obtained at an escapement goal of $2.5(S_{MSY})$, a value approximately 10% less than the equilibrium value of 10,000. A no-fishing simulation was also conducted. Box-plots of mean length and age for the original simulation, the no-fishing simulation, and the alternative fishing simulations with escapement goals of $2.0(S_{MSY})$ and $2.5(S_{MSY})$ are presented in Figures 56 and 57, respectively.

Simulation 21 was a low-productivity simulation conducted with a mesh size of 8.5 in, an exploitation rate of $\gamma = 0.85$, and an escapement goal of $0.5(S_{MSY})$ (Table 5). Alternative fishing simulations were conducted for an additional 200 years using a reduced mesh size of 7.5 in and the original exploitation rate of $\gamma = 0.85$. A simulation was conducted at the original escapement goal of $0.5(S_{MSY})$ and at each increment of $0.5(S_{MSY})$. A substantial response in mean length and age was not obtained until the escapement goal was increased to $2.5(S_{MSY})$, a level of escapement approximately equal to the equilibrium value of 10,000. A no-fishing simulation was also conducted. Box-plots of mean length and age for the original simulation, the no-fishing simulation, and the alternative fishing simulations with escapement goals of $2.0(S_{MSY})$ and $2.5(S_{MSY})$ are presented in Figures 58 and 59, respectively. When the exploitation rate was also reduced from $\gamma = 0.85$ to $\gamma = 0.50$, a substantial response in mean length and age was observed at a lower escapement goal of $1.5(S_{MSY})$ (Figures 60 and 61).

Simulation 26 was a low-productivity simulation conducted with a mesh size of 8.5 in, an exploitation rate of $\gamma = 0.50$, and an escapement goal of $1.5(S_{MSY})$ (Table 5). This is one of the simulations in which the modeled population had not yet reached a new equilibrium after initiation of fishing (e.g., Figure 10). An alternative fishing simulation was conducted for an
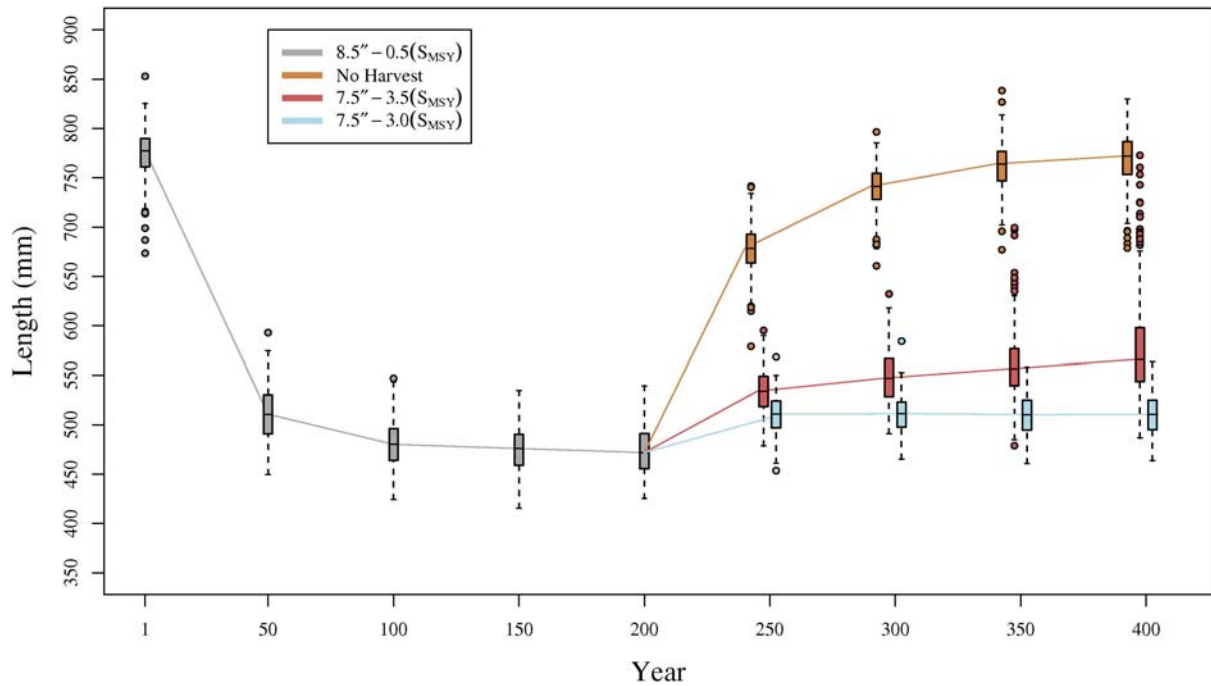
Figure 52. Box-plots of mean length observed in Simulation 8 and three extended simulations under alternative fishing scenarios, with escapement goals of 3.0(S_{MSY}) and 3.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing , mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was held constant at $\gamma = 0.85$.
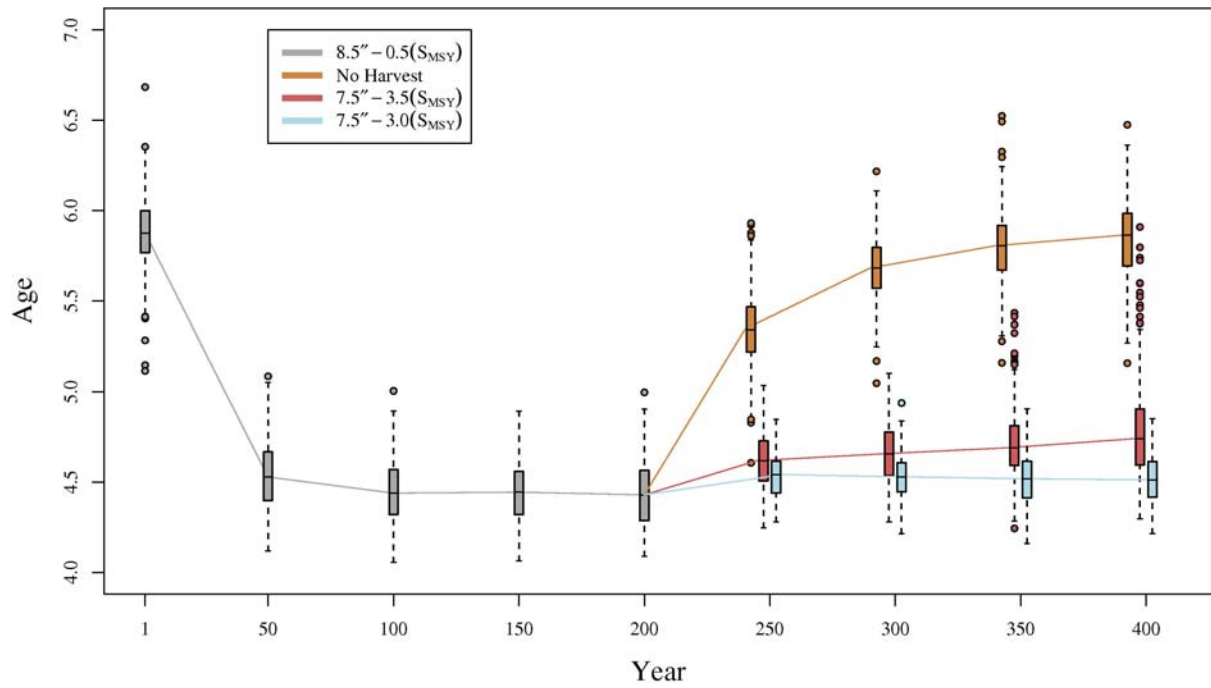

Figure 53. Box-plots of mean age observed in Simulation 8 and three extended simulations under alternative fishing scenarios, with escapement goals of 3.0(S_{MSY}) and 3.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was held constant at $\gamma = 0.85$.
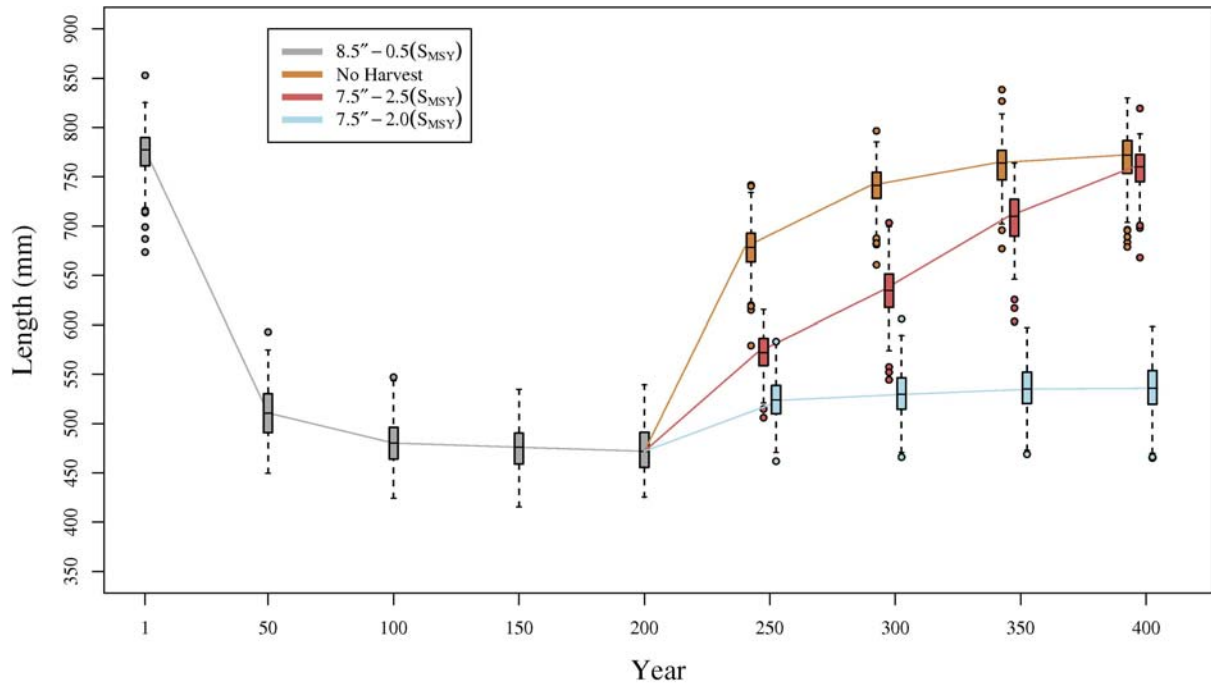
Figure 54. Box-plots of mean length observed in Simulation 8 and three extended simulations under alternative fishing scenarios, with escapement goals of 2.0(S_{MSY}) and 2.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was reduced from $\gamma = 0.85$ to $\gamma = 0.50$.
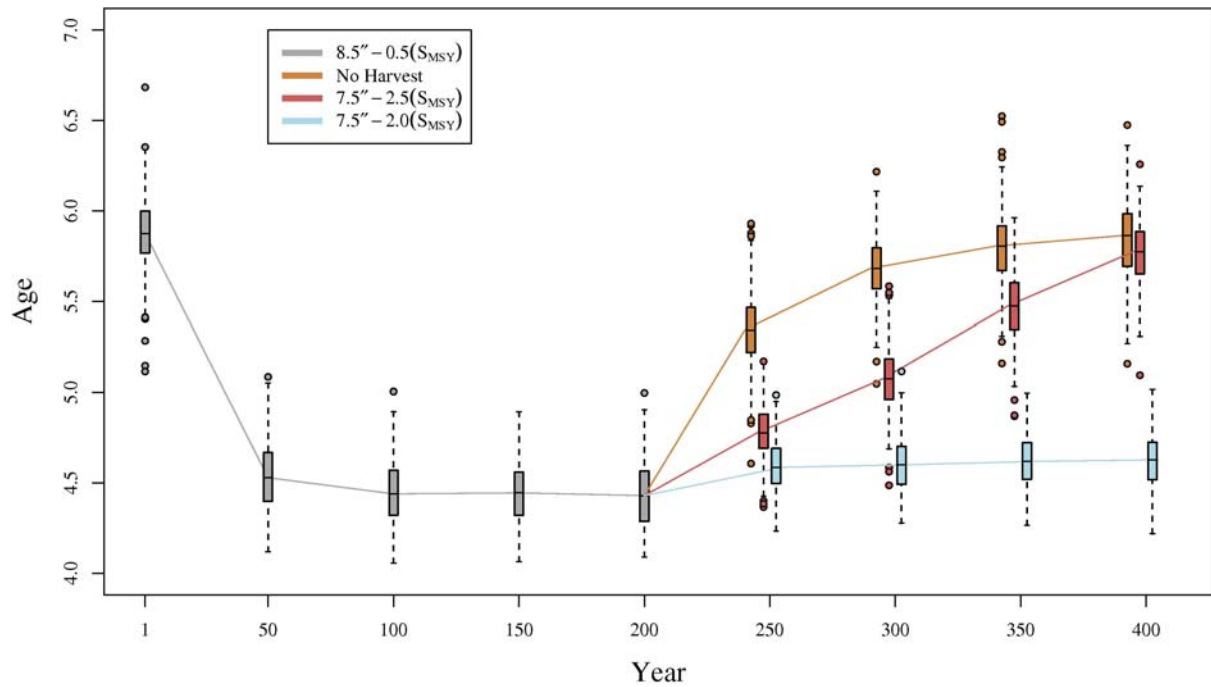

Figure 55. Box-plots of mean age observed in Simulation 8 and three extended simulations under alternative fishing scenarios, with escapement goals of 2.0(S_{MSY}) and 2.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was reduced from $\gamma = 0.85$ to $\gamma = 0.50$.
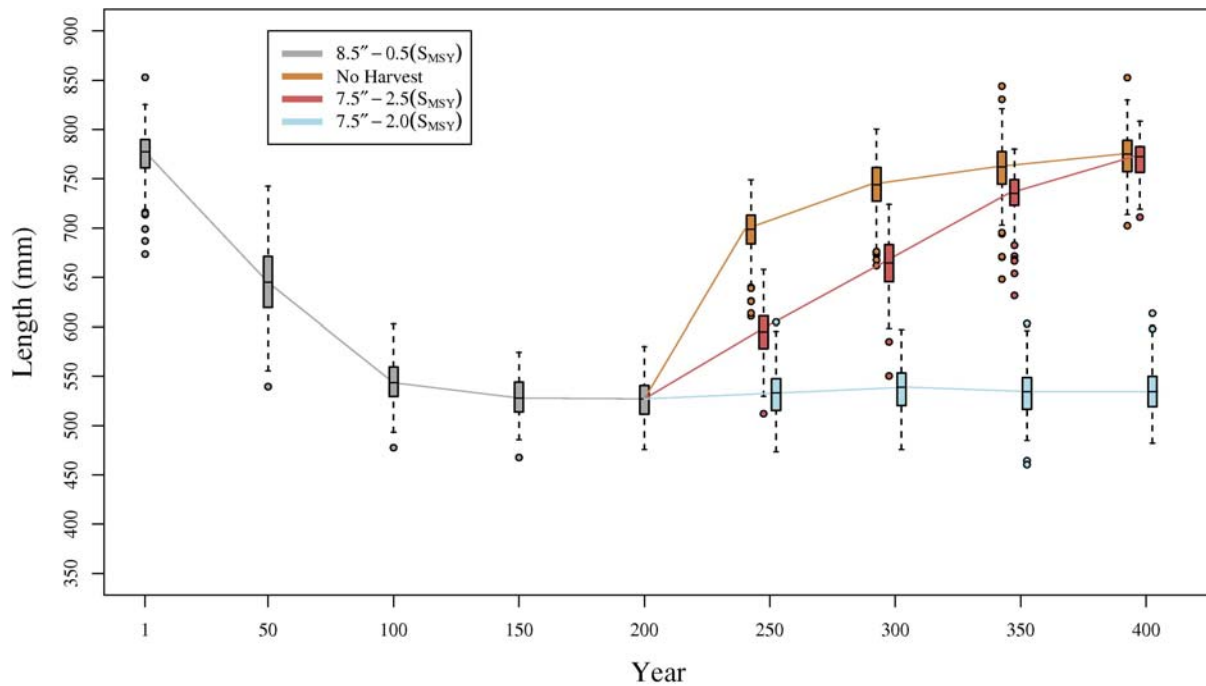
Figure 56. Box-plots of mean length observed in Simulation 13 and three extended simulations under alternative fishing scenarios, with escapement goals of 2.0(S_{MSY}) and 2.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was held constant at $\gamma = 0.50$.

Figure 57. Box-plots of mean age observed in Simulation 13 and three extended simulations under alternative fishing scenarios, with escapement goals of 2.0(S_{MSY}) and 2.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was held constant at $\gamma = 0.50$.

Figure 58. Box-plots of mean length observed in Simulation 21 and three extended simulations under alternative fishing scenarios, with escapement goals of 2.0(S_{MSY}) and 2.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was held constant at $\gamma = 0.85$.
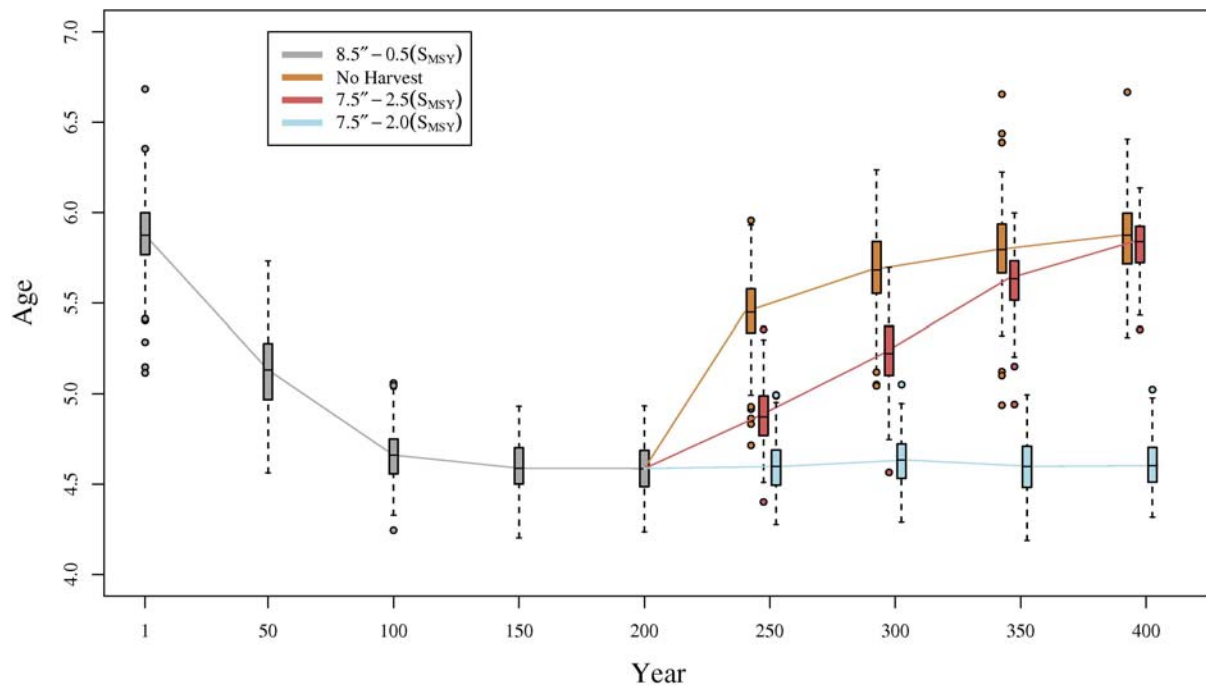

Figure 59. Box-plots of mean age observed in Simulation 21 and three extended simulations under alternative fishing scenarios, with escapement goals of 2.0(S_{MSY}) and 2.5(S_{MSY}) and a no-fishing. In the two extended simulations with fishing, mesh size nwas reduced from 8.5 in to 7.5 in and the exploitation rate was held constant at $\gamma = 0.85$.
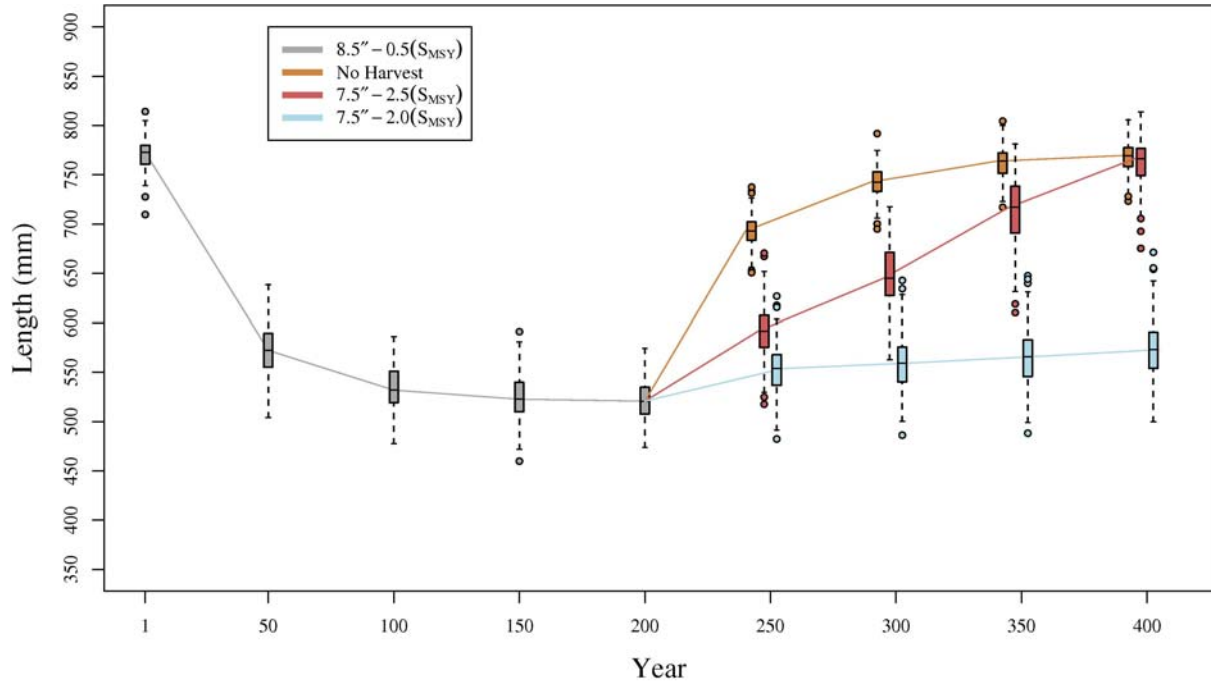
Figure 60. Box-plots of mean length observed in Simulation 21 and three extended simulations under alternative fishing scenarios, with escapement goals of 1.0(S_{MSY}) and 1.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was reduced from γ = 0.85 to γ = 0.50.
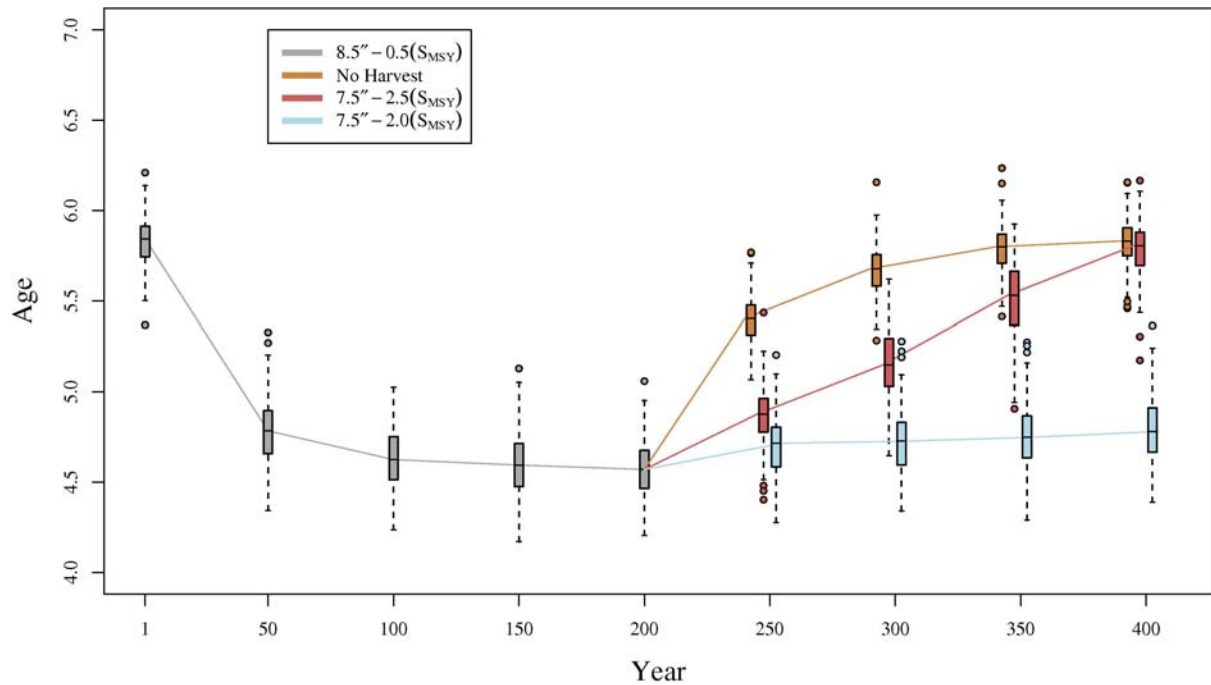

Figure 61. Box-plots of mean age observed in Simulation 21 and three extended simulations under alternative fishing scenarios, with escapement goals of 1.0(S_{MSY}) and 1.5(S_{MSY}) and a no-fishing scenario. In the two extended simulations with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was reduced from γ = 0.85 to γ = 0.50.

Figure 62. Box-plots of mean length observed in Simulation 26 and two extended simulations under alternative fishing scenarios, with an unchanged escapement goal of $1.5(S_{MSY})$ and a no-fishing scenario. In the extended simulation with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was held constant at $\gamma = 0.50$.
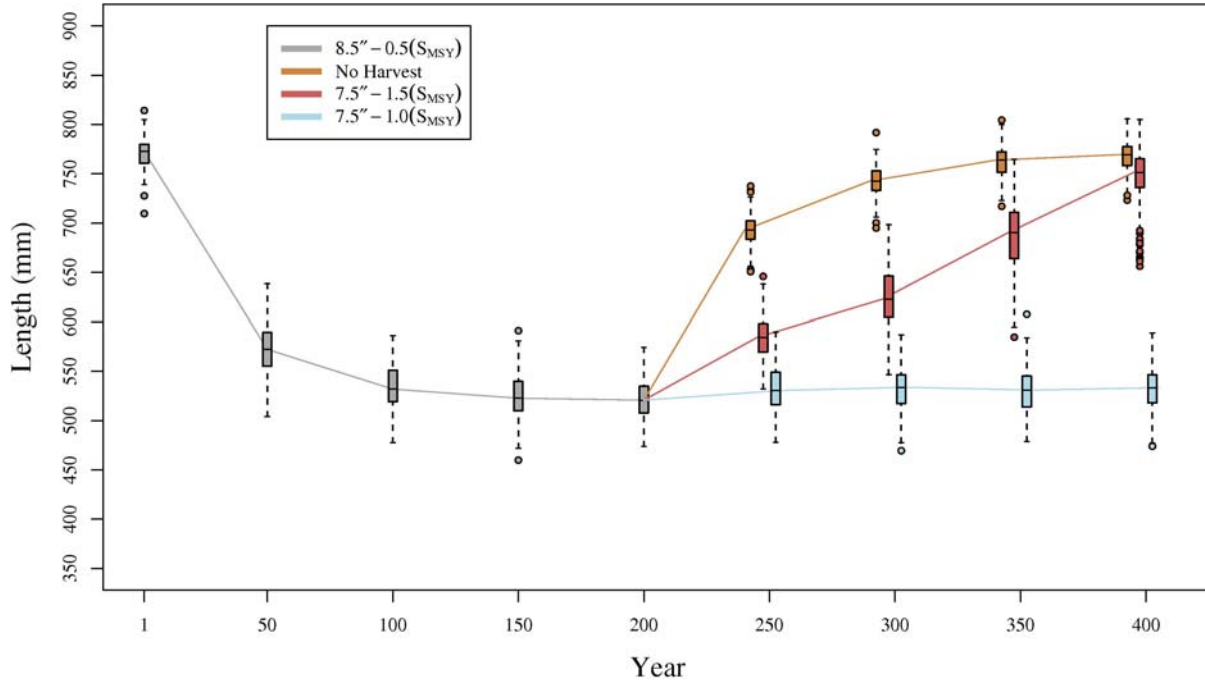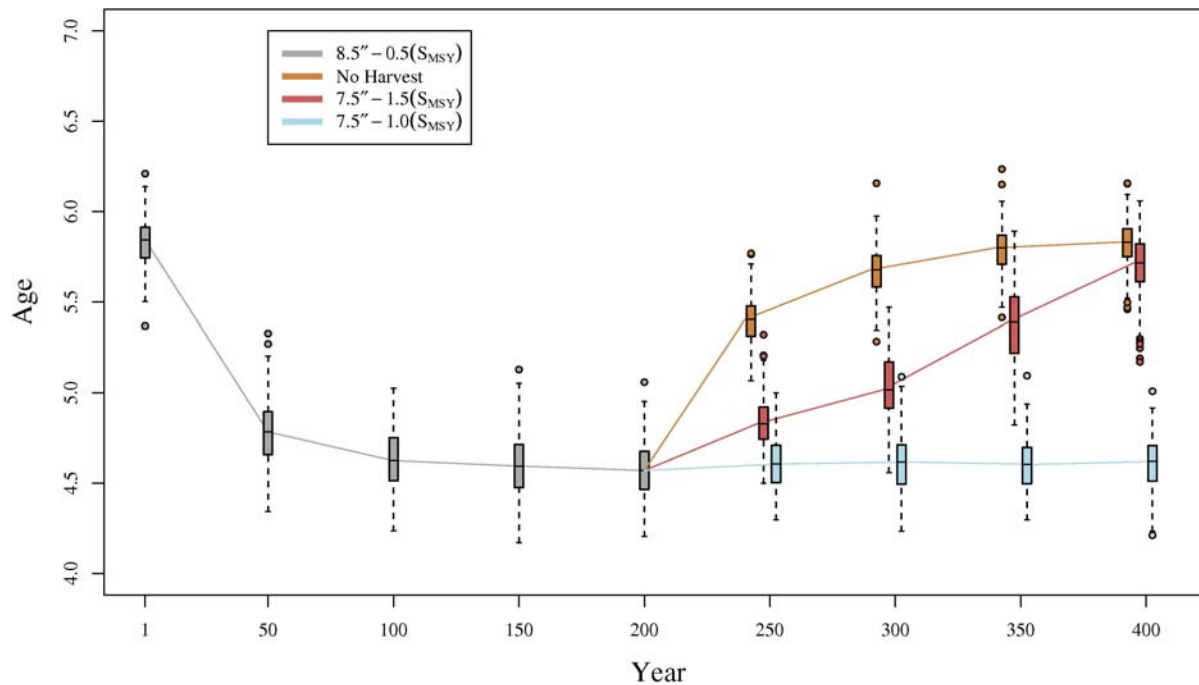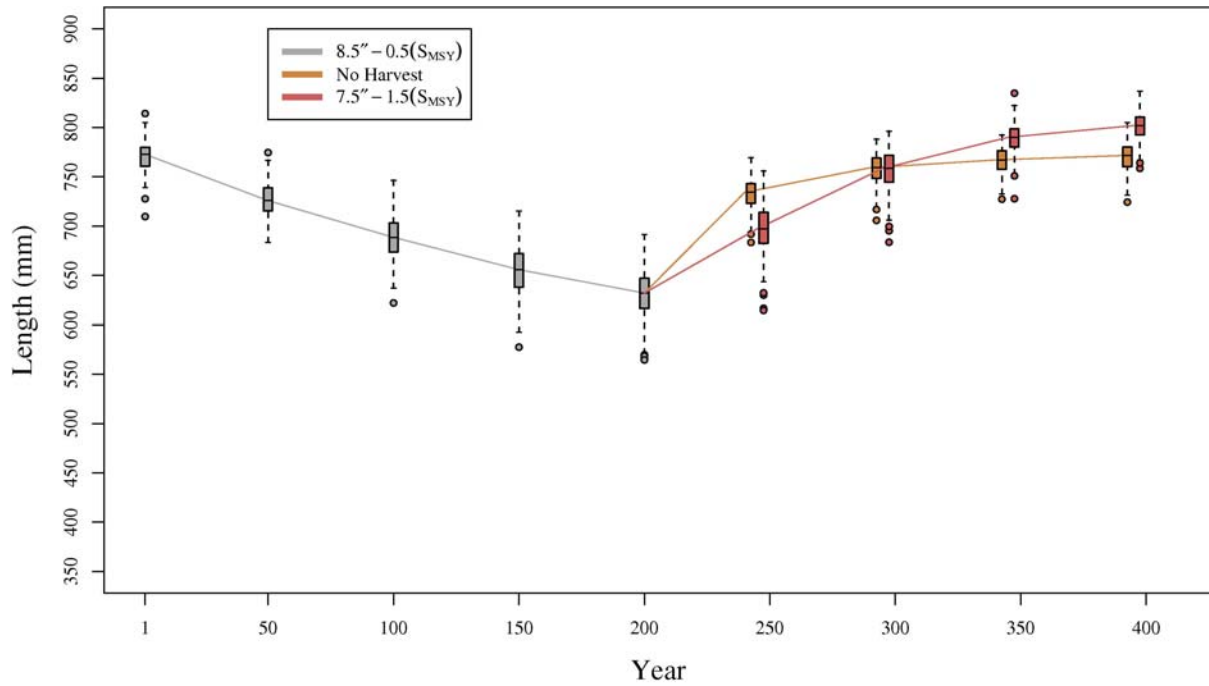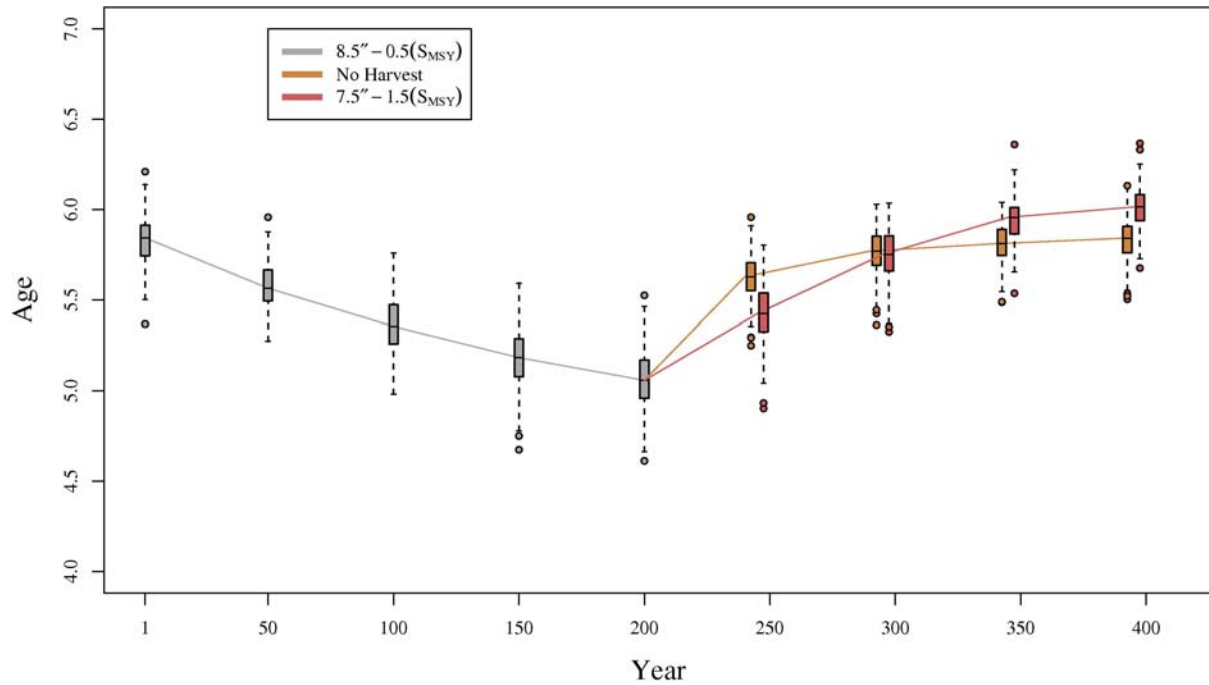

Figure 63. Box-plots of mean age observed in Simulation 26 and two extended simulations under alternative fishing scenarios, with an unchanged escapement goal of $1.5(S_{MSY})$ and a no-fishing scenario. In the extended simulation with fishing, mesh size was reduced from 8.5 in to 7.5 in and the exploitation rate was held constant at $\gamma = 0.50$.

additional 200 years using a reduced mesh size of 7.5 in and the original exploitation rate of γ = 0.50. The reduction in mesh size alone was sufficient to produce a substantial response in mean length and age without increasing the escapement goal (Figures 62 and 63).

Discussion

Like some other northern Chinook salmon populations, Yukon River Chinook salmon are characterized by a high proportion of large-bodied, older individuals. Natural selection and other evolutionary processes acting on these long-lived, anadromous fish have favored larger size for reasons which remain unclear. The location and physical characteristics of spawning and rearing habitat, as well as competition among breeding females for redd sites and assortative mating that results in mates of similar sizes (Roni and Quinn 1995), may have selected for larger, older spawners in this population. Unlike many southern populations of Chinook salmon, those in the Yukon River have not experienced major impediments to freshwater migration that could affect these traits, but these fish have been subjected to commercial exploitation for more than a century.

The declines in average weight documented by Bigler et al. (1996) and the reduced frequency of large ($\geq$ 900 mm) Chinook salmon in several spawning populations (Hyer and Schleusner 2005), combined with unexpectedly low abundance in recent years and a widespread public perception that mean size and age have declined, have precipitated concern that fishery management practices or other unknown factors may be changing fundamental characteristics of this iconic run of fish. Whether these apparent changes 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.

The myriad of interacting fishery and natural selective pressures operating on the wild population and the lack of experimental controls makes it a challenge to definitively address these questions using empirical observations. For that reason, we chose to probe one aspect of this controversy by investigating the potential for selective exploitation to alter population productivity and demographics using computer simulation. We developed an individual-based, stochastic model that integrated population dynamics and evolution through the inheritance of correlated phenotypes (length and age-at-maturation). Because of the current concern regarding Yukon River Chinook salmon, the model was parameterized to approximately mimic their recent demography and life history. We sought to identify general patterns of response to selection using approaches commonly used in analyses of phenotypic evolution to inform fisheries managers about the potential genetic consequences of selective fishing practices.

There are several advantages to initially approaching a problem through computer simulation (e.g., Elphick 2008). The most important is that models allow one to isolate individual factors or combinations of factors and investigate their influence on the characteristics of interest, while holding potentially confounding factors constant and thereby eliminating their influence. In addition, sample sizes are virtually unlimited and numerous issues, such as sampling bias and variation or bias caused by unidentified factors, which are often troublesome in analyses of empirical data, can be avoided completely. The outcomes of computer models can be replicated numerous times; the range, variation, and mean of outcomes observed across replications can be informative with respect to the reliability of predictions. Because of these advantages, computer simulation can be extremely efficient at identifying important explanatory factors and predicting

the type of response they will likely produce. An additional advantage of computer modeling is that a complex biological system can be represented by a model that is comparatively simple and easy to comprehend. This last advantage is also a limitation of modeling; a model is a caricature of reality rather than reality itself, and the utility of a model usually depends on the validity of the assumptions made during model construction.

Our model encapsulates a number of assumptions, through either model structure or parameterization, about the life history and evolutionary responsiveness of Yukon River Chinook salmon. Most of the demographic, phenotypic, and productivity components were based upon empirical observations, and so are expected to provide reasonable approximations. The value 2.25 for the productivity parameter α was based on available productivity estimates for three sub-populations of Yukon River Chinook salmon. However, recent estimates of abundance for one of these sub-populations obtained via sonar suggest that the productivity estimates may provide positively biased estimates of productivity (Danielle Evenson, Alaska Department of Fish and Game, personal communication), so this value may be too large. The low-productivity value of 1.5 was simply selected as a reduced value. We anticipated that the underlying productivity of a population would be important in determining how a population would respond, and felt that the selection of low and high values would be effective in displaying the range of potential outcomes for a variety of wild Chinook salmon populations with characteristics similar to the Yukon River population.

The structure of some of the sub-models was less firmly founded on either empirical observations or tested models. For example, the mating behavior of Chinook salmon is known to be more complex than the mating model we implemented (e.g., Berejikian et al. 2000), though we had little information on which to base a more complex model structure and parameterization. There is little doubt that length, age, and other key traits are heritable in Chinook salmon and would therefore respond to selection (Carlson and Seamons 2008); heritability parameters used in the model were estimated from Chinook salmon data, although not from populations within the Yukon River. The combination of a small correlation between the lengths of mated pairs and fecundity increasing with female size (unequal family size), and the co-heritability of traits necessitated a slight departure from the heritability model of Ronningen (1974), Olausson and Ronningen (1975), and Réale and Roff (2001) to achieve a stable population. Our incorporation of a fitness sub-model was an attempt to impart population resilience to selection imposed by fishing via a stabilizing natural selection on length and age. This sub-model had a strong influence on how far mean length and age declined in response to selective exploitation before stabilizing at reduced levels. Resilience to selection has not, to our knowledge, been estimated from empirical data on salmon, and our parameterization was determined during model calibration. The lack of information on the resilience to selection reduces the ability of our model to make absolute predictions regarding the magnitude of a response to selective exploitation.

Other prominent assumptions include that length and age at maturation are genetically linked, that the genetic characteristics underlying these traits are not rapidly eroded by selection, that plasticity has a negligible contribution to phenotypic variation, and that productivity is stationary and responds predictably to changes in spawner abundance and composition. Because some of these features of the model are less firmly founded on empirical observations of Yukon River Chinook salmon, their suitability is more difficult to assess.

One potential concern with the model is the decline in length of fish too small to be directly vulnerable to the fishery. This is a predictable outcome of the genetic covariance of length and age and, if this covariance is inaccurately estimated or varies across the life history, could produce misleading results. Nevertheless, theory predicts such correlated responses to selection when selection is directional (e.g., Hard et al. 2008); directional selection against large fish when the maturation is influenced by both size and age might be expected to alter growth rate in a way that changes size at younger ages. Our approach may overestimate the responses in lengths expressed at younger ages to selection on large fish, but it is unlikely to misconstrue the direction of these responses to selection over the relatively short term because the estimate of genetic correlation between the traits was also positive. In the absence of empirical estimates for the genetic covariance of lengths at age, the model is constrained. Nevertheless, it can produce increasing lengths at younger ages under specific forms and intensities of selection on length (authors' unpublished data).

Given environmental stationarity, an unexploited and naturally reproducing population of Chinook salmon should display stability over long time periods. Our approach to dealing with uncertainties regarding model suitability and the lack of information on important model inputs was to modify initial inputs until such stability was obtained. This model calibration was challenging because of the nonlinear interaction of some model components, especially the interaction between inheritance of length and age, the dependence of fecundity on length, and the weakly assortative mating model. Although we succeeded in producing stability and reasonable demographic and life-history characteristics in the unexploited population, we recognize that the adjustments we made to achieve these values may not reflect the natural mechanisms that produce these features in the wild. Nevertheless, we believe that this model represents a reasonable first attempt to develop such an individual-based model for Chinook salmon, and that the model is unlikely to be wrong in predicting the direction of fishery-induced evolution. For example, the responses in length and age, and demography presented in this report are qualitatively similar to those of a deterministic model of fishing-induced evolution in Chinook salmon in the Arctic-Yukon-Kuskokwim region (Hard et al., in press). However, like Riddell (1986), we acknowledge that our model, being primarily based upon selection for a single trait (length), may well present an over-estimate of the magnitude of the effects. Indeed, the magnitude of the response depends directly on the strength of stabilizing natural selection, a multifaceted factor for which we have no information.

Simulation Results

Our results suggest that size-selective fisheries for Chinook salmon employing large-mesh gill nets (imposing directional selection against larger fish) could shift population demography and reduce productivity through evolution of length and age at maturation within less than ten generations (about 50-60 years). In most scenarios examined, mean length and age declined rapidly in response to the onset of the fishery and stabilized at considerably lower levels within 50 to 100 years. In general, mean length and age declined more when the escapement goal was a smaller fraction of S_{MSY} (0.5 vs. 1.5) and when exploitation rate was higher (0.85 vs. 0.50); more precision in management (15% vs. 30%) also tended to increase effectiveness of exploitation and the effects of selective fishing. This suggests that exceeding escapement goals in years of small returns may impart magnified resiliency to selection in subsequent generations. Any realized reduction in mean length and age for Yukon River Chinook salmon can be expected to correspond to a reduction in mean weight, fecundity, and productivity.

Several important responses of the modeled population, some expected from theory and others less predictable, were apparent in the results. For example, the changes in length and age under a constant exploitation rate affected run size and escapement in ways that depended on population productivity. Because the base escapement goal S_{MSY} was independently established for the high- and low-productivity simulations, and S_{MSY} occurs at lower escapements for more productive populations, exploitation rates tended to be greater in the high-productivity simulations, which exacerbated the effects of selective exploitation. Regardless of the productivity, higher escapement goals were associated with higher run sizes and with smaller changes in length and age. Because improved management precision increased the effectiveness of catching larger, older fish, especially when the population was more productive, there was a tendency for run size and escapement to decline relatively more under these circumstances. This indicates that high productivity may not by itself ensure resilience to high exploitation rates. We found that a closely managed fishery on a more productive population tended to increase the selection differential on length and reduce run size and escapement over the long term, a result that highlights the importance of surplus escapement to adequately seed spawning habitat with sufficient numbers of larger and older fish.

Overall, the responses of males and females to fishing selection followed the same general pattern, but the differences were instructive. In both cases, selection differentials on length increased initially, followed by a reduction in selection intensity over several years. However, males tended to have higher initial selection differentials on both length and age, followed by a more rapid reduction in selection intensity, especially in the high-productivity scenarios, except when the escapement goal was large relative to S_{MSY}. In that case the negative selection differential tended to increase in magnitude slowly but consistently over the course of the simulations. The contrast between male and female responses undoubtedly reflects the differences in how gear selectivity and the distribution of length at age corresponded between the sexes. Relative to males, a greater proportion of females tended to mature at lengths most susceptible to gear interception, which tended to reduce their ability to rebound in size, especially when the population was less productive. The reduction in selection intensity over time tended to be weakest when both run size and exploitation rate were high, the conditions under which selection is expected to be most effective.

In each of the two productivity scenarios, reductions in mean length and age after 200 years of fishing tended to be affected most strongly by escapement goal and exploitation rate; the effect of management precision was consistently smaller. Similar patterns were observed for changes in individual fecundity and total egg deposition as a result of variation in escapement goal, exploitation rate, and management precision. Clearly, the interaction between exploitation rate and escapement level was key in determining evolutionary response over this period. This interaction suggests that management based on maintaining escapement above the level derived from traditional stock-recruit analysis may help to minimize fishing-induced declines in size and age of adult fish, although what level of escapement is optimal remains uncertain.

In most of the cases we considered, management intervention after 200 years had meager success in reversing declines in mean length and age over a subsequent 200 years unless multiple changes were implemented in the fishery. The reduction in mesh size from 8.5 in to 7.5 in was modest in comparison to the large reduction in length after 200 years of fishing with 8.5 in gear, so the smaller-meshed gear continued to target the largest individuals and effectively preclude recovery in the absence of other remedies. Management options to reduce exploitation rate and mesh size were much more effective in increasing length and age when implemented jointly,

rather than individually. Reducing exploitation rate from 0.85 to 0.50 was an effective intervention if the escapement goal was sufficiently high (on the order of 1.5(S_{MSY}) or higher). Reducing mesh size from 8.5 to7.5 in was effective in increasing mean length and age if the exploitation rate was reduced to 0.50 and the escapement goal was at least 1.5(S_{MSY}). As expected, eliminating fishing completely produced the most rapid recoveries in size and age, because genetic variation present in both traits permitted responses to relaxed selection. The simulations showed convergence of final phenotypes between the no-fishing and reduced fishing/reduced mesh size scenarios, but generally this required at least 150 years.

Our findings are qualitatively similar to those of other exploratory studies. In particular, our results show strong similarities to those of Hard (2004) and Hard et al. (in press), who used a deterministic, distribution-based model of phenotypic evolution in Chinook salmon populations with similar life-history parameters to show that size-selective fishing could produce a detectable evolutionary response in size at age within a few decades if both exploitation rate and size selectivity are sufficiently strong. Hard et al. (in press) predicted that the lengths of adults of most ages would decline under selection within 100 years even if the selection differential is small on fish of older ages, due to the correlated heritabilities of lengths expressed at different ages. They argued that adaptation to fishing could reduce population viability because both run size and fishery yield were predicted to decline detectably within 10 generations unless stabilizing selection on length (through natural or sexual selection on size of breeding adults) is sufficiently strong. A modest but realistic heritability of length ($h^2 \sim 0.3$) appeared to permit some recovery of length at age after cessation of fishing. Thus, given sufficient genetic variability, a population could adapt to fishing selection to reach a higher abundance, but fishery yields were likely to take much longer to respond to management intervention.

Management Implications

Resolving the uncertainties that exist for the effects of fisheries-induced evolution for Yukon River Chinook salmon will require careful monitoring of long-term trends in exploited populations that differ in features that do not confound fishing effects, or carefully designing fishing 'experiments' to quantify these effects (NRC 2005). It is difficult to identify practical situations where these attempts could be carried out; therefore, we believe it is important for managers to be precautionary about the potential genetic effects of fishing in managing salmon fisheries.

Fisheries that exert substantial mortality are expected to affect the demographic characteristics and intrinsic reproductive potential of populations; this is a basic tenet of population biology and fisheries management. We observed such effects under all the fishing scenarios we explored, results that are consistent with those of others who have argued that any extra mortality exerted by fishing is likely to produce changes in population characteristics as adaptation to fishing occurs (e.g., Policansky 1993a,b). At equivalent exploitation rates, size-selective fisheries that remove larger, older fish disproportionately can reduce intrinsic potential more than those that are not selective because of the greater fecundity (and perhaps gamete quality and habitat selectivity) of these individuals. Because size and age are both heritable in Chinook salmon, these challenges to population resilience can be compounded over time through evolutionary response to selection on those traits.

If exploited populations are to cope with the ecological and evolutionary pressures posed by fishing they must retain the adaptive capacity to respond. Fisheries-induced evolution might

compound the demographic risk posed by over-exploitation, and this evolutionary trend could be difficult to reverse. As fish adapt to exploitation, they are likely to evolve away from configurations that natural and sexual selection alone would favor. Given sufficient genetic variability and a predictable fishing regime typified by moderate to high exploitation rates, salmon ought to respond to fishing selection by increasing growth rate and reducing the mean age at maturation. Both of these adaptations will act to reduce fishing mortality and, therefore, yield. Whether such adaptations can improve population viability in the face of continued fishing depends largely on two conditions: genetic variability in size and age is not diminished by selection, and productivity is not eroded by consequent changes in size, age, and fertility of breeding adults. Even if aggressive reduction of fishing mortality is sufficient to permit a population to recover total run size, achieving original age and size distributions is likely to take much longer.

The management of Yukon River Chinook salmon should encompass all aspects of the fishery and their ecology, including the potential for fishery-induced adaptation. Our results provide important indications of how Yukon River Chinook salmon populations might be expected to respond to long-term, selective exploitation of the largest individuals. Reductions in mean length, maturation age, population productivity, and related traits seem highly likely to occur, even though the magnitudes of the declines are difficult to predict with confidence. Our findings also suggest that socially and economically disruptive management intervention might be required to accomplish population recovery if the oldest and largest fish are extirpated from the population. A modest reduction in mesh size alone may not be an effective management response in that eventuality. Although there are indications that the size structure of the population may have shifted to smaller fish in the past (Bigler et al. 1996; Hyer and Schleusner 2005), the population appears to remain relatively robust and some large individuals persist within the population. Management of the fishery would benefit by adopting a more risk-averse perspective and explicitly linking exploitation rates and selectivity of the fishery to the degree of certainty in the condition of the breeding population (Gerrodette et al. 2002). The adoption of such a precautionary perspective with respect to the potential consequences of selective exploitation for adaptive capacity might forestall future decline and increase the potential for the Yukon River Chinook salmon population to persist as a viable and phenotypically diverse resource that can support a fishery as well as adapt successfully to future natural challenges.

Conclusions and Recommendations

Conclusion #1: That many phenotypic traits, such as size and age at maturation, are heritable seems irrefutable, not withstanding the important influence that environmental factors have on the same phenotypic traits.

Conclusion #2: Insufficient information exists, in the form of theoretically-justified models and empirical observations with which to parameterize such models, to accurately predict the magnitude of a population-level response to selective exploitation.

Conclusion #3: Size-selective exploitation, particularly directional selection for the largest and most fecund individuals, has the potential to rapidly reduce fish size and age at maturation, as well as population productivity.

Conclusion #4: Unless scientific experiments are conducted at a scale in which individual populations are the experimental units, which is unlikely to be socially acceptable even if logistically feasible, analysis of empirical observations is unlikely to conclusively reveal the true relationship between fishery exploitation and the phenotypic traits and demographic characteristics of salmon populations.

Recommendation #1: Maintain the abundance of the reproductive component of a population well above the level suggested by traditional analysis of stock-productivity data to maintain the resiliency of the population to both fishery and natural selective forces.

Recommendation #2: Reduce or eliminate directional selection for larger and more fecund individuals to maintain genetic and phenotypic diversity, capacity to utilize diverse habitat, and population productivity.

Acknowledgments

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