Fishery selection and Pacific salmon life histories: patterns and processes

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Abstract

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Life history traits of wild animals can be strongly influenced by anthropogenic activities, including hunting and fishing. Recent research has warned of adverse evolutionary changes resulting from the exploitation of wild populations. My PhD research fills gaps in our understanding of long-term fishery selection patterns and the potential for evolutionary change in harvested populations. I first examined how genetic and environmental effects impact age and size at maturation in sockeye salmon (*Oncorhynchus nerka*) using data from a common garden study. I found that genetic effects are likely to play a role in influencing these traits, suggesting that fishery selection has the potential to contribute to microevolution. Next I quantified multi-decadal fishery selection patterns in a range of Alaskan Pacific salmon fisheries. I quantified and compared commercial and recreational fishery selection on Chinook salmon (*O. tshawytscha*). I discovered that selection by the recreational fishery, which consistently caught larger fish, but not the commercial fishery, which has caused variable selection but overall caught smaller fish, has been consistent with the size trends towards smaller fish over time. Analyses of nine commercial sockeye salmon fisheries showed that size selection varied over time but in most years larger than average fish were caught. Next, I found that size-selective fishing on sockeye salmon, where males are typically larger than females, can also result in sex selection, specifically more males being removed than females. Sex-selection patterns varied across populations, and skewed sex ratios may change sexual selection, competition, and behavior on the spawning grounds. Finally, I found that length at age at maturation has decreased over the last half-decade in most but not all Bristol Bay sockeye salmon populations while age composition has not changed. I quantified temporal trends in maturation length thresholds to determine whether fishery selection likely contributed to microevolutionary changes and found decreasing values over time for most, but not all, populations. Environmental changes in the ocean combined with adaptive microevolution have likely combined to produce the observed patterns. These findings suggest that fishery managers should consider both selective fishing and environmental factors affecting fish growth when successfully managing exploited fish populations.

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General Introduction

Life history traits of wild animals can be strongly influenced by anthropogenic activities, including hunting and fishing (Darimont et al. 2009). Through domestication, selective breeding has been used to rear animals, birds, and plants to have specific, beneficial traits (Hazel 1950). Increased harvest can have significant ecological effects on exploited stocks, including reductions in density and decreases in mean age and size (Policansky 1993; Trippel 1995). Hunting and harvesting can have selective effects on wildlife behavior and morphology and plant morphology (Harris et al. 2002; Coltman et al. 2003; Mooney and McGraw 2007). Fishing gear often selectively removes individuals with respect to size (Hamley 1975) and can thus alter the distribution of life-history traits such as size and age at maturation among the fish surviving to breed (Law 2000; Allendorf et al. 2008). Thus, fishing can be seen as an experiment in life history evolution (Rijnsdorp 1993).

Recently, the effects of fishery selection on wild populations' life history traits have received a great deal of attention, with the literature warning of adverse evolutionary changes (Allendorf and Hard 2009). Selective harvest on wild fish populations has been associated with shifts towards smaller fish, younger age distributions, and decreased age and size at maturation (Fenberg and Roy 2008) and is linked to changes including decreased fecundity (Walsh et al. 2006), increased sexual dimorphism (Wolak et al. 2010), lowered reproductive rates (Venturelli et al. 2009), decreased reproductive potential (Marteinsdottir and Begg 2002; Hutchings 2005), loss of yield (Conover and Munch 2002), increased variability in abundance (Hsieh et al. 2006; Anderson et al. 2008), and even fishery collapses (Olsen et al. 2004). Numerous studies have emphasized the importance of older, larger fish for stock stability and sustainability (Birkeland and Dayton 2005; Law 2007; Hsieh et al. 2010). However, research has been hampered by the difficulties in quantifying fishery selection over time and understanding its association with evolutionary changes in harvested fish (Law 2007; Heino and Dieckmann 2008).

Fishery managers and scientists have questioned how to manage fisheries to minimize adverse phenotypic and genetic changes in their stocks associated with size-selective harvest (Jørgensen et al. 2007; Allendorf et al. 2008). "Evolutionary management" of exploited fish stocks considers the effects of removing fish of different sizes from a stock and consequential evolutionary changes in fish age, length, and growth (Heino and Godø 2002; Ashley et al. 2003; Jørgensen et al. 2007). This perspective also considers how evolution of life history traits affects ecological relationships and management strategies (Jørgensen et al. 2007). Before it is possibly to reliably evaluate the consequences of fisheries-induced selection, it is necessary to carefully document the extent to which a fishery is indeed selective over an appropriate period of years. For example, Kuparinen et al. (2009) argue that there is great need to evaluate fishery selection regimes and identify less-selective fishing gear and management strategies. According to the Breeder's Equation, evolutionary response is a product of selection on a trait and that trait's heritability (Falconer and Mackay 1996), so quantifying selectivity is an essential first step to understanding the evolutionary consequences of size-selective fishing on affected traits. However, research evaluating the implications of fishing has been hampered by the difficulties in quantifying fishery selection, including selection differentials, over time (Law 2007; Kuparinen et al. 2009). Data required to accurately estimate fishery selection, including the size or age composition of fish being caught and not being caught (Quinn et al. 2006), are often difficult to obtain. Few studies have empirically examined long term size-selectiveness of fisheries due to the lack of available data on fish both caught and not caught.

Fortunately, studies of fishery selection on Pacific salmon (*Oncorhynchus spp.*) are aided by their anadromous and semelparous life history. Because all salmon migrating into freshwater are maturing adults, they can be counted and life history data can be collected, which can then be directly compared with data from the catch. Given the effects of density and climate on growth and age at maturation of salmon (e.g., Rogers 1987; Rogers and Ruggerone 1993; Pyper and Peterman 1999; Ruggerone et al. 2003), it is necessary to carefully document fishery selection patterns over sufficient time periods over which evolutionary changes can occur before associating fisheries with life history trait changes. It is also important to understand if and how genetic and environmental effects impact age and size at maturation in salmon. Individual spawning populations separated by space are likely to exhibit local adaptations for age and size at maturation, which may be enabled by phenotypic plasticity and/or genetic adaptations (Taylor 1991; Wood 1995). These changes can also affect how the populations are influenced by size-selective fishing (Kendall and Quinn 2009). Common garden studies and the use of probabilistic maturation reaction norms to examine maturation length thresholds can help to understand the influences of each factor on life history traits (Dieckmann and Heino 2007; Kuparinen and Merilä 2007; Heino and Dieckmann 2008).

Chapter One: Comparative maturation schedules of two Columbia River sockeye salmon, *Oncorhynchus nerka*, populations

Introduction

Growth, maturation, reproduction, survival, and mortality are essential processes in the life cycles of all animals, and life history traits associated with these processes characterize populations within species. Environmental conditions, evolutionary pressures, and contemporary selection regimes experienced by individuals in different populations often result in varying life history patterns. The separate and combined influences of environmental conditions and genetic control on a population's life history traits result in local adaptation and have strong implications for its conservation and management (Taylor 1991). Populations should be managed in ways that recognize and sustain their diverse traits (Wood 1995) and successful restoration and enhancement programs need to consider adapted characteristics (Taylor 1991). Life history diversity, especially in growth and age at maturity, buffers populations and groups of populations from environmental variability and increases their productivity (Koellner and Schmitz 2006; Greene et al. 2010; Schindler et al. 2010). Thus, maintaining productivity may be done best by conserving as many locally adapted populations as possible (Wood 1995). Identification of life history differences among populations and understanding how they are shaped, including interactions between genotypic and environmental factors, is critical to population conservation (Waples et al. 2001).

Populations may vary in growth and age and size at maturity as a direct consequence of environmental differences. They may also evolve genetic differences in growth rate and the relationship between growth and maturation that are adaptations to their environment. Environmental and genetic influences can be additive (genetic tendency to grow rapidly in a population whose environment facilitates rapid growth), and in other cases these tendencies are opposite, resulting in diminished phenotypic variation—a process known as countergradient variation (Conover and Schultz 1995).

For example, individuals in a cool environment may grow more slowly than those from a population experiencing warmer water. However, when both groups are raised in a common, warm environment, individuals adapted to the cooler environment may grow faster than those adapted to the warmer environment if they have an inherently greater capacity for growth and are only limited by temperature. Countergradient variation in growth (Conover and Present 1990; Conover et al. 1997; Arendt and Wilson 1999) and other traits including body size and shape (Marcil et al. 2006), developmental rate (Laugen et al. 2003), and coloration (Craig and Foote 2001; Grether et al. 2005) have been reported in many fish species. For example, Craig & Foote (2001) found that kokanee salmon (landlocked sockeye salmon, *Oncorhynchus nerka*) and anadromous sockeye salmon both display similar shades of red in their respective natal environments. However, when they are exposed to low-carotenoid diets under laboratory conditions, kokanee sequester carotenoids to the flesh musculature three times more efficiently than sockeye and thus appear redder in color, indicating a genetic compensation for the more limited carotenoids in lakes compared to marine waters. Examination of such countergradient variation can help to understand variability in life history traits among individuals from different populations, can contribute to effective management of these populations, such as through effective stocking and introduction (Conover and Schultz 1995), and help anticipate their responses to changes in the environment and in selection regimes.

Size and age at maturation are especially well-studied life history traits in salmonid fishes. These species home to natal sites for breeding, resulting in reproductive isolation, complex population structure, and adaptations to the environmental conditions of the natal site (Ricker 1972; Taylor 1991; Wood 1995; Garcia de Leaniz et al. 2007). Life history diversity in salmon populations can both increase productivity and buffer size fluctuations (Greene et al. 2010; Schindler et al. 2010). However, altered selection regimes through fishing (Kendall et al. 2009), artificial propagation (McLean et al. 2005), and environmental change (Holtby 1988; Pyper et al. 1999; Beechie et al. 2006) can affect age and size at maturation of salmonids, with implications for the conservation. For example, reduction of the number of age classes in exploited fish stocks can result in decreased reproductive rates and stock productivity (Hsieh et al. 2006; Venturelli et al. 2009) and hatchery supplementation programs can limit life history diversity expressed in the stocked populations (Ayllon et al. 2006).

In natural salmonid populations, age and size at maturation patterns reflect both environmental and genetic influences. Environmental conditions can affect smolt size (Thorpe 1986; Randall et al. 1987), which in turn influences age and size at maturation (Randall et al. 1986; Thorpe 1987; Hutchings and Jones 1998). Genetic factors also affect age and size at maturity (Ricker 1972; Hard 2004; Carlson and Seamons 2008); offspring age at maturity is often linked to that of their parents (Tipping 1991; Hankin et al. 1993). It can be difficult to determine if both genetic and environmental factors influence population-level life history variation from sampling in the field (Beacham and Murray 1987; Roni and Quinn 1995) because of the interplay between these factors, and thus experiments can yield important insights.

In this study, we examined age and size at smolt transformation and maturation of sockeye salmon in two populations using data collected from fish in the wild and in a controlled laboratory experiment. The populations originated in the Okanagan River of British Columbia, Canada, which has been labeled a stock of special concern, and Redfish Lake, in the Stanley Basin, Idaho, USA, where the stock was listed as endangered in 1991 under the U.S. Endangered Species Act (status of both populations given in Gustafson et al. 1997). These populations spawn in distant parts of the Columbia River system (Fig. 1.1) so have been subjected to different environmental conditions and regimes of selection. In contrast to the healthy populations in the northern end of their range where there are abundant long-term data on life history patterns (e.g., Bristol Bay, Alaska: Quinn et al. 2009), these depleted populations are operating under extreme conditions for the species and data on their life history patterns are sparse. Their critical status is likely to be exacerbated by changing climate conditions (Crozier et al. 2008).

We first collect and summarize historical and recent data on life history transitions (size and age at smolt transformation and maturation) of fish spawning in the wild to understand life history variation between the populations. We then report data on fish from each population that were spawned and reared under controlled laboratory conditions. The laboratory study was designed for another purpose (specifically, to study olfactory imprinting; Dittman et al. 2009) but the data provide a rare opportunity to shed light on the genetic and environmental influences on maturation in these fish. We tested the null hypothesis that age and size at maturation would be similar between the populations in captivity because their juvenile growth rate, smolt size, and post-smolt environment were similar, against two predicted alternative hypotheses: 1) age and size at maturity patterns observed in wild fish would be mirrored in the laboratory due to genetic controls over these traits; or 2) the patterns observed in wild fish would be less divergent, or even reversed, in the laboratory due to environmental influences interacting with genetic control, such as countergradient variation in growth rate and/or maturation. To test these hypotheses, we compared average age and size at the smolt transformation and at maturity between the populations and calculated probabilistic maturation reaction norms (PMRNs) for the experimental fish, giving another perspective on age and size at maturation differences. PMRNs describe the probability of an individual maturing at a given time as a function of age and body size (Heino et al. 2002a). Differences in age and size at maturation between the populations in both wild and captive settings would be consistent with the presence of local adaptations in these populations.

Methods

Study sites

Redfish Lake is at 1996 m elevation and is 1444 km from the Pacific Ocean via the Columbia, Snake, and Salmon rivers (Bjornn et al. 1968; Fig. 1.1). The Okanagan River and Osoyoos Lake, where Okanagan River sockeye salmon spawn and then rear as juveniles, respectively, are at 278 m elevation and are 986 km from the Pacific Ocean via the Columbia River (Burgner 1991; Fig. 1.1). Consistent with the higher elevation, Redfish Lake is cooler, with monthly average lake surface water temperatures ranging from 0.3˚C in February to 17.9˚C in July (1996-2008; Robert Griswold, Biolines Environmental Consulting, unpublished data), compared to 2.2˚C in February to 22.3˚C in July for Osoyoos Lake (2002-2005; Margot Stockwell, Department of Fisheries and Oceans Canada (DFO), unpublished data). At 25-35 m depth, where sockeye salmon are likely to rear, Osoyoos Lake has averaged 7.8˚C across all months from 1971-2000 (Margot Stockwell, DFO, unpublished data) compared to 4.8˚C in Redfish Lake from all months from 1996-2008 (Robert Griswold, Biolines Environmental Consulting, unpublished data).

Review of historical and recent data on life history transitions

Historic and recent data on wild sockeye salmon of the Okanagan River and Redfish Lake populations, including smolt and adult age and size, were compiled from a combination of peer-reviewed literature, agency reports, and personal communications. To collect these data, we searched Web of Science for published data, spoke with scientists and managers studying and working with these fish, and searched agency websites (including Bonneville Power Administration (BPA), Idaho Department of Fish and Game (IDFG), Columbia River Inter-tribal Fisheries Commission (CRITFC), and DFO) to find publications, reports, and unpublished data. Detailed information about the historical and recent data on life history transitions included in this paper is available in Table 1.2.

Currently, Redfish Lake sockeye salmon are intensively managed due to their endangered status. In recent years many Redfish Lake sockeye salmon have been spawned and reared as juveniles in captivity and released into Redfish Lake at various developmental stages. We did not use data from these fish in our analysis, though some of the naturally spawning fish contributing to the datasets may have been their offspring. Though the paucity of data from overlapping years when the fish were abundant and largely wild limited direct annual comparisons of age and size of smolts and adults from the two populations, we analyzed all data available to characterize life history patterns of these two populations as naturally reproducing entities. Specifically, we compared qualitatively or quantitatively, using t-tests or Mann-Whitney-Wilcoxon (MWW) tests (when data were not normally distributed), differences in age and size at smolt and maturation transitions.

Laboratory experiment

Captive sockeye salmon from both populations were reared from embryo to adulthood at the University of Washington's Big Beef Creek research station, which is on a tributary of Hood Canal in western Washington, USA. The project began in fall 2004 with the establishment of the two populations: Okanagan River sockeye salmon were first filial general (F1) offspring of captively reared fish originally obtained from the Colville Tribe's Cassimer Bar Salmon Hatchery and Redfish Lake fish were the 4th generation of fish captively reared in the National Marine Fisheries Service captive broodstock program at Burley Creek, Washington. The Okanagan River sockeye salmon were the offspring of two age 4 females crossed with four age 4 males, and the Redfish Lake fish were the offspring of an age 3 female crossed with two age 3 males. A larger and more diverse set of sires and dams would have been desirable, but the status of populations did not permit it.

Eyed eggs from both populations were transferred to the Big Beef Creek field station in December 2004 and reared in constant 10°C well water throughout their lives. Okanagan River fry (n = 1159) were reared in six different tanks and the Redfish Lake fry (n = 843) were reared in four tanks. All fish were fed the same food. From fry to smolt stage their rations were adjusted after periodic weighing and measuring events to keep all fish at the same length and target mass (~30 g) by June 2006, by which time they were expected to have completed the smolt transformation process. To assess smolting, 50-80 fish were sacrificed and each fish was measured for length and weight and gill samples were collected for later gill ATPase measurements. This process was repeated, approximately every three weeks, a total of seven times between February and June of 2006. Filaments from three gill arches were placed in a solution of sucrose, EDTA, and imidazole according to methods described by Zaugg (1982) and then frozen on dry ice and stored at -80°C. Gill Na+,K+-ATPase activities were measured using the method of McCormick (1993).

In July 2006, after smolt transformation, all fish were fin clipped to identify their tank grouping and transferred to three 4.1 m-diameter circular outdoor freshwater tanks where they were raised communally to maturity on an *ad libitum* diet. On nine dates between March and November of 2007, 8-135 fish from each population were sacrificed, measured for length, weighed, and plasma and gonads were collected to determine maturation (i.e., at age 3; Dittman et al. 2009). Maturation status for females was established by weighing total body weight and gonads of all fish and calculating the gonadosomatic index (GSI) as [gonad weight/body weight] x 100. All female fish with a GSI greater than 0.5 were considered to be maturing. Maturation status for males was established by determining the plasma 11-ketotestosterone concentrations for each fish as described by Larsen et al (2004). Fish from both populations were represented during each sampling. Fewer fish were sampled during the first two dates, in March and May ($n = 64$ of the 2040 fish in the olfaction study), than during the later dates (June through November). On these earliest two dates, the status of maturing fish was clear ($n = 38$) but if a fish had not yet begun the process of maturation it was unclear whether it would or would not have matured later that year. Therefore, these fish were not included in our study. By June it was very evident whether a fish would or would not mature that year, so both immature and maturing fish could be distinguished and were included in our study. The experiment was terminated in November 2007 and it was assumed that all fish that had not matured would have done so the following year, at age 4. This assumption was supported by data from other Redfish Lake sockeye salmon reared in freshwater, under similar conditions and temperatures as those in our study, showing that >99.9% of the fish matured as 3- or 4-year-olds (Redfish Lake sockeye salmon captive broodstock program; Frost et al. 2008).

For our analyses, including the PMRN calculation, it was necessary to use lengths of all experimentally reared smolts and immature/maturing adults at a common date (June 2006 for smolts and November 2007 for adults). To calculate these, we modeled juvenile growth (length averaged for all fish sampled each month) using exponential functions and post-smolt growth (again, length averaged for all fish sampled each month) using logarithmic functions. Except for Okanagan River immature length, all model fits had R^2 values > 0.9 (Fig. 1.2). The length of each individual smolt and immature/maturing adult was then extrapolated to the common date (June for smolts and November for adults) using the regression equations (as follows: smolts in June 2006, Okanagan: y = $y = 101.81e^{0.061x}$, $R^2 = 0.97$; Redfish Lake: y = $y = 102.02e^{0.06x}$, $R^2 = 0.96$. Fish in November 2007, Okanagan maturing: y = $y = 83.2\ln(x) + 258.56$, $R^2 = 0.94$, immature: $y = 43.04\ln(x) + 295.91$, $R^2 = 0.36$; Redfish Lake maturing: y $y = 89.9\ln(x) + 243.93$, $R^2 = 0.92$, immature: y = $y = 89.59\ln(x) + 206.16$, $R^2 = 0.95$; Fig. 2).

We calculated a PMRN midpoint (specifically, the length at which the probability of maturing was 50%; L_{p50}) for immature/maturing fish from each captive population, based on the environmental conditions to which the fish were exposed, to further understand life history divergence. Though less accurate than calculation of full PMRNs based on a wider range of growth trajectories and environmental conditions (Dieckmann and Heino 2007), these midpoints provide a useful index of the relationship between length and maturation probability. We combined data from males and females for each population because maturation status and body size were similar between sexes. The probability of maturing (*m*) increased with fish length (*L*) from 0 (immature) to 1 (mature) in a sigmoid shape, suggesting the use of the logistic function. We estimated the L_{p50} for each population by fitting a logistic regression (glm with a logit link function) with *m*(*L*) as the response and *L* as the predictor. L_{p50} values were calculated by dividing the negative intercept by the slope of the logistic regressions (equations 1 and 2):

(1) $$\text{logit}(m(L)) = \log_e\{m(L)/[1 - m(L)]\} = \beta_0 + \beta_1 * L$$

(2) $$L_{p50} = -\frac{\beta_0}{\beta_1}$$

We used likelihood ratio tests to assess significant differences in maturation thresholds (L_{p50} values) between the two populations. To do this, we calculated the likelihood of maturation, with the same parameters for all fish and with separate parameters for each population, using the logistic likelihood function with a binomial error distribution.

Results

Historical and recent data on life history transitions

Smolt age and size

Most wild Okanagan River sockeye salmon smolts were age 1, presumably because their rearing lake, Osoyoos Lake, is warm, shallow, and eutrophic (data from sources 2, 4, 19, 23, 34, and 35 in Table 1.2). Between 1946 and 1953, 93% of smolts were yearlings, as were 86% of those between 1986 and 1993. Few Okanagan River fish rear in freshwater for two years and almost none migrate to the ocean as sub-yearlings. On the other hand, Redfish Lake sockeye salmon smolts have historically been age 1 or 2, depending on their length at the end of their first year in freshwater. When the average fork length was < 80 mm, < 50% of smolts left the lake as yearlings, whereas when the fork length was ~100 mm, > 90% of smolts left the lake as yearlings (Bjornn et al. 1968). Thus, wild Okanagan River sockeye salmon smolts have tended to be younger than Redfish Lake smolts.

The average length of wild Okanagan River sockeye smolts from 12 years between 1957 and 2005 was 107.8 mm (range of annual means = 86-131 mm, SD = 13.7 mm; data from sources 4, 23, and 34-35 in Table 1.2; Fig. 1.3a) whereas for 22 years between 1956 and 2007 the average length of wild age 1 smolts from Redfish Lake was 97.8 mm (range = 67-117 mm, SD = 14.1 mm; data from sources 3, 20-22, 24-29, and 31-33 in Table 1.2 including Bjornn et al. 1968; Fig. 1.3a; $t = 1.96$, $df = 32$, $P = 0.03$ for a 1-tailed 2-sample t-test of the annual means assuming that Okanagan River fish were larger given their warm and productive rearing lake). Compared to other North American sockeye salmon populations for length at age 1, Okanagan River smolts are in the 93rd percentile and Redfish Lake smolts are in the 84th percentile (Fig. 1.3b).

Age and size at maturation

In most years the majority of wild Okanagan River fish matured two years after their smolt transformation but in some years more fish matured after only one year in the ocean rather than two (Table 1.1; data from sources 1, 4-18, 30 and 36 in Table 1.2 including Fryer 1995). On the other hand, most Redfish Lake sockeye matured after two years at sea and spawned at age 4 or 5, and almost no adults from this population matured after one year in the ocean (Table 1.1; Bjornn et al. 1968). Wild Okanagan River adult sockeye were significantly shorter at maturation than Redfish Lake fish (average length of ocean age 2 Okanagan = 496 mm across 27 years from 1957-2008 (SD = 20 mm) vs. average length of mostly ocean age 2 Redfish Lake = 544 mm across 28 years from 1953-2008 (SD = 33 mm), data from sources 1, 3-18, 30 and 36-37 in Table 1.2 including Bjornn et al. 1968 and Fryer 1995; Fig. 1.4; W = 80, P < 0.0001 for a MWW test).

Laboratory experiment

Smolt age and size

In captivity, all Redfish Lake and Okanagan River sockeye salmon demonstrated a significant increase in gill Na+/K+ ATPase activity during their second spring (2006), indicating that all fish experienced the parr to smolt transformation as yearlings. Specifically, enzyme activity rose from basal levels of 1.98 (Redfish Lake) and 1.89 (Okanagan River) µmoles of ADP/mg protein/hr in February to peak levels of 6.8 and 10.5 µmoles of ADP/mg protein/hr in May 2006 for Redfish Lake and Okanagan River sockeye salmon, respectively. Captively reared smolts from both populations were larger than those seen in the wild, as the rations were designed to produce large, similarly-sized smolts.

No differences in growth rate or mean length of captive fish were found between the two populations at any of the seven sampling events before and through smolt transformation (2- tailed 2-sample Student's t-test when data were normally distributed or MWW tests when they were not, all P > 0.05). Weights were not different between populations at six of the seven sampling events (2- tailed 2-sample Student's t-test or MWW tests, P > 0.05 for six events and 0.009 for one). Tank effects were minimal; very few differences in mean lengths or weights of fish of a given population among tanks were detected during the sampling events. By June 2006, the final sampling event for smolts, all fish in both populations had smolted, both populations averaged 146 mm long, and Redfish Lake smolts were, on average, 1.5 g heavier than Okanagan smolts (35.0 g vs. 33.5 g, respectively).

Age and size at maturation

The age at maturation patterns of captive fish differed from those of wild fish. While 68% of captive Okanagan River sockeye matured one year after smolting (as 3-year-olds), 98% of captive Redfish Lake sockeye salmon matured at this age ($\chi^2 = 71.31$, df = 1, $P < 0.001$ for a Chi-square test comparing age at maturation between the populations). Mature age 3 captive adults from the two populations did not differ significantly in length (Okanagan = 456 mm and Redfish Lake = 460 mm; WMM test due to non-normal distribution of data, W = 32,484, P = 0.42) or weight (Okanagan = 1,135 g and Redfish Lake = 1,163 g; WMM test, W = 31,559, P = 0.18). Most maturing fish from both populations were between 440 and 480 mm long and between 1000 and 1400 g in mass. Calculated L_{p50} values of the PMRNs, 415 mm for Okanagan River fish and 405 mm for Redfish Lake sockeye salmon, were significantly different (Fig. 1.5a and b; likelihood ratio test, D = 9.69, df = 2, P = 0.008).

Discussion

Data collected between 1946 and 2008 showed that wild Okanagan River and Redfish Lake sockeye salmon differed consistently in age and size at smolt transformation and maturation. Wild Redfish Lake smolts are, on average, smaller and smolt more frequently at older ages than Okanagan River sockeye. This is consistent with the colder conditions and lower productivity in the higher elevation Redfish Lake. Okanagan River sockeye salmon adults have matured at younger ages, often after only one year in the ocean, and at smaller sizes than Redfish Lake adults. Maturation of Okanagan River fish as 3-year-olds is consistent with the very large size of their smolts. Similar results have been observed for sockeye salmon in nearby Lake Washington, where smolts are also very large and age 3 adults are also found (Hendry and Quinn 1997). Under controlled laboratory conditions, age and size at smolt transformation and maturation differed considerably from those shown in the wild. All individuals from both populations smolted at age 1 and at similar sizes in captivity. The relationship between faster growth and greater tendency to undergo smolt transformation at a younger age is widely seen in salmonids (e.g., Hutchings and Jones 1998; Quinn et al. 2009) so this result was not unexpected. The accelerated juvenile growth in captivity may have contributed to all individuals reaching a size or growth rate threshold needed to trigger smolt transformation at age 1.

The controlled laboratory rearing also appeared to strongly affect adult maturation; almost all Redfish Lake sockeye salmon matured one year after smolting, as did two-thirds of Okanagan River fish. Thus, favorable environmental conditions in captivity acted on smolt size and overall growth, which contributed to the observed younger age and larger size at maturation in these sockeye salmon populations. Abundant evidence suggests a negative relationship between smolt size and adult age at maturity in wild (e.g., Hyatt and Stockner 1985; Quinn et al. 2009) and hatchery populations (Quinn et al. 2004; Vøllestad et al. 2004). In addition, limited data from the Redfish Lake hatchery program are consistent with this reduction in age at maturity with increased smolt size. In nine of the last 12 years with data, hatchery smolts were between 20 and 50 g in weight and ocean age 1 adults were never recorded. In the three years when hatchery smolts exceeded 50 g (1998, 2006, and 2007), ocean age 1 adults were seen (D. Baker, IDFG, unpublished data). Reproductive benefits (e.g., fecundity) generally increase with fish size, but these benefits must be balanced against the risks of mortality associated with an additional year at sea, so the largest individuals of a cohort generally mature at an earlier age than smaller ones (Quinn et al. 2009 and references therein). Thus it was not surprising, given their large size as smolts, that most captive Okanagan River and Redfish Lake sockeye salmon matured one year after smolt transformation. However, it was at first surprising that a higher percentage of the captive Redfish Lake than Okanagan River fish matured one year after smolting.

Calculated L_{p50} values from the PMRNs indicated that the maturation size threshold of the Redfish Lake sockeye salmon was lower than that of the Okanagan River fish under the experimental conditions. These differences can be interpreted in light of the different environments in which the populations evolved. Juvenile Redfish Lake sockeye salmon rear in a high elevation, cool, and unproductive lake, and are smaller as smolts than the Okanagan River population. In captivity, the larger than normal size at smolt transformation of the Redfish Lake sockeye salmon may have triggered maturation at a younger age than typically occurs in the wild. The size difference between captive and wild smolts was not as great for the Okanagan River population as for the Redfish Lake population, and the increase in proportion of age 3 adults (relative to wild fish) was also not as great for Okanagan River fish as for Redfish Lake fish. These differences in maturation threshold between these two populations, in addition to the differences in age and size at maturation of wild fish, are consistent with the presence of local adaptation in the populations. PMRNs have been helpful in other studies to understand and evaluate adaptive responses and spatial and temporal variation of maturation schedules (e.g., Olsen et al. 2008; Wang et al. 2008; Vainikka et al. 2009). Olsen et al. (2008) found that spatial diversity in maturation schedules, suggested by different PMRNs, corresponded to genetic differences in coastal Atlantic cod (*Gadus morhua*). Wang et al. (2008) used PMRNs to show spatial and temporal variation in adaptive responses in maturation schedules for lake whitefish (*Coregonus clupeaformis*). Finally, Vainikka et al. (2009) evaluated spatial variation in maturation patterns compensating for environmental gradients in Baltic herring (*Clupea harengus membras*) using PMRNs.

Our results were inconsistent with the null hypothesis that age and size at maturation were similar between the two sockeye salmon populations in captivity. They were most consistent with the second alternative hypothesis, that age and size at maturation patterns in the laboratory would be reversed from those seen in the wild. This latter pattern, due to interactions between environmental and genetic influences, may be an example of countergradient variation in Redfish Lake and Okanagan River sockeye salmon maturation size threshold. If maturation thresholds are lower for Redfish Lake than Okanagan River fish, then the similar growth rates in the laboratory would result in higher proportions of Redfish Lake salmon maturing at an early age. In contrast, under the natural conditions (slower growth for the Redfish Lake fish), a lower proportion would mature at an early age. Both variation in maturation rate and threshold under experimental conditions and differences in maturation age and size in wild fish suggest genetic influences on the age and size at maturation patterns.

Factors such as different smolt weights and unequal variances in length and weight of maturing fish between the captive populations may have influenced our results, and the extrapolation used to calculate length of immature and maturing fish on a common date may have increased the uncertainty of the estimation of the PMRN L_{p50} values. Still, our results are consistent with other indications of population-specific variation in life history traits in salmonids (Taylor 1991; Wood 1995). Research on the evolution of life history traits in newly established Chinook salmon (*O. tshawytscha*) populations in New Zealand indicated that populations diverged most strongly in growth rates rather than maturation probability (Kinnison et al. 2010). Thus, the evolution of maturation thresholds as an adaptation to local conditions may occur more slowly than differences in growth. Future work exposing the captive sockeye salmon used in our study to a variety of temperatures and rations, and thus growth rates, would allow for a better understanding of complete PMRNs. This would also enable a better determination of maturation thresholds and genetic differences between the populations.

Life history data from wild Okanagan River and Redfish Lake sockeye salmon are limited due to lack of sampling in many past years and recent scarcity of Redfish Lake sockeye salmon. Hatchery practices, introduction of different stocks, and other factors may have affected life history patterns of these populations over time. The Redfish Lake sockeye salmon population declined to a small number of individuals before the captive rearing program began (Peterson et al. 2008), so the population may be genetically bottlenecked. Thus, a reduced range of life history traits may be expressed in the current population if genes influencing such traits were lost with the population’s decline. Still, salmonid populations can retain significant levels of genetic variation even after declining in abundance (e.g., Neville et al. 2007) and differences in age and size at smolt transformation and maturity between the wild Redfish Lake and Okanagan River sockeye salmon have persisted over time. We believe that the available data are broadly representative of the populations’ patterns, though we recognize the inter-annual variation and effects of multiple factors on these traits.

Ideally, the ancestors of the fish used in our study would have been the same age, come from many different families within a balanced study design, been taken directly from their wild settings and been free of hatchery influence, and been maintained for several generations in a common environment (Conover and Schultz 1995). We cannot rule out a genetic influence on age at maturity stemming from that of the parents of the fish in this study or maternal influences resulting from the parents of these fish being reared at separate locations. Thus, the findings of the laboratory experiment portion of this study could suggest hatchery adaptation rather than supporting the finding of local adaptation. However, the Redfish Lake sockeye salmon captive breeding program has been managed with the specific goal of preventing domestication selection (Kozfkay et al. 2008). While genetic erosion in supportive breeding programs can result from unbalanced sex ratios, inadequate strategies of crossing fish, and decreases in population sizes (Wang and Ryman 2001; Machado-Schiaffino et al. 2007), the Redfish Lake sockeye salmon captive breeding program has specifically sought to develop strategies that minimize domestication selection, inbreeding, and loss of genetic diversity while increasing effective population size (Kozfkay et al. 2008). While this breeding program produces almost exclusively age 3 adults, likely because the warmer water temperature in which the fish are reared (10°C) and the feeding regime allow rapid growth (Frost et al. 2008 and C. McAuley, NOAA Fisheries, Captive Broodstock Programs, personal communication), when the offspring of these fish are released into the wild they have matured mostly as 4- or 5-year-olds (D. Baker, IDFG, unpublished data).

Effective conservation and management requires the identification of biologically relevant units, and thus differences among populations within species (Waples 1991; Neville et al. 2007). But this is just the first step. Life history diversity among populations within a given stock, such as Columbia River sockeye salmon, should be maintained to allow continued productivity and ecosystem services (Greene et al. 2010; Schindler et al. 2010). Selective fishing regimes on mixed stocks can overharvest certain populations, which may result in a loss of some local adaptation (Walters and Martell 2004). Shifts in environmental conditions, such as climate change, are likely to affect smolt size and maturation patterns, potentially strengthening local adaptation or homogenizing populations. Finally, introduction of individuals to a new habitat, supplementation of current populations, or population transplantations will be more successful when life history trait variability is considered. Okanagan River and Redfish Lake sockeye salmon displayed different maturation rates and size thresholds in the lab and differed in age at maturation in the wild. As these populations experience complex combinations of changes in growing conditions at sea, artificial propagation (Dininny 2009), and exposure to fishing, the effects on size and age at maturity may reflect the underlying connections between genetic and environmental controls. The persistence of the populations may depend on the outcome of these interactions.

Table 1.1. Proportion of wild Okanagan River and Redfish Lake sockeye salmon maturing at different ocean ages over time.

		Percent		
Population	**Years**	**Ocean age 1**	**Ocean age 2**	**Ocean age 3**
Okanagan River	1953-1974	0.41	0.59	
Okanagan River	1985-2008	0.17	0.78	0.05
Redfish Lake	1953-1964	0.04	0.88	0.08

Table 1.2. Sources of historical and recent data on Okanagan River (OR) and Redfish Lake (RFL) sockeye salmon life history transitions.

Number	**Author(s)**	**Year**	**Title**	**Source**	**Information contained**
1	Allen, R.L., and T.K. Meekin	1980	Columbia River sockeye salmon study, 1971-1974	Progress report 120, State of Washington Department of Fisheries	OR age and size at maturation
2	Anas, R.E., and J.R. Gauley	1956	Blueback salmon (*Oncorhynchus nerka*) age and length at seaward migration past Bonneville Dam	Special scientific report--fisheries No. 185, U. S. Fish and Wildlife Service	OR smolt age
3	Bjornn, T.C., D.R. Craddock, and D.R. Corley	1968	Migration and survival of Redfish Lake, Idaho, sockeye salmon, *Oncorhynchus nerka*	Transactions of the American Fisheries Society 97: 360-373	RFL smolt age and size; RFL age and size at maturation
4	Chapman, D., C. Peven, A. Giorgi, T. Hillman, F.M. Utter, M. Hill, J. Stevenson, and M. Miller	1995	Status of sockeye salmon in the mid-Columbia region	Don Chapman Consultants, Inc., Boise, ID	OR smolt age and size; OR age and size at maturation
5	Fryer, J.K.	1995	Columbia basin sockeye salmon: causes of their past decline, factors contributing to their present low abundance, and the future outlook	PhD, School of Fisheries, University of Washington, Seattle, WA	OR age and size at maturation

6	Fryer, J.K.	2004	Identification of Columbia Basin sockeye salmon stocks in 2003	Technical report 04-1, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
7	Fryer, J.K.	2005	Identification of Columbia Basin sockeye salmon stocks in 2004	Technical report 05-2, Columbia River Inter-Tribal Fish Commission, Portland, OR.	OR age and size at maturation
8	Fryer, J.K.	2006	Identification of Columbia Basin sockeye salmon stocks in 2005	Technical report 06-4, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
9	Fryer, J.K.	2007	Identification of Columbia Basin sockeye salmon stocks in 2006	Technical report 07-03, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
10	Fryer, J.K.	2008	Use of PIT tags to determine upstream migration timing and survival of Columbia Basin sockeye salmon in 2007	Technical report 08-02, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
11	Fryer, J.K.	2009	Use of PIT tags to determine upstream migratory timing and survival of Columbia Basin sockeye salmon in 2008	Technical report 09-03, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
12	Fryer, J.K., and M. Schwartzberg	1991	Identification of Columbia Basin sockeye salmon stocks based on scale pattern analyses, 1990	Technical report 91-2, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation

13	Fryer, J.K., and M. Schwartzberg	1993	Identification of Columbia Basin sockeye salmon stocks based on scale pattern analyses in 1992	Technical report 93-2, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
14	Fryer, J.K., and M. Schwartzberg	1994	Identification of Columbia Basin sockeye salmon stocks based on scale pattern analyses in 1993	Technical report 94-2, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
15	Fryer, J.K., and D.A. Kelsey	2001	Identification of Columbia Basin sockeye salmon stocks based on scale pattern analyses in 2000	Technical report 01-2, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
16	Fryer, J.K., and D.A. Kelsey	2002	Identification of Columbia Basin sockeye salmon stocks based on scale pattern analyses in 2001	Technical report 02-2, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
17	Fryer, J.K., and D.A. Kelsey	2003	Identification of Columbia Basin sockeye salmon stocks based on scale pattern analyses in 2002	Technical report 03-2, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
18	Fryer, J.K., C.E. Pearson, and M. Schwartzberg	1992	Identification of Columbia Basin sockeye salmon stocks based on scale pattern analyses in 1991	Technical report 92-2, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
19	Gustafson, R.G., T.C. Wainwright, G.A. Winans, F.W. Waknitz, L.T. Parker, and R.S. Waples	1997	Status review of sockeye salmon from Washington and Oregon	NOAA Technical Memorandum NMFS-NWFSC-33, National Oceanic and Atmospheric Administration, Seattle, WA	OR smolt age

20	Hebdon, J., M. Elmer, and P. Kline	2000	Snake River sockeye salmon captive broodstock program research element: annual progress report 1999	Bonneville Power Administration, Portland, OR.	RFL smolt age and size
21	Hebdon, J., J. Castillo, C. Willard, and P. Kline	2003	Snake River sockeye salmon captive broodstock program; research element: annual report 2001	Bonneville Power Administration, Portland, OR	RFL smolt age and size
22	Hebdon, J.L., J. Castillo, and P. Kline	2002	Snake River sockeye salmon captive broodstock program research element: annual progress report 2000	Bonneville Power Administration, Portland, OR	RFL smolt age and size
23	Hyatt, K.D., and D.P. Rankin	1999	A habitat based evaluation of Okanagan sockeye salmon escapement objectives	Research Document 99/191, Fisheries and Oceans Canada, Ottawa	OR smolt age and size
24	Johnson, K.A.	1995	Research and recovery of Snake River sockeye salmon: annual report for April 1993-1994	Bonneville Power Administration, Portland, OR	RFL smolt age and size
25	Johnson, K.A., and J.J. Pravecek	1996	Research and recovery of Snake River sockeye salmon: annual report for April 1994-April 1995	Bonneville Power Administration, Portland, OR	RFL smolt age and size
26	Kline, P., and J.A. Lamansky Jr.	1997	Research and recovery of Snake River sockeye salmon: annual progress report April 1, 1995-April 1, 1996	Bonneville Power Administration, Portland, OR	RFL smolt age and size

27	Peterson, M., B. Moore, K. Plaster, and P. Kline	2007	Snake River sockeye salmon captive broodstock program; research element: annual report 2006	Idaho Department of Fish and Game, Boise, ID	RFL smolt age and size
28	Peterson, M., K. Plaster, L. Redfield, J. Heindel, and P. Kline	2008	Snake River sockeye salmon captive broodstock program; research element: annual report 2007	Idaho Department of Fish and Game, Boise, ID	RFL smolt age and size
29	Plaster, K., M. Peterson, D. Baker, J. Heindel, J. Redding, C. Willard, and P. Kline	2006	Snake River sockeye salmon captive broodstock program; research element: annual report 2005	Idaho Department of Fish and Game, Boise, ID	RFL smolt age and size
30	Schwartzberg, M., and J.K. Fryer	1989	Identification of Columbia Basin sockeye salmon stocks based on scale pattern analyses, 1988	Technical report 89-2, Columbia River Inter-Tribal Fish Commission, Portland, OR	OR age and size at maturation
31	Willard, C., K. Plaster, and J. Castillo	2005	Snake River sockeye salmon captive broodstock program; research element: annual report 2003	Bonneville Power Administration, Portland, OR	RFL smolt age and size
32	Willard, C., J. Hebdon, J. Castillo, J. Gable, and P. Kline	2004	Snake River sockeye salmon captive broodstock program; research element: annual report 2002	Bonneville Power Administration, Portland, OR	RFL smolt age and size
33	Willard, C., M. Peterson, K. Plaster, J. Castillo, D. Baker, J. Heindel, J. Redding, and P. Kline	2006	Snake River sockeye salmon captive broodstock program; research element: annual report 2004	Bonneville Power Administration, Portland, OR	RFL smolt age and size

34	Wright, H., K. Long, D. McQueen, K.D. Hyatt, D.P. Rainkin, N. Audy, L. Weins, M. Walsh, G. Traxler, S. Wolski, S. Lawrence, and R. Benson	2007	Experimental re-introduction of sockeye salmon (*Oncorhynchus nerka*) into Skaha Lake, 2005 brood year report, year 2 of 12	Okanagan Nation Alliance, Westbank, BC	OR smolt age and size
35	Wright, H., K. Long, D. McQueen, K.D. Hyatt, D.P. Rainkin, M. Walsh, G. Traxler, S. Wolski, S. Lawrence, J. Tamblyn, L. Weins, E. Tonasket, and F. Joseph	2006	Experimental re-introduction of sockeye salmon (*Oncorhynchus nerka*) into Skaha Lake, 2005 brood year report, year 1 of 12	Okanagan Nation Alliance, Westbank, BC	OR smolt age and size
36	Fryer, J.K.		unpublished data	Columbia River Inter-Tribal Fish Commission	OR age and size at maturation
37	Baker, D.		unpublished data	Idaho Department of Fish and Game	RFL age and size at maturation

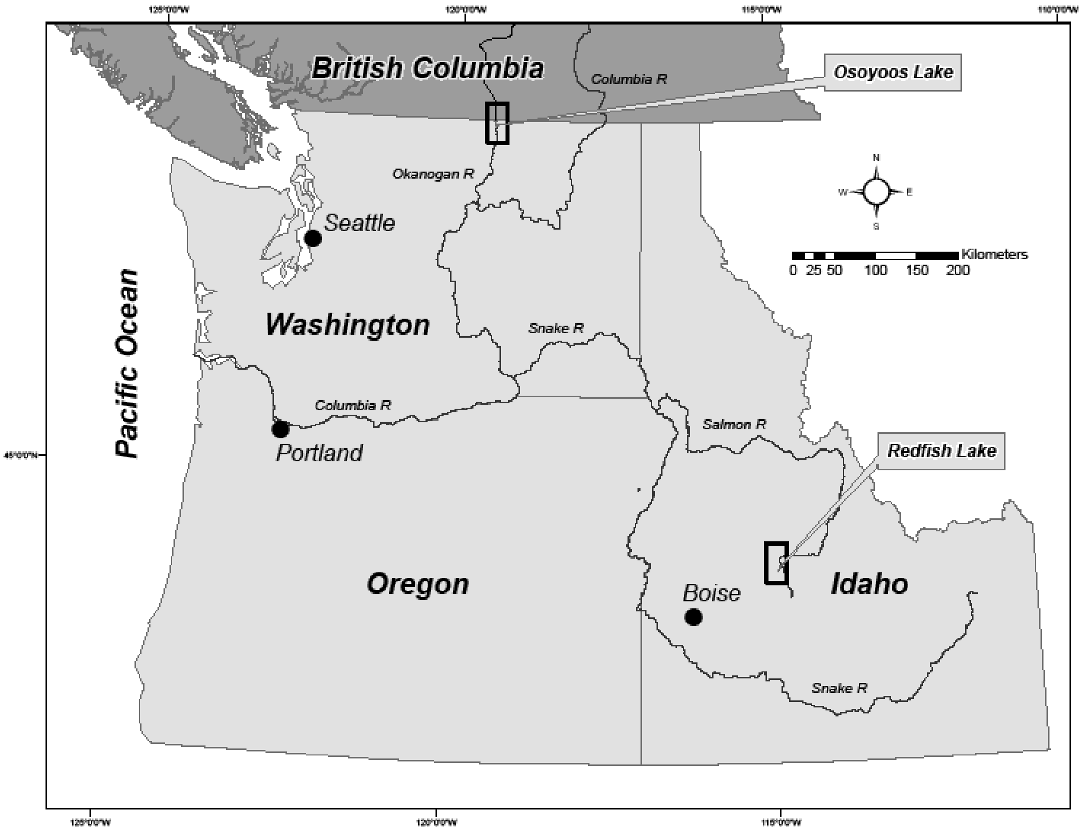


Fig. 1.1. Locations of the spawning and rearing sites of the two sockeye salmon populations under study: Okanagan River and Osoyoos Lake, British Columbia, Canada and Redfish Lake, Idaho, USA.

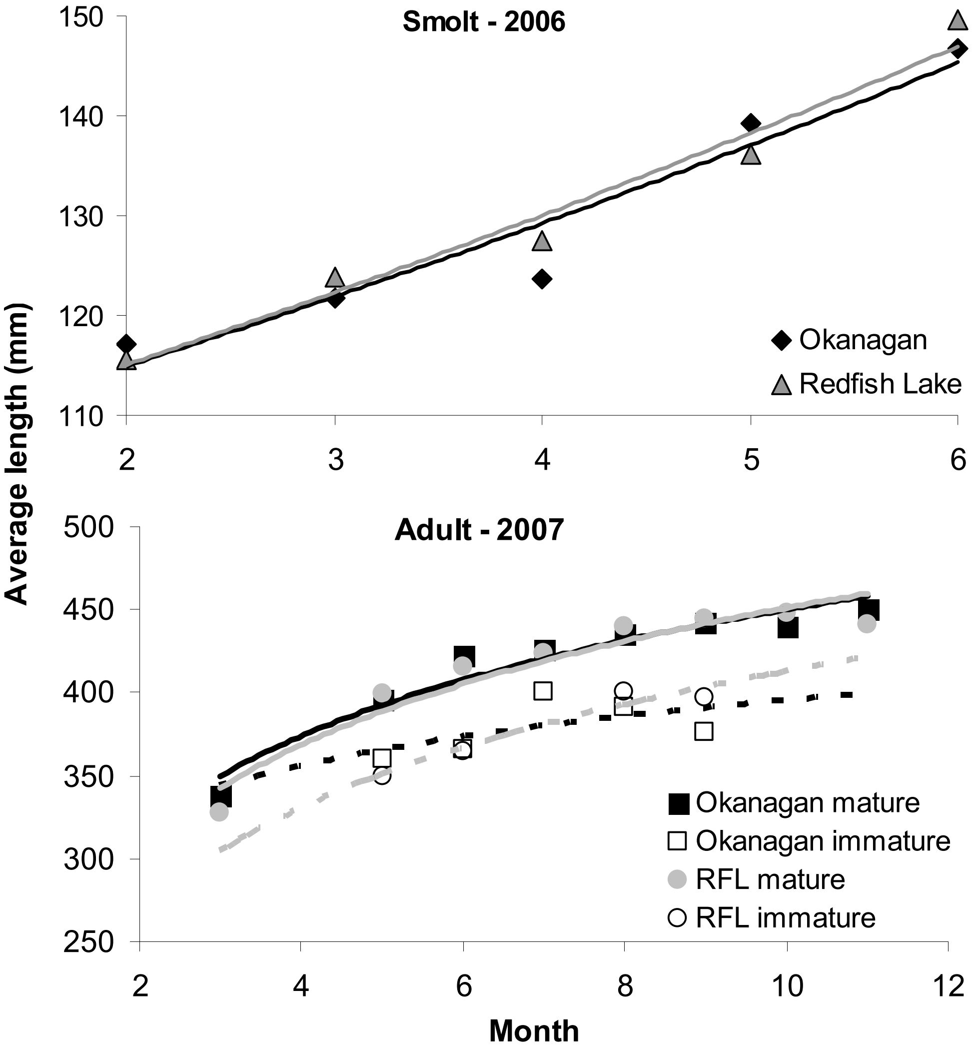


Fig. 1.2. Average length of captively reared Okanagan River and Redfish Lake sockeye salmon sampled between February and June of 2006 (smolts) and between March and November of 2007 (adults). Fitted regression lines (black for Okanagan fish and grey for Redfish Lake) using exponential functions were used to predict length of smolts in June of 2006. For adults, fitted regression lines (black for Okanagan fish and grey for Redfish Lake, solid for mature adults and dashed for immature adults) using logarithmic functions were used to predict length of fish in November of 2007 (see ‘Materials and methods’ for details).

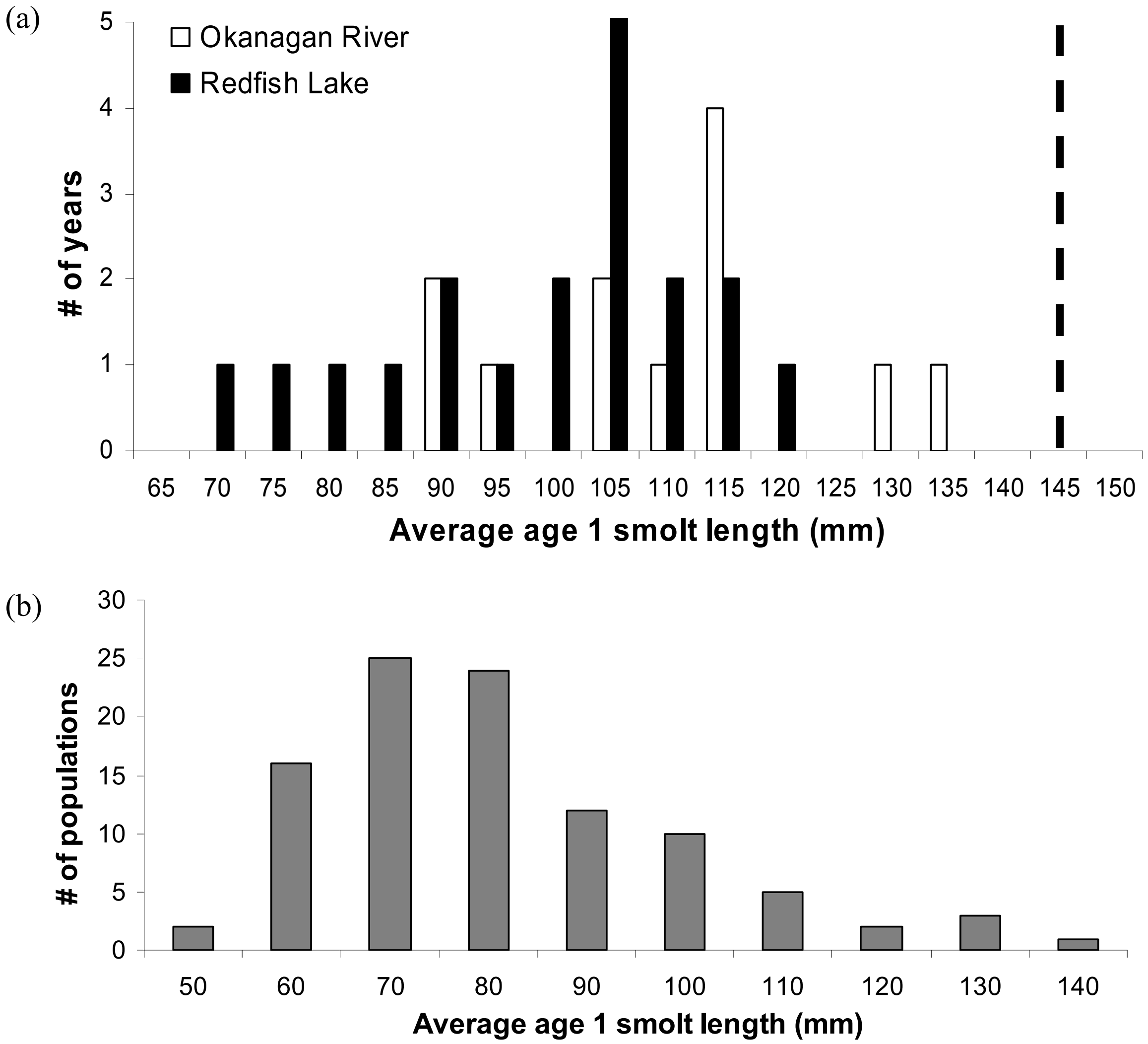


Fig. 1.3. (a) Frequency histogram of average wild sockeye salmon age 1 smolt lengths from Redfish Lake (n = 22 years) and Okanagan River (n=12 years) between 1954 and 2007 (data from sources 2-4, 19-22, 23-29, and 31-35 in Table 1.2 including Bjornn et al. 1968). The dashed line represents the average smolt length observed in the lab (146 mm for both populations). (b) Frequency histogram of average wild sockeye salmon smolt age 1 lengths across their North American range (Okanagan River average length = 97.8 mm, Redfish Lake average length = 107.8 mm, overall mean across populations = 81.3 mm; data compiled by T. Quinn).

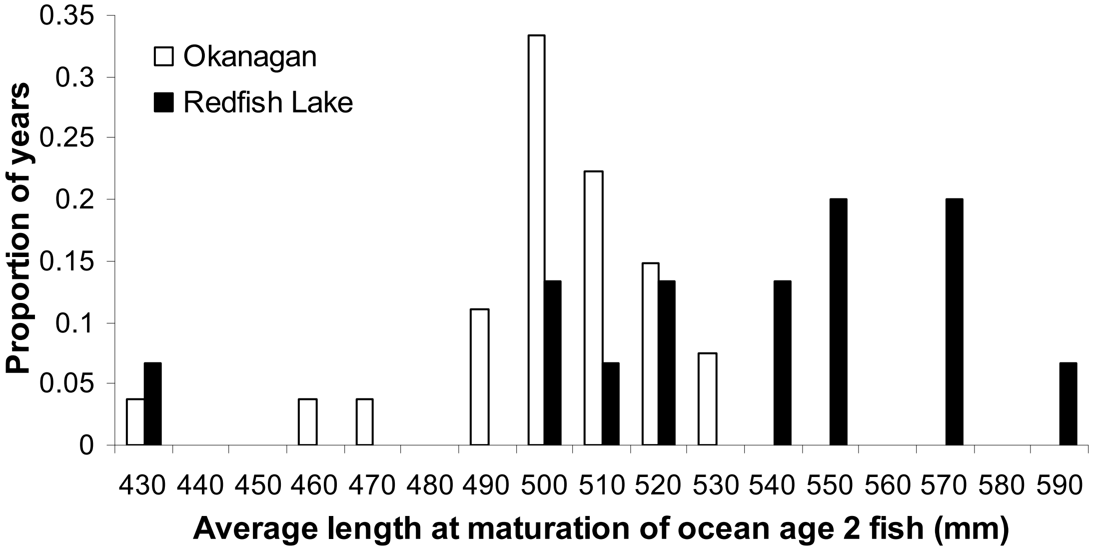


Fig. 1.4. Proportion frequency histogram of individual years' average lengths, between 1953 and 2008, of maturing ocean age 2 wild Okanagan River (n = 27 years) and Redfish Lake (n = 28 years) adult sockeye salmon (data from sources 1, 3-18, 30, and 36-37 in Table 1.2 including Bjornn et al. 1968 and Fryer 1995). Whereas year-specific average length values were available for most years, the lengths of all Redfish Lake fish sampled between 1953 and 1965 were given as one average value (Bjornn et al. 1968); this value is represented by the arrow and was incorporated into the overall average.

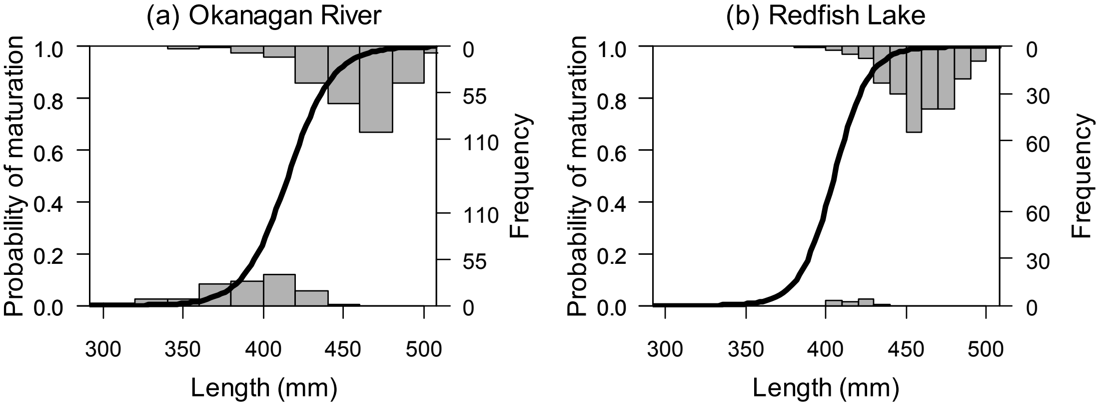


Fig. 1.5. Histogram of lengths of immature (bottom) and maturing (top) captively reared Okanagan River (a) and Redfish Lake (b) sockeye salmon with fitted logistic curves describing the probability of maturation by length. L_{p50} values were calculated as the length at which the probability of maturation is 50%, and are represented by the star on each figure. The grey circle and line represent the average length and standard deviation of wild smolt and ocean age 1 Okanagan River (400 mm, SD = 10.0 mm) and Redfish Lake (451 mm, SD = 12.5 mm) sockeye salmon (data from sources 3, 6-13, 15-18, 30, and 36 in Table 1.2 including Bjornn et al. 1968).

Chapter Two: Length and age trends of Chinook salmon in the Nushagak River, Alaska related to commercial and recreational fishery selection and exploitation

Introduction

Demography, the study of spatial and temporal patterns in the size, structure, and distribution of natural populations, is an important component of life history theory (Stearns 1992). Trends in life history traits, such as age and size at maturation, of exploited fish populations are also important for conservation and management, including anticipating population growth rates and stability. Ricker (1981) discussed the importance of tracking size and age at maturation of exploited stocks over time and suggested that such trends were often correlated with fishery selection. Simply by increasing mortality rates and decreasing population density, fisheries reduce the average age and length of fish in the population (Policansky 1993). Moreover, many commercial fisheries are selective for larger individuals, resulting in ecological (Trippel 1995; Hutchings 2004) and evolutionary (Law 2000; Olsen et al. 2004; Swain et al. 2007; Heino et al. 2008) effects on associated traits. Shifts towards smaller or younger fish have been associated with decreased fecundity (Walsh et al. 2006), lowered reproductive rates (Venturelli et al. 2009), loss of yield (Conover and Munch 2002), increased variability in abundance (Hsieh et al. 2006), and fishery collapses (Olsen et al. 2004). Concerns about mortality rates and size-selectivity of recreational fisheries have increased recently (Cooke and Cowx 2006; Lewin et al. 2006; Arlinghaus et al. 2009).

In general, recreational fisheries are thought to be more benign than commercial fisheries because they catch fewer fish, are less damaging to the environment, overfish fewer populations, and are less selective (Cooke and Cowx 2006; Lewin et al. 2006). However, participation in recreational fishing is widespread, and in some systems recreational fisheries harvest as many or more fish than do commercial fisheries (Coleman et al. 2004; Cooke and Cowx 2006; Lewin et al. 2006). Few studies have compared recreational and commercial harvest and selectivities (Murray-Jones and Steffe

2000; Cooke and Cowx 2006); depending on the patterns of selection, the two fisheries might augment or counter each other's selective effects. Potential impacts of angling on fish populations and their ecosystems have been less extensively researched compared to commercial fisheries (Lewin et al. 2006), and consideration of evolutionary consequences of recreational fishing is rare. However, recreational fishing is usually selective with respect to fish size (mainly attributed to trophy fishing but also caused by regulations), age, sex, or behavioral traits (Lewin et al. 2006) and thus may exert directional selection pressure on adaptive traits (Diana 1983; Nuhfer and Alexander 1994; Arlinghaus et al. 2009; Philipp et al. 2009).

Quantifying fishery selectivity is a first step to understanding its consequences. However, few fisheries have successfully quantified long term selection on heritable traits (but see Sinclair et al. 2002; Carlson et al. 2007b); the required data, including the size or age composition of the fish not being caught (Quinn et al. 2006), are often difficult to obtain. Data from recreational fisheries are rarer than that from commercial fisheries due to the difficulties and costliness of collecting recreational fishery data (Murray-Jones and Steffe 2000; Lewin et al. 2006; Rangel and Erzini 2007).

Because they are anadromous and semelparous, Pacific salmon (*Oncorhynchus* spp.) present especially good opportunities to study possible selective effects of fisheries on life history traits (Kendall et al. 2009; Kendall and Quinn 2009). All salmon migrating into freshwater are maturing adults so they can be counted and life history data (e.g., age, sex, and length) can be collected, facilitating direct comparisons between fish that are caught and those escaping to spawn. For the most part, pink (*O. gorbuscha*), sockeye (*O. nerka*), and chum (*O. keta*) salmon are exploited only as maturing adults on their homeward migration, and recreational fisheries for them are minor in comparison to commercial fisheries. In contrast, Chinook salmon (*O. tshawytscha)* present special challenges because they are exploited in both commercial and recreational fisheries and their duration of marine residence and coastal distribution make some populations vulnerable as both immature and maturing fish. This species achieves a larger size at maturation and is less numerous than other Pacific salmon (Quinn 2005), and is typically the most prized in recreational fisheries and most valuable to commercial fisheries on a *per capita* basis. Analysis of trends in Chinook salmon size and age at maturation is complicated by contributions from hatcheries, harvest of immature fish in different places and at different times, and complex population structure (Ricker 1980). Fortunately, three decades of both catch and escapement data are available for Nushagak River Chinook salmon of Bristol Bay, Alaska, USA (Fig. 2.1), a discrete population of wild fish that are harvested by both commercial and recreational fisheries. The Nushagak River supports the one of the larger runs of wild Chinook salmon in the world (Clark et al. 2006).

We quantified trends in age and size of Nushagak River Chinook salmon, both heritable traits (Carlson and Seamons 2008), and related them to calculated fishery exploitation and selection patterns. Chinook salmon in Bristol Bay have been subjected to an intense commercial gillnet fishery since the late 1800s (Bue 1986; Link et al. 2003; Kendall et al. 2009) and caught in significant numbers by recreational fishers since the late 1970s (Nelson 1987). Alaska Department of Fish and Game (ADFG) manages Bristol Bay salmon fisheries to achieve and maintain sustained production (Clark 2005). Our specific goals were to determine 1) if there has been a decline in body size over time in the Nushagak River Chinook salmon population; 2) whether the decline reflected a change in age and/or length at age at maturation; 3) whether similar patterns were seen in males and females; 4) trends in overall exploitation rate and relative magnitude of the commercial and recreational fisheries; and 5) the size-selectivity of both fisheries. We used these findings to assess whether one or both fisheries might be responsible for the changes in size over time, as opposed to an alternative hypothesis related to some aspect of growth influence by environmental conditions.

Methods

Study site and data collection

Bristol Bay, Alaska supports one of the most abundant and diverse sockeye salmon runs in the world (Hilborn et al. 2003a) and also has significant Chinook salmon populations, the largest of which spawns in the Nushagak River (Fig. 2.1). An economically important commercial gillnet fishery, with temporally variable management, has exerted strong, size-selective fishing pressure on Bristol Bay salmon since the 1890s (Bue 1986; Kendall et al. 2009). Recreational fishing for Nushagak Chinook salmon began in 1963, and the accessibility of the river to floatplanes and boats has contributed to the rapid growth of the fishery, especially since the late 1970s (Nelson 1987). However, most of the land adjacent to ideal fishing locations of the Nushagak River is privately held, which has limited commercial lodges hosting sport fishers to some degree (Jason E. Dye, ADFG, pers. comm.). Fish are also taken for subsistence uses, which are recorded separately from recreationally-caught fish. Nushagak River Chinook salmon runs declined in the late 1980s, leading to the adoption of the Nushagak–Mulchatna Chinook Salmon Management Plan in 1992, which guides recreational harvest to ensure sufficient Chinook salmon spawning in these rivers and sustained yield, especially by subsistence users. Since the mid-1990s, managers have been concerned that Nushagak River Chinook salmon have become younger than in previous years (Brookover III et al. 1997).

Commercial catch and escapement daily count data, along with age, sex, and length (ASL) data on individual fish, have been collected for Nushagak River Chinook salmon by ADFG in most years since 1966. Fish are caught by commercial fishers in the Nushagak Fishing District (Fig. 2.1). Directed commercial Chinook salmon fisheries have been allowed annually since 2002 in early- to mid-June, with minimum gillnet mesh size regulations of 191 mm (7 ½ inches) in effect to target Chinook salmon rather than the smaller-bodied sockeye salmon. In years with concerns about sufficient Chinook salmon escapement through the Nushagak District fishery (1981-1986, 1988-1990, 1993-1995, 1997-2001, and 2008-2009), early season (early June) fishery closures or temporary maximum gillnet mesh sizes of 140 mm (5 ½ inches) have been specified to reduce exploitation of these salmon. At commercial fish processing plants, total catches are estimated and samples are measured for length and weight, scales are collected for age determination, and sex of each fish is recorded. A sonar device enumerates upstream migrating salmon that have escaped the commercial fisheries about 65 km upriver from the mouth of the Nushagak River (Fig. 2.1). Beach seine nets, which collect adult salmon of all sizes, and drift tangle nets are used to sample the escapement for ASL data each day.

Recreational Chinook salmon fishing occurs upstream of the Nushagak District commercial fishery, on the lower Nushagak River and middle Mulchatna River (Fig. 2.1), so fish vulnerable to recreational harvest have escaped the commercial fishery. Recreational fishing regulations between 1980 and 1987 mandated that sport fishers could keep up to five Chinook salmon daily, only two of which could be > 711 mm (28 inches) long. In 1997 regulations were modified to allow one fish between 508 and 711 mm (20-28 inches) and one fish > 711 mm or two fish between 508 and 711 mm on a daily basis and a yearly limit of four Chinook salmon ≥ 508 mm. In 2003 regulations were changed and up to five Chinook salmon < 508 mm (20 inches; these fish are predominantly males that spent only one year at sea, known as jacks) could be retained each day. Recreational harvest count data have been collected annually since 1977, though data on individual fish size and age, reported in creel surveys conducted by ADFG, have been collected in fewer years (1986, 1987, 1991, 1994, 2001, and 2007). Creel surveys have assessed sport fishing effort and harvest, collecting data on counts and individual fish age and length (Minard 1987; Minard and Brookover III 1988; Jason E. Dye, ADFG, unpublished data; Dunaway and Bingham 1992; Dunaway and Fleischman 1995; Cappiello and Dye 2006). Most have been roving surveys conducted in mid-June to mid-July, the peak of the recreational fishing season. No data on size or age of fish caught by the subsistence fishery are available.

Length and age characterization

ASL data were used to characterize annual age, length, and length at age of Nushagak River Chinook salmon commercial fishery catch and escapement, treating males and female separately. Over 99% of Nushagak River Chinook salmon spend one year in freshwater before migrating to the ocean so fish were categorized by their ocean age, which largely determines their overall size (Quinn 2005) and thus vulnerability to gillnets. Because fish of different ages, sizes, and sexes may enter the fishery and escape upriver at different times, and fish abundance varies greatly throughout the season, it would be imprecise to average length and age data on a seasonal basis to characterize the catch and escapement. Thus, daily ASL data were used to estimate the distribution and abundance of Chinook salmon sizes and ages. On days when ASL data were not collected, fish lengths were estimated by interpolation from adjacent days with data. To calculate the total number of fish being caught by commercial gear or escaping of a given age, we multiplied the total catch or escapement by the proportion of fish of a given age group on a daily basis. This analysis assumes that fish of all sizes and age groups have, on average, equal contact with the fishery (i.e., opportunity to get caught) in a given year, and that differential fishing mortality is due to the effects of the gillnet fishery rather than some other attribute, such as migration route.

Annual creel surveys (Minard 1987; Minard and Brookover III 1988; Jason E. Dye, ADFG, unpublished data; Dunaway and Bingham 1992; Dunaway and Fleischman 1995; Cappiello and Dye 2006) reported the total number of fish sampled by age and sex and the average length for each category and its standard deviation. To characterize the length distribution of recreationally-caught fish for a given year, we assumed a normal distribution of fish of a given sex and ocean age described by the mean length and standard deviation given in the creel surveys. This was justified as commercially-caught Chinook salmon, whose lengths are well described by catch and escapement ASL data, also have a normal distribution of lengths by sex and ocean age. Based on this distribution and the total number of fish caught by the recreational fishery, we calculated the number of fish per 10 mm length bin. We subtracted this estimated number of recreationally-caught Chinook salmon, by length bin, from the commercial escapement, resulting in the number and length distribution of the recreational fishery escapement for a given year. The mean length of the recreational fishery escapement was then estimated from this distribution for calculation of selection metrics.

Analyses

We quantified the average age, length, and length at age at maturation of Nushagak River Chinook salmon in the total run (pre-fisheries) in all years with available ASL data and catch and escapement counts for both the commercial and recreational fisheries, including 1981-1983, 1985-1999, and 2001-2009. Data on fish length at various ocean ages were absent for some years. Age and length at maturation could be affected by different selective processes and have different effects on population structure and sustainability. Specifically, we plotted, for males and females separately, the average annual ocean age of all fish (i.e., the total run, pre-fishing), the proportion of fish of each ocean age, the average length of all fish, and the average length at the most common ocean ages (2, 3, and 4). We also estimated the proportion of fish of each sex (*s*) in a given cohort (*c*) that are mature at each ocean age (*a*) to understand changes in maturation at age of the Nushagak River Chinook salmon. Based on the total number of fish of each age in a given cohort returning to spawn ($N_{s,a,c}$), we extrapolated the number of fish that would have been alive at ocean ages 2 through 4 ($B_{s,a,c}$) as:

$$B_{s,a,c} = N_{s,a,c} * \frac{B_{s,a+1,c}}{m_a} , \tag{1}$$

where *m* is a survival rate for fish of different ages (0.7, 0.8, and 0.9 for survival between ages 2 and 3, 3 and 4, and 4 and 5, respectively; Ricker 1976). For ocean age 5 fish (the oldest age group observed), $B_{s,5,c} = N_{s,5,c}$. Then the proportion of fish that were mature at each age, by sex and cohort ($M_{s,a,c}$), was estimated as:

$$M_{s,a,c} = \frac{N_{s,a,c}}{B_{s,a,c}} . \tag{2}$$

For a given cohort of fish, this value would increase for each ocean age group as more fish mature and be 1 for ocean age 5 fish.

Next we plotted the total counts of Chinook salmon returning to the Nushagak River annually since 1966 and the proportion of these fish that were caught by the commercial fishery, caught by the recreational fishery, and that escaped both fisheries since 1977. We then calculated the annual exploitation ratio (total proportion caught) for fish of each sex and age group and for each fishery (*f*; commercial and recreational) on a yearly (*y*) basis ($P_{s,a,f,y}$; Equation 3).

(3) $$P_{s,a,f,y} = \frac{C_{s,a,f,y}}{C_{s,a,f,y} + E_{s,a,f,y}},$$

where $C_{s,a,f,y}$ is the number of fish caught and $E_{s,a,f,y}$ is the number of fish that escape the fishery so are not caught. We also estimated the proportion caught by each fishery (commercial and recreational) in each year.

In addition, we calculated yearly length-based selection differentials ($SD_{s,f,y}$) and standardized selection differentials ($SSD_{s,f,y}$) for each sex and fishery, all ages combined (Equations 4 and 5). While fishery selection by the commercial fishery could be estimated most years between 1981 and 2009, data to calculate selection metrics for the recreational fishery were only available in 1986, 1987, 1991, 1994, 2001, and 2007. We first calculated the mean length of fish in the total run (pre-fishery) in a given season for each sex of fish and fishery ($\overline{L}_{R_{s,f,y}}$). Second, we calculated the mean length of fish of each sex that escaped the fishery and thus had a chance to go on and spawn in that season ($\overline{L}_{E_{s,f,y}}$). The selection differential is the difference in mean length of fish in the pre-fishery run and fish in the escapement (Law and Rowell 1993). Thus, selection differentials represent the overall difference in the average length of the population before and after a potentially selective event (i.e., fishery harvest).

(4) $$SD_{s,f,y} = \overline{L}_{E_{s,f,y}} - \overline{L}_{R_{s,f,y}}$$

To standardize the selection differential, the calculated difference is divided by the standard deviation of length of fish in the run (S_{R_y}), which allows comparison among years and also facilitates comparison with other studies.

(5) $$SSD_{s,f,y} = \frac{\overline{L}_{E_{s,f,y}} - \overline{L}_{R_{s,f,y}}}{S_{R_{s,f,y}}}$$

SDs and SSDs were calculated separately for the commercial and the recreational fisheries. We also calculated average annual combined commercial and recreational fisheries' SD and SSD by adding together the mean of all available annual SDs and SSDs from each fishery. Because SDs and SSDs measure the net effect of each year's fishery on that cohort, they implicitly incorporate inter- and intra-annual variability in fishery management regulations and run sizes. In fact, such effects shape the SDs and SSDs (Kendall et al. 2009). This allows comparisons among years of selection resulting from such regulations and changes in abundance. Thus, SDs and SSDs do not need to be weighted by the number of individuals in the total run or escapement, as this information is implicitly integrated into the calculation.

Finally, we related the trends in age and size of the Nushagak River Chinook salmon between 1981 and 2009 with the patterns of fishery exploitation and selection to see if they were correlated. Because age and size at maturation in Chinook salmon are heritable traits (Carlson and Seamons 2008), consistent, directional selection by a fishery can contribute to trends in age and size at maturation over time as described by the Breeder's equation (response equals heritability multiplied by selection; Falconer and Mackay 1996).

Results

The average length of both female and male Chinook salmon returning to spawn in the Nushagak River decreased significantly between 1981 and 2009 (Fig. 2.2a and b; t-tests: females: $F = 34.2$, $df = 25$, $P < 0.001$; males: $F = 12.7$, $df = 25$, $P = 0.001$). These patterns were driven by significant changes in age composition and length of maturing fish at various ocean ages. The average ocean age of both sexes of Chinook salmon has also decreased significantly over time (Fig. 2.2c and d; t-tests: females: $F = 22.7$, $df = 24$, $P < 0.001$; males: $F = 17.7$, $df = 24$, $P < 0.001$). These trends were driven primarily by the significant decrease over time in the proportion of ocean age 4 fish and increase in ocean age 2 fish in the total run (Fig. 2.3a and b; t-tests: $P \leq 0.005$ for ocean ages 2 and 4, $P > 0.05$ for age 3 for both sexes). Additionally, despite the high allowance for ocean age 1 fish (jacks) by the recreational fishery, these fish were rarely caught. For fish of both sexes, ocean age 2 fish did not change significantly in length over time, but ocean age 3 and 4 fish became shorter between 1981 and 2009 (Fig. 2.3c and d; t-tests: females: ocean age 3: $F = 10.8$, $df = 24$, $P = 0.003$, ocean age 4: $F = 8.0$, $df = 25$, $P = 0.009$; males: ocean age 3: $F = 4.2$, $df = 24$, $P = 0.05$, ocean age 4: $F = 24.1$, $df = 25$, $P < 0.001$). Thus, Nushagak River Chinook salmon of both sexes decreased in length, age, and length at most ages between 1981 and 2009. Finally, for both male and female fish, the proportion of fish mature at each ocean ages increased over time, though most were not significant at the 0.05 level (Fig. 2.3e and f; linear regression: ocean age 4 females: F = 4.916, df = 15, P = 0.04).

Between 1966, when Nushagak River Chinook salmon harvests were first recorded, and 2009, the average total run size was 162,520 fish. The run has fluctuated greatly, from a low of just over 75,000 fish in 1973 and a high of 356,190 in 1982 (Fig. 2.4a). Since 1977, when data on recreational harvests became available, the proportions of the total run composed of commercially-caught fish, recreationally-caught fish, subsistence harvest, and fish that have escaped to spawn have also varied greatly over time, though the commercial catch has typically exceeded either of the other fisheries (Fig. 2.4b). On average, 35% of the total run has been caught by the commercial fishery, 4% by the recreational fishery, 8% by subsistence users, and 53% has escaped to spawn. We also examined the proportions of the fish available to the commercial, recreational, and subsistence fisheries that were caught each year (Fig. 2.5). On average, 35% of the Chinook salmon returning to the Nushagak River have been caught by the commercial fishery annually, and of the fish that escape the commercial fishery 7% and 15% have been caught in the recreational and subsistence fisheries, respectively. Except in one year (1990) the commercial catch has always had a higher exploitation rate than the recreational fishery, though exploitation rates have been similar in some recent years when commercial fishing decreased and recreational fishing increased.

SDs (Fig. 2.6) and SSDs showed similar patterns as they are derived from the same values; SDs show the actual length difference between the total run and escaped fish and SSDs are standardized so are unitless. The commercial fishery SDs and SSDs varied greatly in direction and magnitude and in a given year often differed between males and females. Between 1981 and 2009, the average female Chinook salmon commercial fishery SSD was 0.06 (standard deviation = 0.22; average SD = 6.6 mm and standard deviation = 25.1 mm) compared to 0.01 for males (standard deviation = 0.24;

average SD = 3.1 mm and standard deviation = 35.8 mm). Thus the fishery has taken smaller than average Chinook salmon and larger fish have escaped. On the other hand, the annual recreational fishery SDs and SSDs have been consistently negative and smaller in magnitude than those of the commercial fishery. The average recreational fishery SSDs from the five years when length-specific data were available were -0.09 for females (standard deviation = 0.05; average SD = -8.6 mm and standard deviation = 5.7 mm) and -0.03 mm for males (standard deviation = 0.01; average SD = -3.6 mm and standard deviation = 1.4 mm), indicating that sport fishers caught and retained larger than average fish, especially females. The commercial and recreational fisheries thus exerted opposite size selection pressures. Because the commercial fishery selection varied between catching larger and smaller than average Chinook salmon, whereas the recreational fishery consistently harvested larger than average fish, the average recreational fishery SDs and SSDs were greater in magnitude than those of the commercial fishery. Both fisheries exhibited stronger size selection averaged across all years, though not necessarily in every year, on females than on males.

Discussion

In this paper we have successfully quantified long term trends in age and size at maturation of Nushagak River, Bristol Bay, Alaska Chinook salmon. We showed that both female and male fish have become younger and shorter between 1981 and 2009. This pattern has been driven by significant decreases in the number of older, and thus larger, fish and declines in the lengths of ocean age 3 and 4 fish of both sexes. The proportion of fish mature at ocean ages 2, 3, and 4 increased significantly during the period of record, suggesting that Nushagak River Chinook salmon chose to return at younger ages. Specifically, most fish in the more recent cohorts were mature by ocean age 4, whereas in earlier cohorts this was the case by the time the fish reached the ocean age of 5. Direct comparisons of recreational and commercial fishery exploitation and selection are rare, but we have presented over 30 years of exploitation data from both fisheries on these Chinook salmon and over 20 years of commercial fishery and five years of recreational fishery size selection results. While the run size of Nushagak River

Chinook salmon and the proportion of the run harvested by each fishery fisheries have varied between 1977 and 2009, the commercial fishery has consistently taken a higher proportion (average harvest rate of 35%) than the recreational or subsistence fisheries (average harvest rate of 7% and 15%, respectively). Also, though the selective nature of the commercial fishery has varied greatly over time, with larger and smaller fish being harvested in greater numbers in different years, the recreational fishery has consistently caught larger than average fish between 1981 and 2009. Both fisheries, averaged over time, have been more selective on females than on males. Data on the size and age composition of Nushagak River Chinook salmon captured by subsistence users are not available so fishery selection cannot be directly calculated. While there are no mesh size or net type regulations for Nushagak River Chinook salmon subsistence fishing gear, most people are likely to use “King gillnets” with 19 cm (7.5 inches) or larger mesh (Tim Sands, ADFG, pers. comm.). These gillnets, and thus the Nushagak River subsistence fishery, are likely to catch larger than average Chinook salmon.

The declining length and age trends of Nushagak River Chinook salmon have a number of possible causes but prominent among them are evolutionary trends driven by selective fisheries and changes in growing conditions. While selectivity by the commercial fishery was not correlated with the trends in age and size of Nushagak River Chinook salmon over time, fishery selection by the recreational fishery was. Females of all ages have shrunk an average of 3.1 mm per year between 1981 and 2009 and males an average of 2.6 mm. The combined average annual SDs for the Nushagak River commercial and recreational fisheries between 1981 and 2009 have been -2.0 mm for female fish and -0.5 mm for males (SSDs: females = -0.03, males = -0.02). It is unlikely that this magnitude of size selection alone could have caused the observed changes in overall length, length at age, and age composition of Nushagak River Chinook salmon. Potential harvest of larger, and thus older, than average Chinook salmon by the subsistence fishery may have contributed. Other factors, including ocean and freshwater conditions (Pyper and Peterman 1999; Wells et al. 2007; Wells et al. 2008), harvest in the ocean while immature (Hard et al. 2008), potential interceptions by the walleye pollock, *Theragra chalcogramma*, fishery (NPFMC 2009), competition with hatchery-released salmon (Cooney and Brodeur 1998; Ruggerone et al. 2003; Ruggerone et al. 2010), and changes in abundances of subpopulation that differ in maturation metrics can also be assessed for possible contributions to the observed trait changes.

First, recent environmental conditions in the ocean, including warming patterns (Grebmeier et al. 2006), climate indices, winds, sea level height, upwelling, and downwelling, can result in earlier maturation of Chinook salmon, as were seen for Nushagak River fish, along with larger bodied fish, which were not seen (Wells et al. 2007; Wells et al. 2008). Additionally, warming of the freshwater environment could result in larger smolts, reducing the duration of marine residence (Vollestad et al. 2004; Quinn et al. 2009) and changing the shape of the recruitment curve through compensatory mechanisms. However, this effect would not necessarily explain the reduction in size at age at maturation. Second, many populations of Chinook salmon are vulnerable to capture as immature fish in coastal waters from California north to southeast Alaska. These interceptions typically have the effect of reducing the population’s age at maturation (Hard et al. 2008). There are no specific data on interceptions of immature Nushagak River Chinook salmon but marine recreational fishing is negligible, as is commercial fishing other than in the terminal areas when the fish return as maturing adults. Interceptions of Chinook salmon as by-catch in fisheries for other non-salmonid fishes, such as pollock, are difficult to estimate, so it is challenging to determine to what extent this could affect age and size composition (NPFMC 2009). The hypothesis that competition with conspecifics or salmonids in general has reduced Nushagak River Chinook salmon size at age is plausible, as such effects have been reported for sockeye salmon (Ruggerone and Nielsen 2004; Ruggerone et al. 2005; Ruggerone et al. 2010). However, reduction in growth would be expected to result in a compensatory increase in age at maturation rather than a decrease, as was observed. Finally, consistent changes in abundances of subpopulations of Nushagak River Chinook salmon that differ in age and size at maturation could also contribute to the observed patterns. Genetic and other analyses to understand Nushagak River Chinook salmon subpopulation dynamics could contribute to our understanding of this mechanism. Our findings can be extrapolated to other salmon populations where fish have become shorter and younger over time, including those discussed by Ricker (1995). In general, it is necessary to consider both anthropogenic and environmental influences on trait shifts over time.

In summary, the observed patterns of reduction in length, age, and length at age at maturation for Nushagak River Chinook salmon are not entirely explainable by commercial and recreational fishery selection. Though the commercial fishery can be highly selective in a given year, overall it spares the larger and thus older fish, which are valuable in natural populations (Birkeland and Dayton 2005; Law 2007; Hsieh et al. 2010) due to their higher reproductive potential through greater fecundity and larger eggs (Beacham and Murray 1993; Quinn 2005), and ability to dig deeper redds (Steen and Quinn 1999). Though other factors related to growing conditions are important, there may still be some concern related to the selective nature of the recreational fishery and potentially the subsistence fishery. The overall magnitude of the difference in size between the recreationally-caught and escaped fish has not been great, but older and larger fish have consistently been harvested. Maturation at a different age, length, or length at age would require a change in the reaction norm between growth and probability of maturation that controls variation in age and size (Stearns and Koella 1986; Kuparinen and Merilä 2007; Quinn et al. 2009). Maturation reaction norms between length at maturation and age at maturation (as in Figures 5 and 6 of Stearns and Koella 1986) can be steeper or flatter and may indicate a population's strategy to avoid exploitation. Age-structured salmonids, such as Chinook salmon, are thought to have relatively flat length-age maturation reaction norms, leading to the prediction that size-selective fishing might favor faster growth and younger and smaller adults (Hard et al. 2008), which we found for Nushagak River Chinook salmon. Thus, regulations that decreased the allowable size and/or the number of large harvestable fish may decrease the size-selectivity of the Nushagak River recreational and subsistence fisheries and potential contributions towards shifts towards smaller and younger Chinook salmon. A stochastic individual-based model of selective fishing of Yukon River, Alaska Chinook salmon

(Bromaghin et al. 2008) concurred with this suggestion. The authors found that management strategies to reverse effects of selective exploitation are more effective when both exploitation rates and selectivity for large individuals are reduced concurrently.

Factors that may confound our results include delayed mortality of fish due to disentanglement from gillnets in the commercial fishery and catch and release mortality by the recreational fishery. Gillnet disentanglement mortality was greater for smaller than average sockeye salmon (positive selection differentials; Baker et al. 2011). If gillnet disentanglement mortality also affects smaller than average Chinook salmon, it may act in a synergistic way with the commercial fishery mortality; larger than average fish may be more likely to survive the fishery. Hooking mortality for Chinook salmon examined in two rivers averaged 7.6% (Kenai River, Alaska; Bendock and Alexandersdottir 1993) and 12.2% (Wilamette River, Oregon; Lindsay et al. 2004). This mortality was most strongly dependent on the hook location but fish length was also a significant factor. Specifically, hooking mortality for Kenai River, Alaska Chinook salmon was highest for small males and lower for large males and females of all lengths (Bendock and Alexandersdottir 1993). This suggests that hooking mortality may amplify mortality on smaller Nushagak River Chinook salmon. Given that the Nushagak River recreational fishery catches larger than average Chinook salmon overall, hooking mortality may counteract this selection somewhat.

Nushagak River Chinook salmon fishery selection patterns are expected to be related to annual variation in total run sizes, gillnet mesh size regulations, and the average length of fish in the total run, which was shown for Nushagak District sockeye salmon (Kendall et al. 2009). For example, the recreational fishery has likely been more consistently size-selective than the commercial fishery because of gear regulations. Specifically, commercial fishery regulations stipulating maximum gillnet mesh sizes or closing the fishery in early June during the peak of Chinook migration through the Nushagak Bay prevented the capture of large Chinook salmon in most years. In addition, and the predominance of sockeye salmon, rather than Chinook salmon, in Bristol Bay has likely contributed to different patterns of selectivity by the commercial and recreational fisheries. Sockeye salmon outnumber Chinook salmon in the Nushagak Fishing District, where the catch ratio in the commercial fisheries averaged 43:1 from 1980-2009. While Chinook salmon are generally more valuable than sockeye salmon, fishers profit overall by harvesting more sockeye salmon, and thus they will often use smaller mesh sizes that target them rather than use larger mesh to catch the Chinook salmon because they would then catch fewer sockeye salmon. Thus the much greater size of the sockeye salmon population may reduce the harvest of large Nushagak River Chinook salmon.

Our findings both concur with and contradict stereotypes about the selective nature of commercial vs. recreational fisheries (Cooke and Cowx 2006; Lewin et al. 2006) and the few comparative studies available. For the most part the recreational Nushagak River Chinook salmon fishery harvests many fewer fish than its commercial counterpart, which has also been demonstrated for other recreational fisheries (Murray-Jones and Steffe 2000; Rangel and Erzini 2007). Additionally, in a given year the Nushagak River Chinook salmon commercial fishery is typically more selective than the recreational fishery, but averaged over time the recreational fishery was more selective due its more consistent selection for larger fish. In comparison, Murray-Jones and Steffe (2000) reported that in the Australian surf clam fishery, commercial fishers and recreational fishers who collected clams for bait were similarly size-selective, whereas the recreational food collectors were less size-selective than the other two fisheries.

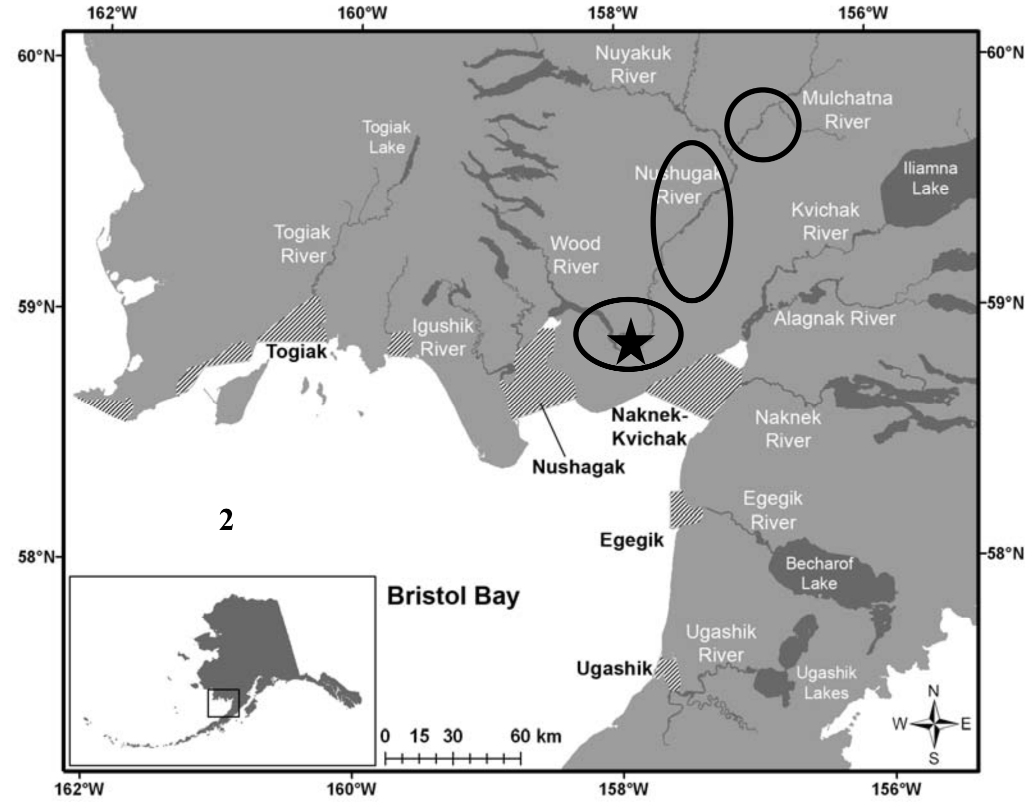


Fig. 2.1. Map of Bristol Bay, Alaska, including the Nushagak Fishing District and the Nushagak River. The hatching indicates where the commercial fisheries occur, the star indicates where the commercial fishery escapement is measured, and primary recreational fishery locations are circled.

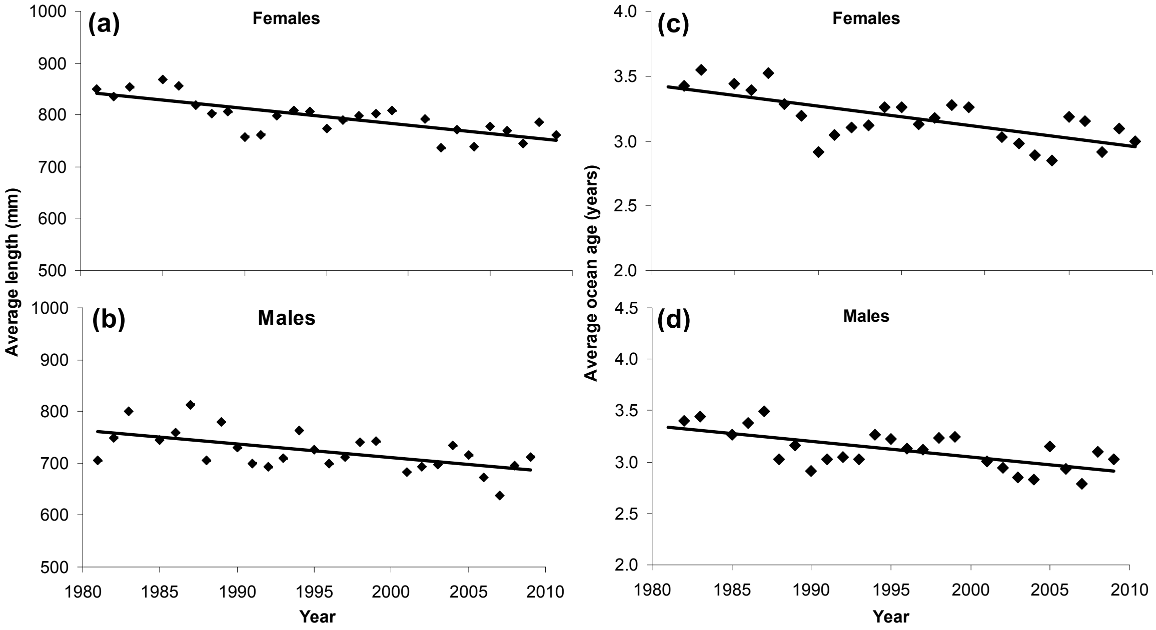


Fig. 2.2. The annual mean length (a and b) and ocean age (c and d), in years, of female and male Chinook salmon returning to the Nushagak River of Bristol Bay, Alaska annually between 1981 and 2009.

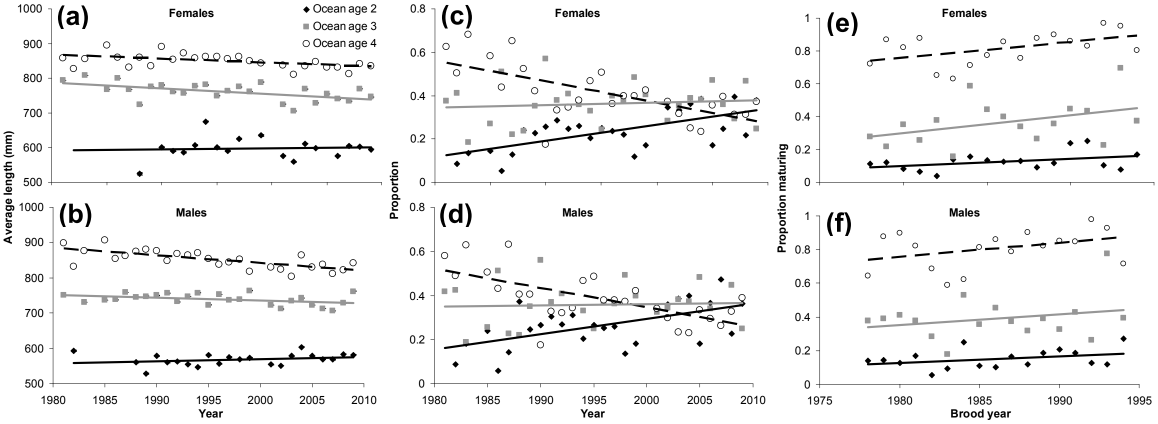


Fig. 2.3. The annual mean length (a and b) and proportion (c and d; in mm) of female and male Chinook salmon of ocean ages 2 (black diamonds with solid trendline), 3 (grey squares with grey trendline), and 4 (open circles with dashed black trendline) returning to the Nushagak River of Bristol Bay, Alaska annually between 1981 and 2009. Also included (e and f) are the proportion of male and female fish, by brood year (1978-1994), mature at ocean ages 2, 3, and 4.

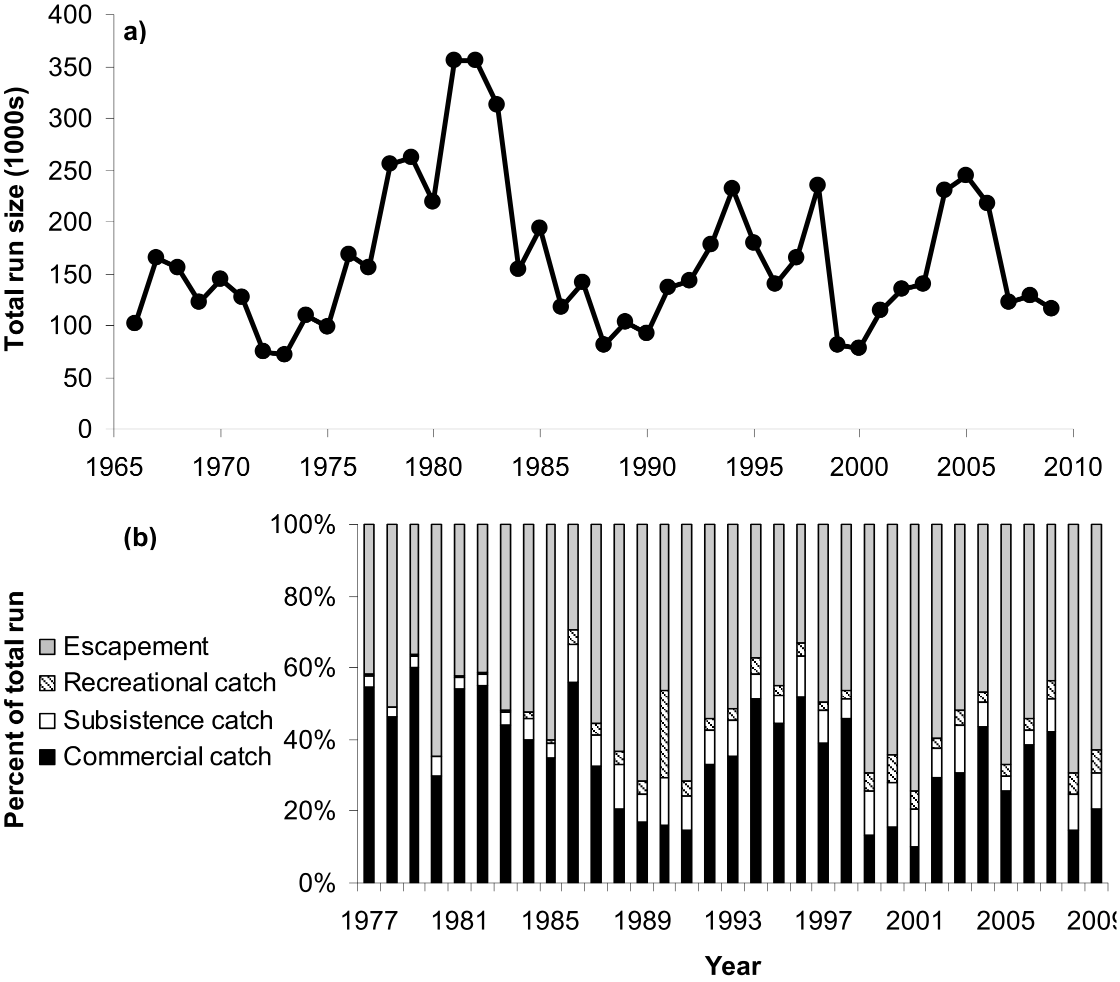


Fig. 2.4. (a) The total number of Chinook salmon returning to the Nushagak River of Bristol Bay, Alaska between 1966 and 2009. (b) The proportion of all Nushagak River Chinook salmon that are captured by the commercial fishery (black), subsistence fishers (white), or recreational fishers (hatched) or that escape to spawn (grey) between 1977 and 2009.

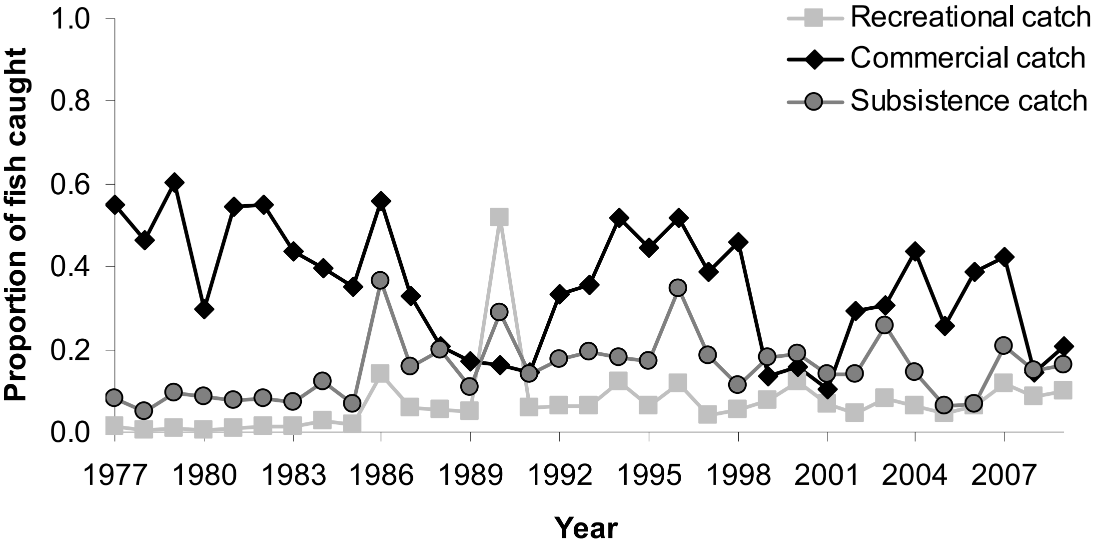


Fig. 2.5. The proportion of all Nushagak River Chinook salmon that encountered the commercial fishery (black diamonds), recreational fishery (grey squares), and subsistence fishery (darker grey circles) and were caught annually between 1977 and 2009.

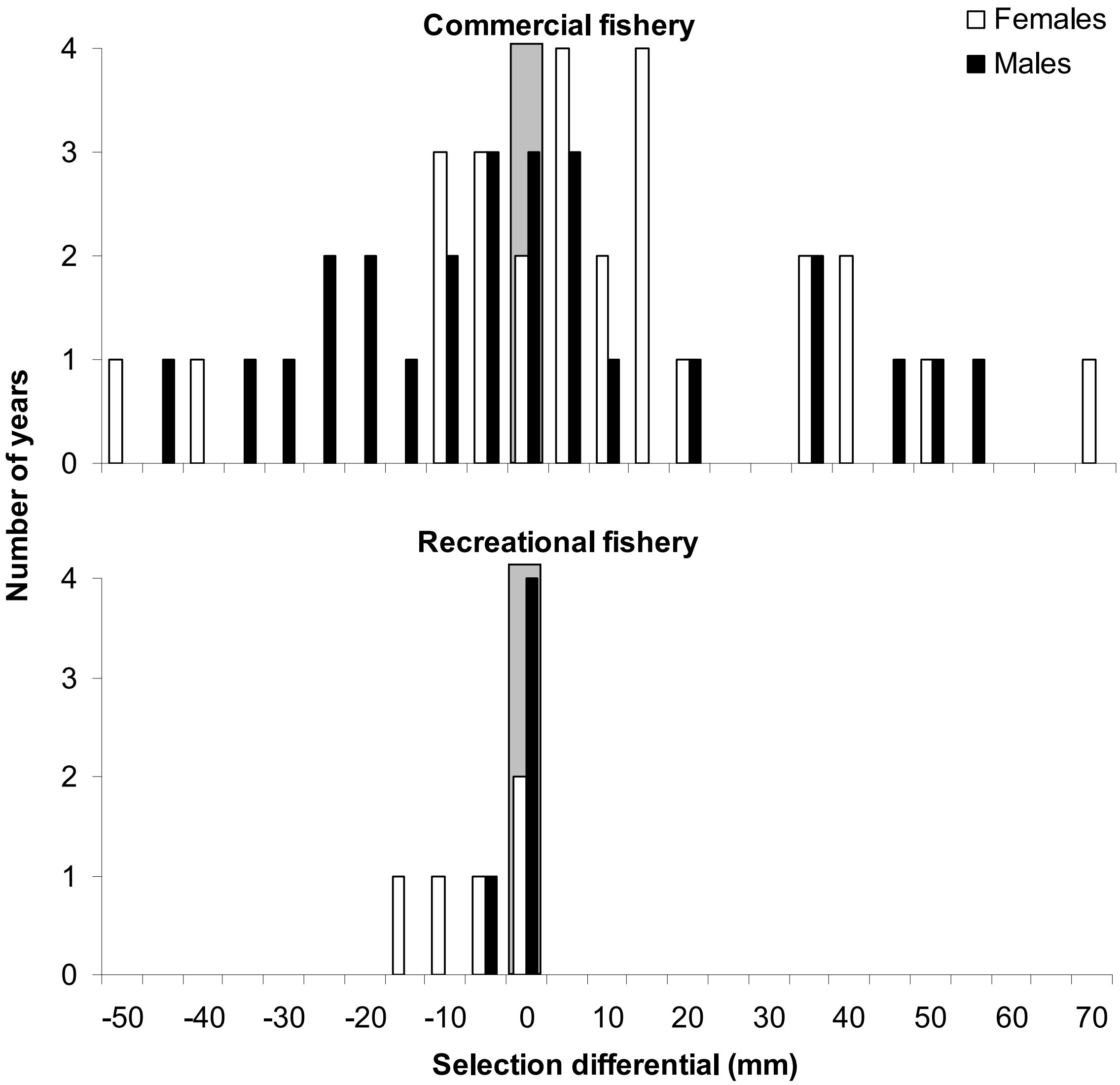


Fig. 2.6. Histograms of annual selection differentials (in mm) of female (white bars) and male (black bars) Chinook salmon of the Nushagak River of Bristol Bay, Alaska for the commercial (top panel) and recreational (bottom panel) fisheries. The grey bar represents a selection differential of 0 (no size-selectivity), the "F" represents the overall average SD for female fish, and the "M" represents the average value for males.

Chapter Three: Quantifying and comparing size selectivity among Alaskan sockeye salmon fisheries

Introduction

Life-history traits of wild animals and plants can be strongly influenced by a variety of anthropogenic activities (Allendorf and Hard 2009; Darimont et al. 2009). Differential mortality patterns from harvest of wild populations can have significant ecological effects, including reductions in density with associated increases in growth and decreases in mean ages and lengths of individuals (Policansky 1993; Trippel 1995; Hutchings 2004). Harvest is often size selective (Todd and Larkin 1971; Sinclair et al. 2002; Coltman et al. 2003; Carlson et al. 2007b; Mooney and McGraw 2007; Kendall et al. 2009), in part because hunters, fishers, and collectors target larger than average individuals (Darimont et al. 2009) and harvesting gear often selectively removes individuals with respect to length (Hamley 1975; Millar and Fryer 1999). This can alter the distribution of age and length at maturation among individuals surviving to reproduce (Law 2000; Coltman et al. 2003; Swain et al. 2007; Allendorf et al. 2008). Maintenance of diverse life-history traits and a broad distribution of ages and lengths at maturation can enhance population productivity and sustainability (Hilborn et al. 2003a; Schindler et al. 2010). Numerous studies have also emphasized the importance of older, larger individuals for population stability and sustainability (Birkeland and Dayton 2005; Law 2007; Hsieh et al. 2010). Accurately understanding the selective pressures generated by harvest and factors influencing size selectivity is therefore important for maintaining the phenotypic diversity and productivity of exploited wild populations.

Fisheries scientists and managers have expressed concerns about adverse ecological and evolutionary effects of selective harvest for over a century (Rutter 1904; Smith 1920; Miller 1957; Handford et al. 1977; Ricker 1981; Allendorf and Hard 2009). Fishery selection may lead to genetic changes in life-history traits (Allendorf et al. 2008), which may be harder to reverse than changes associated only with phenotypic plasticity (Law 2000; Dieckmann and Heino 2007; Dunlop et al. 2009). Selective harvest is generally thought to result in adaptive demographic shifts towards smaller fish and decreased age and length at maturation (Fenberg and Roy 2008). However, continued size-selective harvest has been associated with decreased fecundity (Walsh et al. 2006), increased sexual dimorphism (Wolak et al. 2010), lowered reproductive rates (Venturelli et al. 2009), reduced yield (Conover and Munch 2002), increased variability in abundance (Hsieh et al. 2006; Anderson et al. 2008), and stock collapses (Olsen et al. 2004).

Harvest managers and scientists have considered how to manage fishing and hunting to minimize adverse phenotypic and genetic changes in their stocks associated with selective harvest (Jørgensen et al. 2007; Allendorf et al. 2008). "Evolutionary management" considers consequential evolutionary trait changes in exploited populations (Heino and Godø 2002; Ashley et al. 2003; Jørgensen et al. 2007); such changes have increasingly been shown to affect ecological relationships (Schoener 2011). Evolutionary response in a trait can be expressed as the product of selection on that trait and its heritability, defined as the proportion of phenotypic variance attributable to genetic variance (Falconer and Mackay 1996), so quantifying size-selective harvest is an essential first step to understanding its evolutionary consequences. However, research evaluating the implications of selective harvest has been hampered by the difficulties in quantifying such selection, including selection differentials, over time (Law 2007; Kuparinen et al. 2009). Data required to accurately estimate size selection, including the size composition of individuals being captured and those not captured (Quinn et al. 2006), are often difficult to obtain, so few studies have empirically examined spatial and temporal patterns.

The life-history patterns of salmon make them ideal for quantifying harvest selection and estimating selection differentials. All salmon migrating into freshwater are maturing adults, and they can be counted and data on their life-history traits can be collected. Characteristics of individuals not harvested can be directly compared with similar data from individuals that were caught. Previously, we established protocols and examined long-term patterns of size-selective harvest by the gillnet fishery for sockeye salmon (*Oncorhynchus nerka*) in the Nushagak Fishing District of Bristol Bay, Alaska (Kendall et al. 2009). This fishery has generally caught larger fish than those that escaped to spawn, but selection patterns varied among years. Moreover, the largest fish were often not the most vulnerable to being caught because vulnerability curves generated by the fishery were not simply directional. We also found that the Nushagak River Chinook salmon (*O. tshawytscha*) commercial fishery has been markedly less selective than the fishery for sockeye salmon (Kendall and Quinn 2011), emphasizing that simple selection patterns cannot always be assumed. Other work on size-selective fishing found that larger than average sockeye and pink (*O. gorbuscha*) salmon were caught in most years by Skeena River (Todd and Larkin 1971) and Bristol Bay (Bue 1986; Hamon et al. 2000) gillnet fisheries but selection was inconsistent over time and was often disruptive. The few studies on non-salmonids have found similar patterns. Specifically, Carlson et al. (2007b) showed that a recreational fishery on pike (*Esox lucius*) in England tended to catch larger than average individuals but that there was also some disruptive selection. Sinclair et al. (2002) reported that the fishery on Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence, Canada varied over time between positive directional, negative directional, and disruptive selection.

The goal of the present study was to further characterize harvest selection patterns using additional datasets and test the generality of our previous findings. Specifically, we quantified a total of 283 years of size-selection patterns from nine Alaskan sockeye salmon fisheries with different characteristics under and beyond management control, including fishery and resource characteristics. The direction and strength of fishery size-selection patterns were quantified using annual linear and nonlinear selection differentials, which describe directional selection as the difference in the average length and stabilizing vs. disruptive selection as the difference in variance in length, respectively, of the stock before and after a selective event (Lande and Arnold 1983; Law and Rowell 1993). We examined the relationship between the linear selection differentials and the fishery characteristics and modeled which characteristics best predicted the selection differentials. We hypothesized based on previous research (Kendall et al. 2009) that fisheries with lower exploitation rates, smaller run sizes, and larger than average fish would be less selective on length. Gillnets, with diamond-shaped mesh openings, are thought to have dome-shaped selectivity, catching fish of intermediate lengths (Hamley 1975; Millar and Fryer 1999; Fujimori and Tokai 2001; Kendall et al. 2009). Purse seines, on the other hand, are not thought to be size selective (Yule 2000) as they use small mesh to encircle a group of fish; we predicted that these fisheries would be less selective than those using gillnets. We also expected that more protracted fisheries (longer period between the first and last days of fishing) and those that operated on fewer days in a given season would be less size selective because fishing could be spread throughout the season, catching a wider distribution of lengths of fish in the run, and because fish of all lengths could escape when the fishery was closed. Finally, we hypothesized that because fish of different lengths often vary in run timing (Quinn et al. 2009), differences in fishery timing (i.e., if more fish were caught earlier or later in the season) could affect fishery size selection.

Methods

Study site, study species, and data collection

We used 283 years of sockeye salmon fishery data from nine Alaskan fisheries, including 41 to 61 years (between 1946 and 2009) of data from the five distinct fisheries in Bristol Bay, 19 years of data (1989–2007) of data from Upper Cook Inlet, 18 years (1986–2003) from Chignik Lagoon, 6 years (1985–1988, 1990, 1992) from Alitak Bay, and 5 years (1985–1987, 1989, 1991) from Nelson Lagoon (Fig. 3.1). We obtained annual information on fishery characteristics and attributes of fish returning to each fishery, including gear type, fishery timing, fishing season length, the percent of days during the season when fishing occurred, exploitation rate, run size, and average fish length (summarized in Table 3.1) to use as predictors in evaluating the relationship between fishery characteristics and observed size selection.

Sockeye salmon are especially well-suited to harvest selection analyses compared to other Pacific salmon species. Sockeye, pink, and chum (*O. keta*) salmon are taken almost exclusively in commercial fisheries near their natal areas. However, in many cases the numerous small populations of pink and chum salmon are less closely monitored than the smaller number of larger sockeye populations. Coho (*O. kisutch*) and Chinook salmon are often taken in recreational and commercial fisheries along the coast over a protracted period, so it is more difficult to obtain records of lengths of fish that are caught from a specific population for comparison with the lengths of fish not caught. Analysis of harvest selection depends on the link between data on harvested individuals and those not captured, and this is only valid if both groups are from the same population.

Analyses

Analyses of fishery selection were similar to those carried out by Kendall et al. (2009). At processing facilities, the number of sockeye salmon caught was estimated daily and a sample of fish was measured for length (mid-eye to fork of caudal fin), scales were collected for age determination, and sex of each fish was recorded, providing annual age, sex, and length (ASL) data. Each river into which fish escaped to spawn had a weir, counting tower or sonar device to provide daily counts of upstream migrating salmon that escaped the fisheries. Adult salmon were sampled for ASL near the counting sites using beach seines, tangle nets, or traps designed to catch the entire range of lengths in a non-selective manner. ASL data were used to characterize the lengths of all fish in a given fishery's catch and escapement, which together comprise the total run. Sockeye salmon do not feed or grow during the final stages of migration so the lengths of individuals in the catch and escapement can be directly compared. Males and females were treated separately because males are generally larger and more variable in length than females (Blair et al. 1993).

We used individual length data to quantify fishery size selection (Lande and Arnold 1983). Fishery selection acts on length rather than age, but is important to consider the consequences of this selection on both age and length at maturation as these traits are tightly linked. Fishing can affect the mean length of fish by directional (linear) selection and the variance in length through stabilizing or disruptive (nonlinear) selection (Brodie et al. 1995). Thus, we calculated yearly length-based linear selection differentials ($LSD_{s,f,y}$; Equation 1), linear standardized selection differentials ($LSSD_{s,f,y}$; Equation 2), and nonlinear selection differentials ($NSD_{s,f,y}$; Equation 3) for each sex and fishery, all ages combined. The linear selection differential is the difference in mean length of fish in the total (i.e., pre–fishery) run ($\overline{L}_{R_{s,f,y}}$) and fish in the escapement ($\overline{L}_{E_{s,f,y}}$), and thus it represents the overall difference in the average length of the stock before and after a potentially selective event (i.e., fishery harvest; Law and Rowell 1993).

$$LSD_{s,f,y} = \overline{L}_{E_{s,f,y}} - \overline{L}_{R_{s,f,y}} \tag{1}$$

Linear selection differentials were standardized by dividing them by the standard deviation of length of fish in the run ($\sigma_{R_{s,f,y}}$), which allows comparison among years and fisheries and with other studies.

$$LSSD_{s,f,y} = \frac{\overline{L}_{E_{s,f,y}} - \overline{L}_{R_{s,f,y}}}{\sigma_{R_{s,f,y}}} \tag{2}$$

Nonlinear selection differentials were estimated as the annual difference between the variance in length of escaping fish of a given sex in a given fishery ($\sigma^2_{E\,s,f,y}$) and the variance in length of the total run ($\sigma^2_{R\,s,f,y}$) plus the linear selection differential squared.

$$NSD_{s,f,y} = \sigma^2_{E_{s,f,y}} - \sigma^2_{R_{s,f,y}} + LSD^2_{s,f,y} \tag{3}$$

Larger selection differential values represent stronger selection whereas values close to 0 represent weaker selection. The linear selection differential's sign (+ or -) indicates whether larger or smaller individuals were caught, respectively, whereas a nonlinear selection differential's sign (+ or -) shows whether the variance is increasing (disruptive selection) or decreasing (stabilizing selection).

We used one-sample *t*-tests to examine if the average *LSSD* and *NSD* for each fishery differed from 0. Power tests (Cohen 1988; 1992) showed that for an effect size of 0.80 and significance criterion of $p < 0.05$, significant differences could be detected by these tests 80% of the time (power = 0.80) with as few as 14 years of data per fishery. Thus, power was > 0.80 for all fisheries except for Nelson Lagoon and Alitak, which had 5 and 6 years of data, respectively. We used ANOVA to test if significant differences in mean *LSSD* and *NSD* values existed among the nine fisheries. We performed Tukey HSD post–hoc tests to see which pairs of fisheries differed. For an effect size of 0.40 and significance criterion of $p < 0.05$, significant differences among the fisheries could be detected with a power of > 0.80 with 11 years of data per fishery. For the smallest sample size, Nelson Lagoon's five years of data, the power was 0.35. Finally, we evaluated if male and female *LSSD* and *NSD* values differed using paired *t*-tests or ANOVAs (when variances were unequal between sexes). For the paired *t*-tests, the power tests showed that for an effect size of 0.80 and significance criterion of $p < 0.05$, significant differences could be detected with a power of > 0.80 with 14 years of data per fishery. Finally, for the ANOVAs, power tests showed that significant differences could be detected with a power of > 0.80 with 25 years of data per fishery. Thus, for all fisheries except Nelson Lagoon and Alitak, the power of these ANOVAs was at least 0.65.

We estimated annual exploitation rate (proportion of fish in the run caught) by sex and fishery ($P_{s,f,y}$) as

$$P_{s,f,y} = \frac{C_{s,f,y}}{C_{s,f,y} + E_{s,f,y}}, \tag{4}$$

where $C_{s,f,y}$ was the number of fish by sex caught by a given fishery in a given year and $E_{s,f,y}$ was the number of fish by sex that escaped a fishery in that year. Run size was the total number of fish returning to spawn in a given year, and season length was the total number of days between the dates of the first and last observed catches. Fishery timing was calculated as the percent of the fishing season's duration at which half of the total catch was achieved and describes whether more fish were caught earlier or later in the season. The percent of days during the season when fishing occurred was the percent of days fished during the season with a non-zero catch. Average fish length was the average length of all fish in the total run (catch and escapement). Gear type was a categorical variable (purse seine, gillnet, or mixed purse seine/gillnet).

For any selection regime, the *LSD* can be calculated as a product of two factors: the "length-selectivity value" (the difference in the average length of fish caught vs. those not caught) and the exploitation rate. Consequently, different combinations of the two factors can result in the same *LSD*. We examined which values of these factors were observed in the nine fisheries to determine how the *LSD*s were influenced by exploitation rate and selective removal by length.

Additionally, because many factors can shape a fishery's length selectivity, we explored how the range of predictor variables were related to *LSSD*s using linear mixed effects models (Zuur et al. 2009). We focused our analysis on *LSSD*s in these analyses because they are standardized so can be compared over time and among fisheries and because linear selection differentials are included in the calculation of the nonlinear metric. Mixed effects models minimize bias in estimating random effects when fixed effects are present, and can account for multiple sampling events from a given unit (Smith et al. 2008; Weisberg et al. 2010). These models accounted for the lack of independence among yearly samples from a given fishery. Thus, in our mixed effects models the random effect was the fishery; we had multiple years of data from each fishery. We employed the lme function in the nlme package with a normal error distribution and restricted maximum likelihood as the parameter-estimation method in the program R (R Development Core Team 2009). We first ran linear mixed effects models with each individual variable to understand its relationship with the *LSSD*s. Then, to determine which variables best predicted *LSSD*s, we ran models with different combinations of uncorrelated variables. Exploitation rate, run size, fishing season length, the percent of the season when a fishery was open, and fishery timing were correlated (Pearson correlation and Spearman's rank correlation; $P < 0.05$). Thus, we included year, gear type, exploitation rate, and average fish length as fixed effects in our models.

The models (Equation 5) predicted the absolute value of *LSSD*s from year-specific subsets of predictor variables for all years of data across fisheries. We used the absolute value because we wanted to understand which factors were associated with less-selective fishing (*LSSD* values close to 0). Separate models were created for males and females.

(5) $$|LSSD| \sim a + n_i + X_1 b_1 + X_2 b_2 + \ldots + \varepsilon_i$$

In this equation, a is the intercept, n_i represents a random effect due to fishery i, X values represent one of the above predictor variables, the b values are the coefficients for predictor variable, and ε_i are errors for fishery i. Thus, $|LSSD|$ is the sum of a baseline value, a random effect due to the fisheries, and one or more fixed effects. Models were adjusted with a first-order autoregressive process (AR1) with $\mathrm{cov}(\varepsilon_{i,y}, \varepsilon_{i,y+n}) = \Phi^{|n|}$, where $\varepsilon_{i,y}$ and $\varepsilon_{i,y+n}$ are errors for fishery i separated by n years, which accounts for the finding that within fisheries residuals of the *LSSD* values were correlated with past years' values (Pinheiro and Bates 2000). The best models to explain the |*LSSD*s| for fish of each sex were chosen based on Akaike Information Criterion with a second order correction for small sample sizes ($\mathrm{AIC_c}$) (Burnham and Anderson 2002). $\mathrm{AIC_c}$ values indicate support for models providing a balance between better fits to the data and not being over-parameterized. To understand how the predictor variables were related to |*LSSD*s|, we examined the variables' coefficient values, standard errors, and P-values. We also checked model diagnostics including plotting residual against fitted values to check randomness and lack of any trends and examining Q–Q plots.

Results

Average *LSSD* values across all years for males and females were significantly less than 0 for 7 of the 9 fisheries (*t*-tests, $P < 0.05$; Table 3.2). In 72 and 84% of the years the fisheries caught larger than average male and female fish, respectively, leaving smaller fish to spawn. Additionally, in 77% of all years assessed and for 6 of the 9 fisheries the average *LSSD* values for females were significantly more negative than those of males (paired *t*-tests with equal variance, $P < 0.05$; Table 3.2). Average annual *LSD*s among fisheries ranged from 2.6 mm (Chignik females) to -21.8 mm (Nelson Lagoon males; Table 3.2). The ANOVAs and post–hoc Tukey HSD tests revealed that, except for the Togiak fishery on males and the Chignik fishery on females, *LSSD*s for all fisheries were not different from each other ($P > 0.05$). Specifically, average *LSSD*s for Togiak males and Chignik females were positive whereas for all other fisheries they were negative. *LSSD*s varied greatly over time for a given fishery (Table 3.2; Fig. 3.2). Thus, our findings did not support our first hypothesis that fishery selection patterns would vary across the fisheries. In fact the patterns have been generally similar: fishery selection has varied over time but on average larger fish have been caught.

Average *NSD* values among years were significantly greater than 0, indicating disruptive selection, for 7 of the 9 fisheries for females and 8 of 9 fisheries for males (*t*-tests, $P < 0.05$; Table 3.2). In 92% of years for males and 84% of years for females the *NSD* values were positive, indicating disruptive selection. Additionally, in 71% of all years assessed and for 7 of the 9 fisheries average *NSD* values for males were significantly larger than for females, indicating stronger disruptive selection on males than on females (ANOVAs, $P < 0.05$; Table 3.2). ANOVAs and post–hoc Tukey HSD tests showed similar *NSD*s for female fish among most fisheries, but *NSD*s for males were different among 36% of fishery pairs. Finally, *NSD*s varied greatly over time within fisheries (Fig. 3.3).

Several patterns emerged from our examination of exploitation rates and length-selectivity values (difference in average length of fish caught vs. not caught) along with the *LSD* they combined to produce (Fig. 3.4). For any fishery, the product of the exploitation rate and the difference in length of fish caught vs. not caught is the linear size selectivity (Fig. 3.4a). Specifically, to prevent large *LSD*s, a fishery with a high exploitation rate must exhibit low length selectivity and a fishery that is highly length selective must catch only a small fraction of fish. We found that 62% of annual *LSD*s for females and 69% for males had values of less than ±10 mm (Figs. 4b and c). A wider range of exploitation rate values than length-selectivity values occurred; most *LSD*s resulted from length-selectivity values between -30 mm and +10 mm but exploitation rate values were more evenly distributed between 0.3 and 0.9, with generally similar patterns for males and females.

Fishery selection did not vary among fisheries that used the different gear types in the way we predicted. Male *LSSD*s from the two fisheries that included purse seine gear, Chignik and Alitak, and female *LSSD*s from the Alitak fishery were on average negative and significantly different than 0, suggesting that larger than average fish were caught

(Table 3.2; *t*-tests, $P < 0.05$). These *LSSD*s were also not significantly different from those of the all-gillnet fisheries (ANOVAs, $P > 0.05$). Average *NSD* values for males and females from both the Chignik and Alitak fisheries were all positive (Table 3.2; *t*-tests, $P < 0.05$), suggesting disruptive selection on length. These findings did not support our hypothesis that fisheries that used purse seine gear would be generally less selective than fisheries that used gillnets. The exception was female sockeye salmon from the Chignik fishery—*LSSD*s were not significantly different than 0 (Table 3.2; *t*-test, $P = 0.15$) and were significantly different from the *LSSD*s of other fisheries (ANOVAs, $P < 0.05$).

The findings of the linear mixed effects models agreed with our hypotheses that lower exploitation rates, smaller run sizes, and larger than average fish were associated with smaller *LSSD* values (closer to 0) and thus less size selectivity (Table 3.3). Additionally, fisheries that were open on fewer days each season were less size selective, as predicted. However, longer fishing seasons were correlated with larger *LSSD*s, suggesting greater size selection, contrary to our hypotheses. In years when more fish were caught later in the season (later fishery timing), size selectivity was weaker for males, but the opposite was found for females. Neither of these relationships was statistically significant, though. For males, there was significantly less size-selective fishing in earlier than more recent years, but this relationship was not significant for females. The best models to predict *LSSD*s were similar for males and females (Table 3.3) and included different subsets of predictors including the average length of fish in the run, the exploitation rate, a year effect, and gear type. Model diagnostics, including Q–Q plots, showed that the models fit the data appropriately. Inspection of the plot of residuals vs. fitted values from the best-fit models did not reveal any evident outlier observations or trends.

Discussion

This research improves our understanding of the magnitude of and variation in size-selective harvest patterns on wild fish populations and thus the potential for harvest-induced evolution of life-history traits. The patterns and processes described here can be compared to those of other fisheries to guide further analyses and understand how management and resource characteristics can be related to selection patterns. Long-term patterns of size-selective harvest were similar among nine Alaskan sockeye salmon fisheries despite differences in location and gear. In general, larger than average fish of both sexes were harvested by most fisheries, as revealed by negative average *LSD* and *LSSD* values, though selection varied markedly among years. Linear selection was stronger on longer females than it was on longer males for most fisheries. Male sockeye salmon are generally larger than females (Blair et al. 1993); the longest males are usually less vulnerable to being caught by gillnets (with their dome-shaped selectivity profiles) whereas the longest females are more vulnerable (Kendall et al. 2009). Fishing usually produced disruptive selection, increasing the variation in fish length as shown by the *NSD* values. Disruptive selection was stronger on males than females for all fisheries, associated with the greater variation in length of male sockeye salmon compared to females and the fact that the largest males were less vulnerable than those of intermediate lengths. Overall, more than 60% of observed annual *LSD*s were less than ±10 mm and over 97% were between -30 mm and +10 mm. Such linear and nonlinear selective pressures could contribute to evolutionary decreases in age and length at maturity of these fish.

The temporal variation in *LSSD*s was correlated with changes in fish characteristics, fishing pressure, and management regulations. Specifically, linear mixed effect models revealed that the average length of fish returning to spawn, exploitation rate, year, and fishing gear type were the best predictors of annual fishery *LSSD*s. Though correlations of the *LSSD*s with various management and environmental factors were generally weak, fishery managers should be aware that certain strategies can minimize size-selective harvest and evolutionary consequences (Heino and Godø 2002; Ashley et al. 2003; Jørgensen et al. 2007). In particular, lower exploitation rates confer less potential for evolutionary changes in age and length at maturation given fixed length-selectivity values of a fishery, consistent with previous models (Law and Grey 1989; Ernande et al. 2004; Brown et al. 2008; Hutchings 2009; Bromaghin et al. 2011). A fishery can be very length selective but not greatly affect the length distribution of fish escaping to spawn if only a small percentage of fish are caught (Fig. 3.4a). In addition, though managers cannot control the length of fish entering a fishery in a given year, when smaller than average fish are predicted, special care should be taken as stronger selection on the larger fish in the population may occur. Shorter fishing seasons and a smaller percentage of days fished were also significantly correlated with smaller *LSSD*s and thus less size-selective fishing. Finally, size selection by gear type was not as straightforward as we expected. In general, gillnet fisheries selectively caught larger than average fish. The fishery that used a mix of gillnet and purse seine gear also caught significantly larger fish on average. The purse seine-only fishery, though, caught larger than average males but smaller than average females. Fisheries using all gear types produced disruptive fishery selection. It is unlikely that the purse seine gear is selective *per se*, so the selectivity of these fisheries may result from some other trait associated with fish length such as timing or behavior.

Variation in fish length, subpopulation run timing, fishery timing, and fishery harvest rates within a fishing season contribute to observed fishery size-selectivity patterns. First, populations that are harvested together by a given fishery often differ in lengths, and variation in run timing among these populations can result in fish of different lengths entering a fishery at different times in a given season (Boatright et al. 2004; Chasco et al. 2007). Second, a fishery's harvest rate can vary within a given season due to management strategies. For example, fixed escapement management, applied to many salmon fisheries, often results in higher fishery exploitation rates later in the season once the escapement goal has been met (Quinn et al. 2007). Thus if larger fish arrive earlier in the season, when harvest rates are lower, and smaller fish arrive later, when harvest rates have increased, more small fish may be caught than larger ones, despite the fact that on any given day larger fish may tend to be caught. Another consideration for salmon (and some other fishes; Quinn et al. 2009) is that males tend to migrate earlier in the season than females, further influencing the patterns of selection. To account for these considerations and further understand their influences on fishery size-selection patterns, future work should calculate selection differentials on shorter, within-season time scales.

We also note that the consequences of size-selective harvest may differ among populations due to their differences in size and run timing, emphasizing the importance of estimating size-selective fishing on a population level (Kendall and Quinn 2009). Year-to-year randomization of the days when a fishery is open may reduce the overall strength of selection acting on fish of different lengths or different populations that share the same river system.

We emphasize the need to examine fishery size-selection patterns over many years. Studies over a few years, regardless of the level of detail, may not reveal the true variation in selection patterns and thus the consequences of such selection. Similarly, Olsen et al. (2009) emphasized the importance of examining variation in trait values in addition to mean values. It is also necessary to assess size selection in multiple fisheries to know how much patterns can be generalized. We discovered, when searching for fisheries with appropriate data to calculate size selection, that it is often impossible to make such calculations due to interception of fish in a given stock by multiple fisheries and inconsistent or missing catch and/or escapement data. Knowledge of selection patterns from similar fisheries can be considered when making management decisions for fisheries where selection cannot be calculated. As the rigorous demands of data quality are difficult to meet in salmon fisheries, they will likely be even more challenging in fisheries for other species that are iteroparous, are subject to capture in larger areas, are difficult to enumerate, or grow in size during the period when they are being fished.

A number of studies have modeled the rate of evolution associated with harvest (Law and Rowell 1993; Hard 2004; Andersen et al. 2007; Brown et al. 2008; Andersen and Brander 2009; Hard et al. 2009; Eldridge et al. 2010; Bromaghin et al. 2011) and the optimal age at maturation in exploited populations (Jørgensen et al. 2009; Kuparinen et al. 2009). Our results emphasize that such studies should consider inter-annual variation in harvest selection when predicting the mode and rate of evolution and optimal age and size at maturation. With temporal variation in selectivity, the rates of fisheries-induced evolution may be slower than if constant selection is assumed. Our analyses also indicated that the fisheries generally produced disruptive selection on fish length composition as well as tending to exploit larger than average fish. There are two implications of this result. First, studies that only report whether the exploited individuals were larger than those not taken may miss important non-linear patterns. Second, models of possible evolutionary effects of harvest should account for the combination of directional and disruptive selective.

A next step in this work would be to estimate trends in age and length at maturation over time in the exploited sockeye salmon stocks and assess if fishery selection could lead to genetic changes in traits (Allendorf et al. 2008) and the speed of such changes (Law 2007; Andersen and Brander 2009). Quantifying temporal trends in length at maturation is complicated, though, by the need to assess the average length of fish at specific ages (as age composition could also change over time) and in individual populations rather than at a fishery-scale (due to potential population abundance changes over time). Kendall (2011) found that length-at-age at maturation of sockeye salmon has decreased over time in the majority, but not all, of nine populations associated with two of the Bristol Bay fisheries. Population-specific consequences of size-selective harvest depend on a number of factors including genetic controls over length and age at maturation and correlations of these traits with other life-history traits. Age and length-at-age at maturation are under genetic control to some degree; Carlson and Seamons (2008) found the median heritability value for both traits to be 0.21 in salmonid fishes, and the heritability value for length at maturation in one Bristol Bay sockeye salmon population was estimated to be 0.58 (J. Hard, NOAA Fisheries, pers. comm.). These heritability estimates and our finding that larger than average sockeye salmon have usually been caught by Alaskan fisheries suggests that fishing could result in evolutionary changes towards smaller and younger fish over time (Hard et al. 2008; Allendorf and Hard 2009). The variation in the selection pressure and patterns of disruptive selection, though, could slow the accumulation of such changes, and observed patterns of size and age will also be affected by growing conditions (Rogers 1987; Rogers and Ruggerone 1993; Pyper and Peterman 1999) and other forms of selection.

Table 3.1. Characteristics of the nine Alaskan sockeye salmon fisheries evaluated in this study. See text for descriptions of characteristics.

Characteristic	**Chignik**	**Alitak**	**Togiak**	**Ugashik**	**Nushagak**	**Egegik**	**Naknek-Kvichak**	**Upper Cook Inlet**	**Nelson Lagoon**
Gear type	Purse seine	Mixed purse seine & gillnet	Gillnet	Gillnet	Gillnet	Gillnet	Gillnet	Gillnet	Gillnet
Fishing season length (days)	84	97	42	41	38	42	40	74	98
Percent of days fished	93	75	75	64	74	72	75	30	63
Fishery timing (percent of season when half of catch is reached)									
Males	25	51	61	56	42	43	46	62	34
Females	25	50	61	56	41	44	46	62	35
Exploitation rate									
Males	0.58	0.63	0.64	0.62	0.57	0.74	0.50	0.61	0.51
Females	0.65	0.59	0.66	0.57	0.53	0.73	0.47	0.60	0.66
Run size									
Males	748,973	768,640	273,214	1,574,642	2,362,719	3,172,037	7,013,666	2,798,222	264,456
Females	865,585	718,894	304,968	1,550,552	2,652,391	3,557,465	7,870,714	2,830,674	262,573
Average fish length (mm)									
Males	565	531	576	555	553	555	542	547	530
Females	562	525	548	536	529	540	528	539	536

Table 3.2. Linear standardized selection differentials (*LSSDs*), linear selection differentials (*LSDs*), and non-linear selection differentials (*NSDs*) for male and female sockeye salmon from the nine Alaskan sockeye salmon fisheries evaluated in our study. For each sex of fish, average *LSSD*s and *NSD*s, standard deviation of the *LSSD*s and *NSD*s, and P-values from the *t*-tests examining whether average *LSSD*s for each fishery were significantly different than 0 are listed. We also recorded whether average *LSSD* and *NSD* values were greater for males or females and the P-value from the paired *t*-tests (*LSSD*s) or ANOVAs (*NSD*s) examining these differences. Finally, the average annual *LSD*s for males and females from each fishery are given. All models were adjusted with a first-order autoregressive process (AR1).

	Males			**Females**			**Males vs. females**		**Males**	**Females**
Fishery	**Avg. *LSSD***	***LSSD* std. dev.**	**P-value**	**Avg. *LSSD***	***LSSD* std. dev.**	**P-value**	**Smaller avg. *LSSD***	**P-value**	**Average *LSD* (mm)**	
Chignik	-0.13	0.21	0.02	0.07	0.20	0.15	Male	< 0.0001	-9.1	2.6
Alitak	-0.19	0.10	0.005	-0.22	0.20	0.045	Female	0.58	-9.5	-7.6
Togiak	0.03	0.21	0.41	-0.16	0.24	< 0.0001	Female	<0.0001	0.7	-5.5
Ugashik	-0.09	0.21	0.008	-0.24	0.20	< 0.0001	Female	<0.0001	-4.0	-8.8
Nushagak	-0.10	0.21	0.0005	-0.27	0.24	< 0.0001	Female	<0.0001	-4.2	-9.9
Egegik	-0.15	0.24	0.0002	-0.27	0.23	< 0.0001	Female	<0.0001	-6.2	-9.7
Naknek-Kvichak	-0.15	0.16	< 0.0001	-0.18	0.15	< 0.0001	Female	0.05	-6.2	-6.2
Upper Cook Inlet	-0.25	0.14	< 0.0001	-0.32	0.16	< 0.0001	Female	0.0003	-14.2	-13.6
Nelson Lagoon	-0.34	0.34	0.09	-0.34	0.34	0.09	Female	0.98	-21.8	-11.5
Fishery	**Avg. *NSD* (mm^2)**	***NSD* std. dev. (mm^2)**	**P-value**	**Avg. *NSD* (mm^2)**	***NSD* std. dev. (mm^2)**	**P-value**	**Smaller avg. *NSD***	**P-value**		
Chignik	1188.5	850.70	< 0.0001	459.4	613.2	0.003	Female	0.03		
Alitak	1116.2	603.30	0.006	142.7	246.9	0.21	Female	0.003		
Togiak	199.2	280.86	< 0.0001	300.0	214.2	< 0.0001	Female	0.002		
Ugashik	521.1	557.45	< 0.0001	197.8	247.6	< 0.0001	Female	0.25		
Nushagak	463.4	449.06	< 0.0001	238.0	219.1	< 0.0001	Female	0.003		
Egegik	836.8	794.04	< 0.0001	309.4	267.3	< 0.0001	Female	<0.0001		
Naknek-Kvichak	356.1	273.06	< 0.0001	127.7	169.5	< 0.0001	Female	<0.0001		
Upper Cook Inlet	1110.9	709.68	< 0.0001	487.9	380.8	< 0.0001	Female	0.001		
Nelson Lagoon	636.1	624.96	0.085	256.9	287.3	0.12	Female	0.06		

Table 3.3. Results of linear mixed effects models predicting *LSSD* values from various predictor variables and models using a total of 283 years of data from nine Alaskan sockeye salmon fisheries. The number of parameters, ΔAIC_c values (the difference between each model's AIC_c value and that of the model with the lowest value), regression slope coefficients, standard errors, P values (for continuous variable, "-" for categorical variables), random effect variances, and how individual parameters affected *LSSD*s are included for each model.

Sex	Model	# of parameters	ΔAIC_c	Regression coefficient	Regression coefficient SE	Regression coefficient P-value	Random effects variance	How *LSSD* is affected (**+** means *LSSD*s increase so greater size-selectivity)
Individual variables								
Male	Exploitation rate	1	0.0	0.35	0.054	<0.0001	0.0014	**+** as exploitation rate increases
	Year	1	13.9	0.004	0.0007	<0.0001	0.00013	**+** in later years
	Average length of fish in run	1	26.7	-0.002	0.0005	<0.0001	0.00040	**+** as average length of fish decreases
	Season length	1	30.8	0.002	0.0005	0.0001	0.000027	**+** as season length increases
	Percent of days fished	1	41.0	0.0013	0.0006	0.03	0.00063	**+** as percent of days fished increases
	Gear type	1	42.1	-	-	-	0.00051	**+** for purse seines, **-** for gillnets
	Fishery timing	1	44.6	-0.0006	0.0007	0.45	0.00012	**+** as fishery timing is earlier
	Run size	1	56.2	1.E-08	4.E-09	0.0001	0.0030	**+** as run size increases
Female	Exploitation rate	1	0.0	0.26	0.06	<0.0001	0.0010	**+** as exploitation rate increases
	Average length of fish in run	1	16.4	-0.002	0.0006	0.002	0.0015	**+** as average length of fish decreases
	Gear type	1	18.8	-	-	-	0.0010	**-** for purse seines, **+** for gillnets
	Fishery timing	1	23.7	0.001	0.0008	0.21	0.0010	**+** as fishery timing is later
	Percent of days fished	1	24.7	-0.0007	0.0006	0.26	0.00087	**+** as percent of days fished decreases
	Season length	1	25.0	0.0006	0.0007	0.42	0.0016	**+** as season length increases
	Year	1	25.2	-0.0002	0.0008	0.84	0.0014	**+** in earlier years
	Run size	1	45.5	1.E-08	4.E-09	0.03	0.0026	**+** as run size increases
Best models								
Males	1) Average length of fish in run, exploitation rate, & year	3	0.0				1.6E-11	
	2) Average length of fish in run & exploitation rate	2	0.1				8.8E-11	
	3) Average length of fish in run, exploitation rate, & gear type	3	10.0				3.6E-11	
Females	1) Average length of fish in run & exploitation rate	2	0.0				1.3E-10	
	2) Exploitation rate	1	1.0				0.0010	
	3) Average length of fish in run, exploitation rate, & year	3	6.3				0.00050	
	4) Exploitation rate & gear type	2	7.2				0.00010	

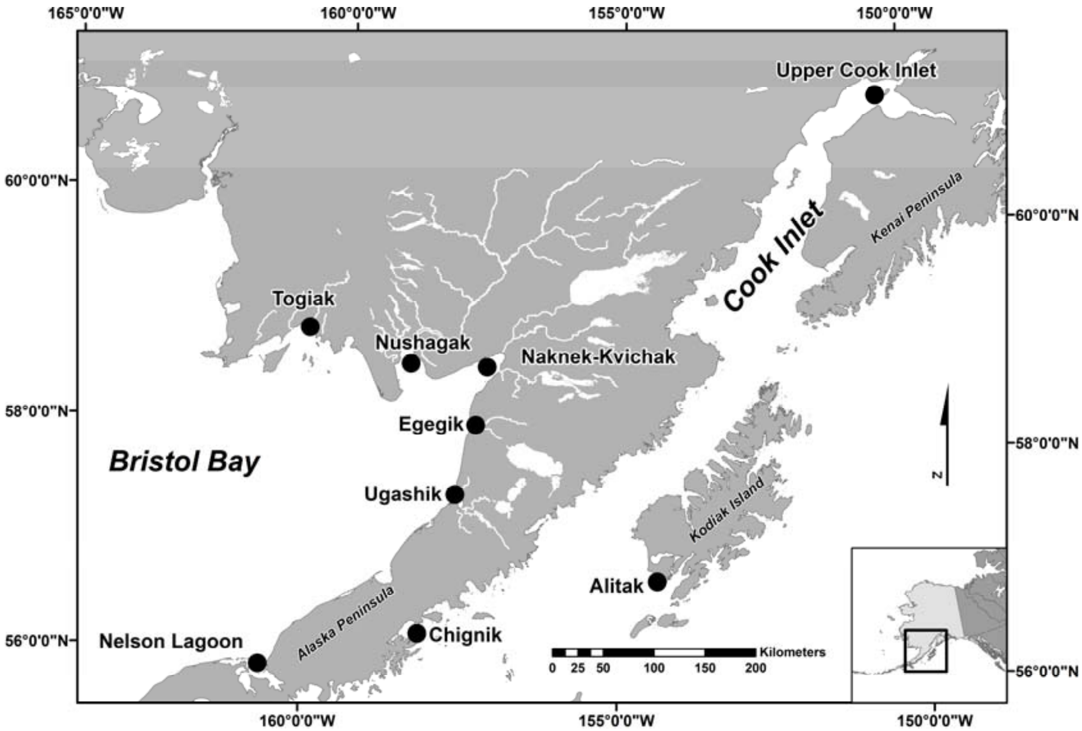


Fig. 3.1. Map of the location of the nine fisheries included in this study.

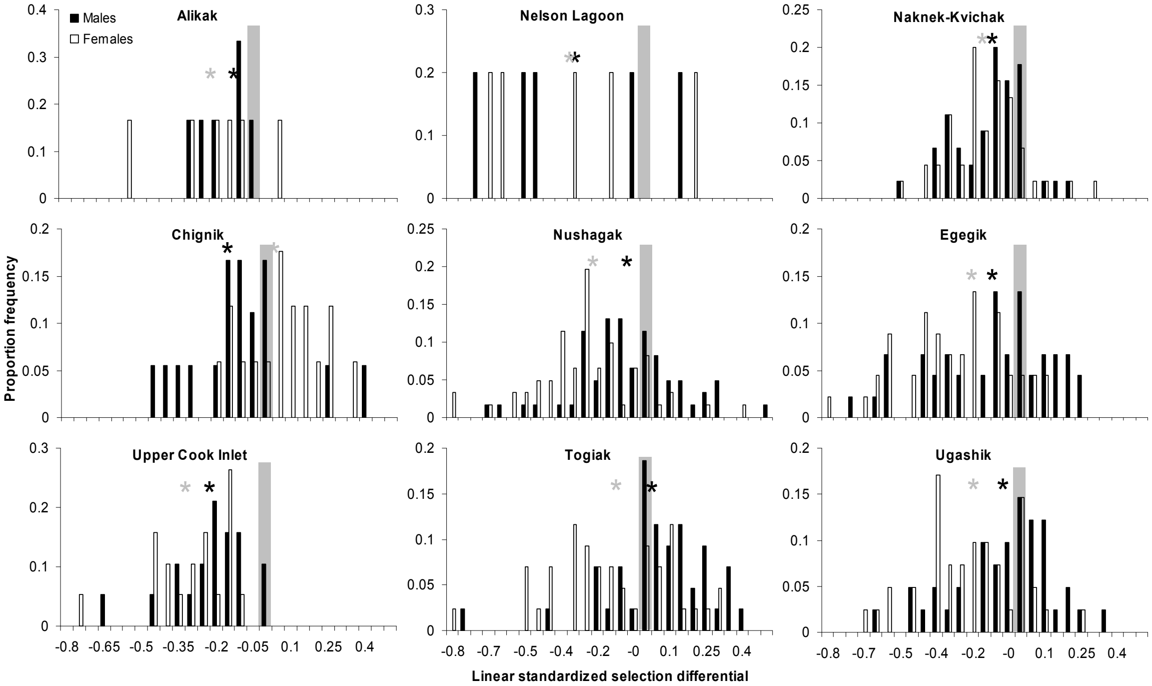


Fig. 3.2. Proportion frequency histograms of yearly *LSSD* values for each of the nine sockeye salmon fisheries included in our study. Males bars are black and females bars are white. The black star is the average *LSSD* for males over all years with available data and the grey star is the average *LSSD* value for females. The grey background bar shows where *LSSD*s are 0 and thus there is no length selection. With *LSSD*s greater than 0, smaller fish were caught, leaving larger fish to spawn, whereas with negative *LSSD* values larger fish were caught.

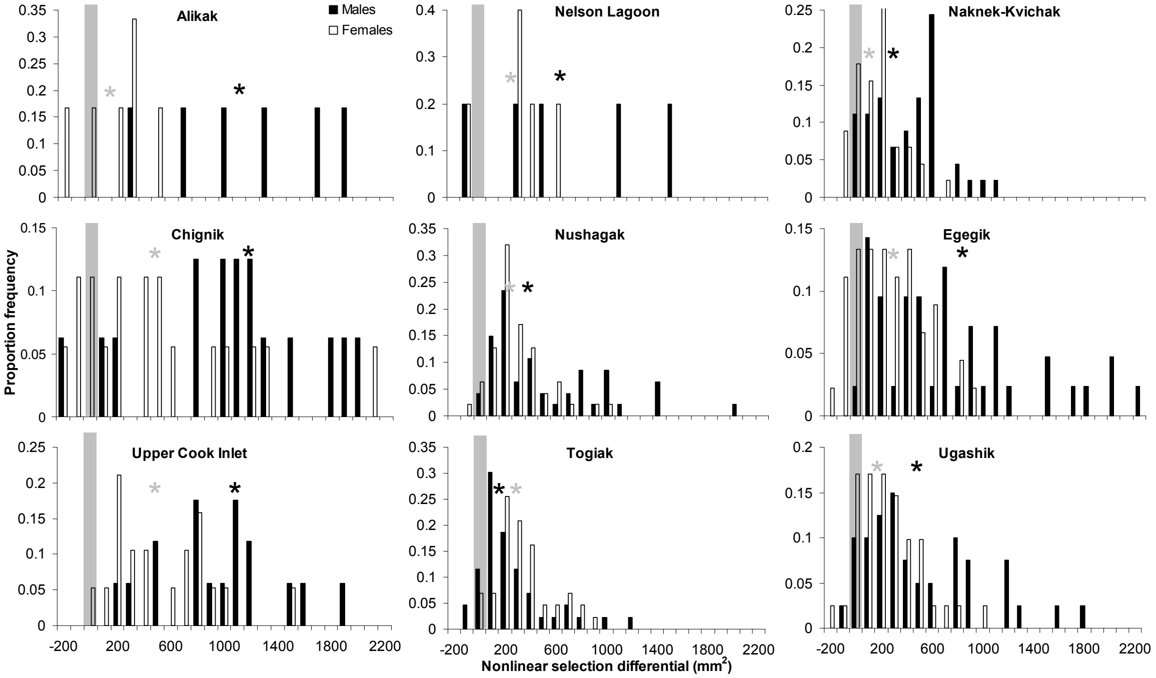


Fig. 3.3. Proportion frequency histograms of yearly *NSD* values (mm^2) for each of the nine sockeye salmon fisheries included in our study. Males bars are black and females bars are white. The black star is the average *NSD* for males over all years with available data and the grey star is the average *NSD* value for females. The grey background bar shows where *NSD*s are 0 and thus there is no length selection. *NSD*s greater than 0 indicate disruptive selection and increases in length variance whereas negative *NSD* values indicate stabilizing selection.

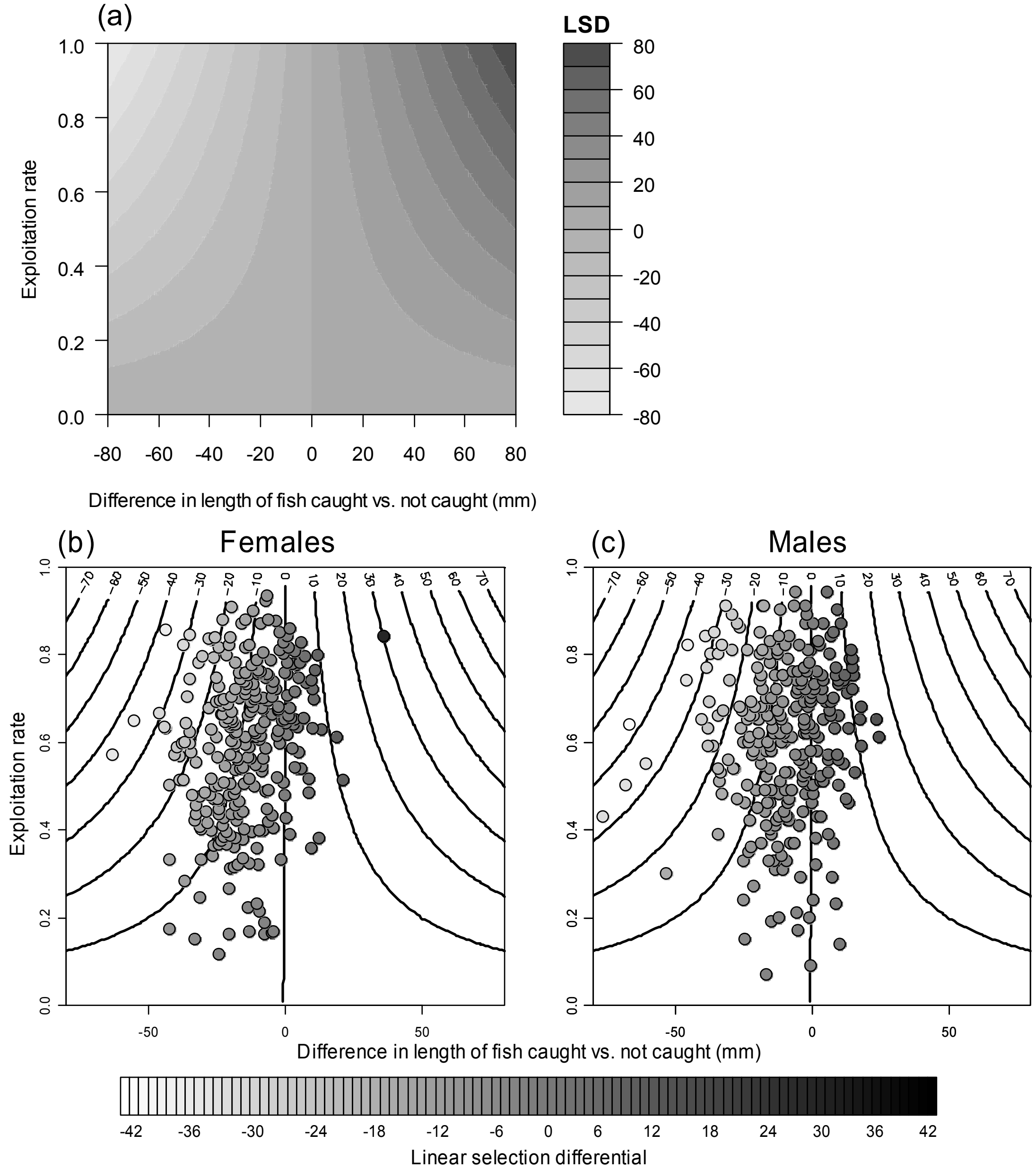


Fig. 3.4. (a) Contour plot of *LSD* values produced by different exploitation rates and "length-selectivity values," the difference in the average length of fish caught vs. those not caught, of a fishery. Actual (b) female and (c) male annual exploitation rates and length-selectivity values, along with the resulting *LSD*s, produced in a total of 283 years by the nine Alaskan sockeye salmon fisheries examined in our study. Background contour lines in (b) and (c) show where the product of a fishery's exploitation rate and length-selectivity value equal a given *LSD* value.

Chapter Four: Size-selective fishing affects sex ratios and the opportunity for sexual selection in Alaskan sockeye salmon *Oncorhynchus nerka*

Introduction

Harvesting by humans increases mortality rates and can reduce size and age in targeted populations (Jennings et al. 2001; Darimont et al. 2009). Harvesting can affect body size by changing the density of individuals in a population and selectively targeting certain individuals, especially larger ones (Coltman et al. 2003; Jørgensen et al. 2007; Allendorf and Hard 2009). Harvesting can shift population sex ratios; many hunting regulations are explicitly sex-biased, as is trophy hunting that targets large animals with pronounced sexual characteristics (Coltman et al. 2003). Some fisheries are also sex-directed, including those targeting crustaceans that only take males (Sato and Goshima 2006). In addition to the above direct effects, human harvest can also indirectly shift population sex ratios if it leads to heavier exploitation on one sex because of differences in size, age, and maturation schedules that influence an individual's susceptibility to capture (Ginsberg and Milner-Gulland 1994; McCleave and Jellyman 2004; Milner et al. 2007; Fenberg and Roy 2008). Sex-selection by fisheries is a function of gear and fish characteristics because there is often no visual selection, and it is usually subtle as fish characteristics, including sex, can only be identified after fish are caught. Additionally, if individuals of one sex mature at older ages, they may be more heavily exploited simply as a function of being exposed to harvest longer.

Variation in spawning ground sex ratios can strongly influence sexual selection including the intensity of intra-sexual competition, mate selection, and breeding success variation (Clutton-Brock 2007). If the sex ratio bias in a wild population is slight or the sex with the greatest influence on population growth (usually females) is less heavily exploited, effects on the population may be negligible (Ginsberg and Milner-Gulland 1994; Milner-Gulland et al. 2003). In some cases, total long term harvest yield can even be higher if males are selectively harvested (Kokko et al. 2001). However, the reproductive biology, demographics, and evolutionary trajectory of the population may be altered as intra-sexual competition and mate choice are affected by a skewed sex ratio (Saether et al. 2003; Carver et al. 2005; Holand et al. 2006; Milner et al. 2007; Fenberg and Roy 2008).

Among vertebrates, fishes display especially diverse patterns of genetic and environmental sex determination; hermaphroditism; mode of reproduction and life history variation; and a range of sexual dimorphism and alternative male life history strategies and mating tactics (Berglund 1997; Jennings et al. 2001). These patterns have evolved to accommodate the range of biotic and abiotic regimes of mortality and other forms of selection that populations experience. Males and females from a range of species commonly differ in body size, age at maturity, and longevity to some degree (e.g., striped bass, *Morone saxatilis*, Atlantic sturgeon, *Acipenser oxyrhynchus*, American eel, *Anguilla rostrata*, bluefin tuna, *Thunnus thynnus*, Atlantic halibut, *Hippoglossus hippoglossus*, and basking shark, *Cetorhinus maximus* (Scott and Scott 1988) and and sexual size dimorphism is especially marked in sequentially hermaphroditic species (Jennings et al. 2001)). The sex ratios at maturity can reflect life history differences, interacting with biases associated with increased exploitation (e.g., Jennings et al. 2001; Platten et al. 2002; Heppell et al. 2006). However, other than hermaphroditic fishes and sex-directed fisheries, few studies have explicitly explored if and how selective fishing can affect sex ratios of exploited fish populations.

In the case of anadromous Pacific salmon, *Oncorhynchus* spp., age and size distributions of males and females are not as skewed as in many other fishes and sex ratios of breeding adults generally approximate 1:1, with deviations usually being ascribed to selective fishing effects (e.g., Heard 1991). The breeding biology of Pacific salmon seems to be linked to patterns of sexual size dimorphism (the difference in size between males and females; SSD). Specifically, in species that commonly spawn at high densities (pink, *O. gorbuscha*, sockeye, *O. nerka*, and chum, *O. keta*, salmon), males are larger, on average, than females and more variable in size (Beacham and Murray 1985; Blair et al. 1993; Quinn 2005), but in those spawning at lower densities (coho, *O. kisutch*, and Chinook, *O. tshawytscha*, salmon), males are often smaller than females (Holtby and Healey 1990; Young 2005). This is, in part, because pink, chum and sockeye salmon seldom display the alternative male life history patterns of "jacks" (males returning from the ocean a year younger and at much smaller sizes than females) and non-anadromous individuals (Quinn 2005).

Our research focuses on sockeye salmon in Bristol Bay, Alaska, where commercial gillnet fishing, which has occurred since the late 1800s, has reduced fish densities, caught larger than average fish, and exploited more males than females (Kendall et al. 2009; Kendall and Quinn 2009). Such patterns have been revealed in part by fishery selectivity curves, which show the vulnerability of fish of different lengths to being caught and are generally dome-shaped and skewed rightwards. Fishing in Bristol Bay may have also shifted breeding sex ratios on spawning grounds, which could affect opportunities for sexual selection and altered population demographics. Specifically, experimental research by Mathisen (1962) on the behavior and reproductive success of sockeye salmon spawning with unequal sex ratios found that males became less competitive and more mobile when there was a surplus of females. Detailed, long term data are available from the Bristol Bay fisheries and spawning populations that can be used to explore sex ratio biases and how they relate to size-selective exploitation.

The first goal of this study was to quantify the sex ratio of all fish that were caught and that were not caught in each of the five Bristol Bay fishing districts over the last half-century. Our second goal was to test two hypotheses about sex ratios of fish in 13 discrete spawning populations, all of which migrate through one of the Bristol Bay fisheries on their way to the spawning grounds, based on fishery size-selectivity and SSD patterns. First, we predicted that populations with larger-bodied fish would experience less sex selection, and therefore have less-biased sex ratios, because their size distributions would place them nearer the apex of the dome-shaped fishery selectivity curves. At that point on the curve, size differences have less effect on exploitation rate variation between the sexes than at other points on the curve. Populations with small- and intermediate-sized fish were predicted to have more biased sex ratios as males and females would be harvested at different rates along the increasing slope of the selectivity curve. Second, we predicted that populations with greater SSD would experience more biased exploitation rates and so display more skewed sex ratios. We tested these hypotheses with 10 years of detailed data from the spawning populations, including sex ratios, average body sizes, and SSD, and knowledge of the fishery size-selection to which these populations are exposed. Finally, we discussed the impacts of skewed sex ratio on sexual selection on the spawning grounds.

Methods

Study site and data collection

We used a hierarchical dataset in this study. First, at a larger spatial scale, we examined over 40 years (between 1963 and 2009) of data on sockeye salmon that were caught (termed the "catch") and that were not caught (the "escapement") by gillnet fisheries within the five fishing districts of Bristol Bay, Alaska (Fig. 4.1). Data collection and analyses of fishery selection were similar to those carried out by Kendall et al. (2009). At fish processing plants in each fishing district, catches were estimated daily and a sample of the fish were measured (mid-eye to fork of tail, MEFT), scales were collected for age determination, and sex of each fish was recorded, providing annual age, sex, and length (ASL) data. Each river into which fish escaped to spawn had a counting tower or sonar device to enumerate, on a daily basis, upstream migrating salmon. Fish were sampled for ASL near the counting sites using beach seines or tangle nets; all gear was designed to be non-selective and catch the entire range of sizes. ASL data were used to characterize length for all sockeye salmon, male and female separately, in each fishery's catch and escapement. The catch and escapement together are equal to the total run. Sockeye salmon do not feed or grow during the final stages of migration and only a few days separate the sampling in the fishery and the river, so lengths in the catch and escapement can be directly compared.

Second, on a finer spatial scale, we collected data from 13 individual Wood River system sockeye salmon populations, which migrate together through the Nushagak Fishing District on their way to the spawning grounds (Fig. 4.1). Detailed information on individual fish from these populations provides complementary data to the larger-scale fisheries data. Analyses of Wood River system spawning ground data were similar to those described by Kendall and Quinn (2009). ASL (length as mid-eye to hypural plate, converted to MEFT) data have been collected annually from sockeye salmon in many discrete spawning sites within this watershed since 1963 but we focused on the past decade (2000-2009) when data were most complete. In a given year we measured 110 females and males from each spawning populations to estimate average size of fish (Fig. 4.1). Fish were sampled at random near the peak of the run to best represent the spawning population. Additionally, each stream's population was counted by a team of scientists on foot, keeping separate track of male and female live and dead salmon. These surveys did not count all fish because some may enter after the survey or have been consumed by bears before the survey. Daily counts over 21 years in one of the streams, Hansen Creek, indicated that peak survey counts were about 75% of the total counts and that the two were highly correlated ($R^2 = 0.89$; Quinn, unpublished data). In populations with more protracted spawning, the counts might be somewhat lower, but we expect that they too should be closely correlated with the total run size.

Analyses

At the larger scale, we used ASL data to estimate sex ratios in the catch, escapement, and total run for each of the five Bristol Bay fishing districts between 1963 and 2009. We calculated the sex ratio as the proportion of fish that were male. For each fishery we performed t-tests to examine whether annual catch, escapement, and total run sex ratios were significantly different than 0.5 and ANOVAs and Tukey HSD post-hoc tests to assess significant differences among the sex ratios in each group. Power analyses of the t-tests (Cohen 1988) showed that for a large effect size (0.8) with a significance criterion of $p < 0.05$, significant differences could be detected > 99% of the time (power > 0.99) for all fishing districts. Power analyses for the ANOVAs found that for a large effect size (0.4) and significance criterion of $p < 0.05$, significant differences in sex ratios among the fisheries could also be detected with a power of > 0.99.

At the finer scale, we calculated annual sex ratios, average lengths of males and females, and sexual size dimorphism (SSD) for fish in each of the 13 stream-spawning populations using the spawning ground survey data between 2000 and 2009. SSD was estimated for each year as the average length of males minus the average length of females. We employed ANOVAs and Tukey HSD post-hoc tests to evaluate differences in sex ratios and average lengths of fish among populations. Between 3 and 10 years of length data were available for each population (in some years data were not collected), so the power to detect significant differences among populations ranged from 0.22 to 0.85 with a large effect size (0.4) and significance criterion of $p < 0.05$. Sex ratio data were available for each population in 9 or 10 years, so under the same conditions the power was > 0.78. Finally, to evaluate how populations with different sizes of fish varied in sex ratios, we plotted the average length of males and the proportion of males in each population averaged between 2000 and 2009. In this analysis, each population was given equal weight so populations with more years of available data wouldn’t drive the results. We first transformed the average proportion offish that were male in each population by taking the arcsine square-root. We then fit linear and quadratic models to these data to understand the form of the relationship and calculated each model’s likelihood based on the normal error distribution. We evaluated which model fit the data best without being over-parameterized using the Akaike Information Criterion (AIC) and a likelihood ratio test.

To evaluate if and how size-selective fishing patterns could influence sex ratios of fish on the spawning grounds, we first calculated the proportion of fish of each length that were caught annually (2000 to 2009) by the Nushagak District fishery (Kendall et al. 2009). Specifically, fishery selectivity curves were calculated as

$$(1) \qquad P_{y,s,l} = \frac{C_{y,s,l}}{C_{y,s,l} + E_{y,s,l}},$$

where P is the proportion of fish caught by year (y), sex (s; male or female), and length (l; mid-eye to fork of tail), C is the number of fish that were caught, and E is the number of fish that escaped the fishery. We assumed that sockeye salmon in all Wood

River system populations had a similar risk of being caught by the Nushagak District fishery because there is broad overlap in migratory timing through the fishery among the populations (Doctor et al. 2010). We estimated the mean fishery selectivity curve between 2000 and 2009 by averaging the proportion caught for each length across the years (again to give each population equal weight). To understand how size-selective fishing was related to sex ratios of different spawning populations, we compared the sex ratios, average lengths of fish, and SSD values of the populations to this curve.

Results

On the larger spatial scale, we found that since the early 1960s, significantly fewer than 50% of the sockeye salmon returning to 4 of the 5 Bristol Bay fishing districts (the total run) have been male (Table 4.1). Specifically, an average of 47% of fish returning four of the five fishing districts, including Nushagak, Naknek-Kvichak, Togiak, and Egegik, were male. In 4 of the 5 fishing districts, males were harvested at a higher rate than they were represented in the total run. This sex-selective harvesting contributed to more skewed sex ratios of the fish in the escapement. For example, males represented 47% of the total run to the Nushagak District, 48% of the fish in the catch, and 44% of the fish that escaped to spawn. T-tests using the mean sex ratio for each year revealed that the total run, catch, and escapement sex ratios for the Nushagak, Naknek-Kvichak, Togiak, and Egegik Fishing Districts were all significantly different from 0.5 ($p < 0.05$). Additionally, the annual escapement sex ratios of the Ugashik District differed from 0.5 ($p = 0.0045$), though the total run and catch sex ratios did not differ ($p > 0.05$). ANOVAs comparing annual sex ratios among the catch, escapement, and total run suggested that significant differences existed between the catch and escapement and the total run and escapement sex ratios for only the Nushagak and Ugashik districts, but the total run and catch sex ratios were not significantly different in these districts.

At the finer spatial scale, boxplots of the annual sex ratios (Fig. 4.2a) and lengths of male sockeye salmon (Fig. 4.2b) in the 13 Wood River system populations 2000-2009 revealed variation among populations and also among years within a given population. Annual proportions of fish that were male ranged from 0.36 to 0.47 and annual average lengths (MEFT) of male fish varied from 455 to 537 mm. The ANOVAs and Tukey HSD post-hoc tests revealed that sex ratios were significantly different between 6% of population pairs and average lengths were significantly different between 28% of population pairs. Across the populations, average SSD values ranged from -7 to +31 mm. In populations with relatively small fish, average SSD values were close to 0 (males and females were similar in size), and sometimes females were on average larger than males (Fig. 4.3a). Average SSD increased for populations with fish of intermediate and larger sizes, and males were longer than females (Fig. 4.3a).

For a given population, regressions showed that the average proportion of males increased as the average length of males increased (Fig. 4.3b). However, the best-fit model was not linear but a quadratic function, revealed by its lower AIC value and the likelihood ratio test ($D = 7.9$, $df = 1$, $p = 0.005$). This function showed that the smallest- and longest-bodied populations had higher proportions of males than populations with fish of intermediate lengths. This relationship was clarified when we compared the sex ratios, average lengths of fish, and SSD in the spawning populations to the Nushagak District fishery selectivity curves. Between 2000 and 2009 these curves were generally dome-shaped (Fig. 4.5); vulnerability increased as fish increased in size, the curve peaked at slightly larger than average fish, and then vulnerability decreased for the largest fish. The mean fishery selectivity curve was approximately dome-shaped (Fig. 4.4).

We overlaid the average sizes of male and female sockeye salmon from the spawning populations on the mean Nushagak District fishery selectivity curve to illustrate how population sex ratios could be influenced by size-selective fishing (Fig. 4.4). First, the slope of the selectivity curve corresponding to populations with the smallest-bodied fish (including Eagle, Mission, and Hansen creeks) was slightly less than that of populations with intermediate-sized fish (A, C, Hidden Lake, and Lynx creeks), so the difference in the proportion of males and females caught was less for the smallest-bodied fish than for fish of intermediate sizes. More importantly, though, males and females from short-bodied populations were more similar in size (smaller SSD), so they experienced similar rates of fishery selection. Thus, sex ratios of the smallest-bodied populations were less skewed and closer to those observed in the escapement as a whole. Second, fish of intermediate lengths fell along the portion of the selectivity curve with a steeper slope, and the greater size difference between males and females (SSD) than for the smallest-bodied populations resulted in different harvest rates between the sexes. Higher proportions of males were caught than females, skewing the sex ratios of populations with fish of intermediate lengths. Finally, the longest fish of both sexes fell along the peak of the dome-shaped selectivity curve, so there was less difference in proportion caught between males and females despite their higher SSD values. Thus, populations with the longest fish (Yako, Pick, Bear, Happy, and Ice creeks) showed less-skewed sex ratios than populations with intermediate-sized fish.

Discussion

Size-selective exploitation can alter the distribution of wild populations' life history traits and result in adverse ecological and evolutionary consequences (Coltman et al. 2003; Allendorf and Hard 2009). Here we empirically documented that size-selective fishing can also affect the sex ratios of wild populations, even those that exhibit only moderate sexual size dimorphism, potentially affecting patterns of sexual selection and breeding dynamics.

Our analyses showed, on a large spatial scale, that overall sex ratios of sockeye salmon were slightly but significantly female-biased. There are currently very few interception fisheries that might affect these populations and so we assume that the differences were largely if not entirely natural. Males are on average larger and older than females (Quinn et al. 2001b) and thus they may incur some greater risk of predation associated with foraging at sea for the additional year, as was hypothesized for the reverse pattern of size and sex ratio in coho salmon (Holtby and Healey 1990). Specifically, male sockeye salmon were older than females in 61-73% of years with data between 1963 and 2009 in four of the five commercial fishing districts, including Naknek-Kvichak, Egegik, Ugashik, and Nushagak. Males returning to the Togiak Fishing District were older than females in only 38% of years. This did not entirely correlate with the sex ratios of fish in the total run among fishing districts as the only district with a 1:1

sex ratio was Ugashik; in all others, including Togiak, males represented less than 50% of the fish returning to spawn. Regardless of the processes giving rise to the female-biased sex ratios, we found that most fisheries exaggerated this by catching a higher proportion of males. This tendency to catch males likely results from both their larger size and greater changes in body depth, jaws, and teeth than females. These features become fully developed when maturation is complete (Blair et al. 1993) and make males more vulnerable to gillnets than females. Only the Togiak District fishery caught fewer males than were present in the total run, and in this case males were, on average, younger than females.

Each of the five Bristol Bay gillnet fisheries exploits multiple discrete spawning populations, and these populations differ markedly in size at age, age composition, and morphology (Blair et al. 1993; Quinn et al. 2001b). These differences affected the overall exploitation rate among populations (Kendall and Quinn 2009). Our results demonstrated that fishing also affected sex ratios on the spawning grounds, and in some cases only slightly more than one-third of potential breeders were males. Fishery selection influenced Wood River system sockeye salmon spawning population sex ratios not only because of differences in the average size of fish among populations but also because SSD (the difference in length between males and females) differed. Sex ratios of populations with fish of intermediate lengths were most impacted by size-selective fishing both because males and females differed in length and because, due to the shape of the fishery selectivity curve, males and females were exploited at different rates. In the smallest-bodied populations, SSD was slight and this reduced the sex ratio effect, and in the largest-bodied populations the SSD was large but the sizes of the fish made both sexes similarly vulnerable.

The breeding system of salmonids (Fleming and Reynolds 2004) is characterized by intense male-male competition for access to mates (Fleming and Gross 1994; Quinn and Foote 1994) and some degree of female choice (Foote 1989; Berejikian et al. 2000). The strength of these processes is governed largely by the operational sex ratio (OSR: sexually active males to sexually active females). This ratio is typically male-biased at the very beginning of the season because males often arrive before females (Morbey 2000) but approaches unity as females arrive. At this point competition among males for mates may not be intense. However, the OSR becomes increasingly male-biased as females complete spawning and are no longer available as mates. Consequently, groups of 5-10 or more males may be seen courting the few remaining ripe females towards the end of the spawning season (Quinn et al. 1996). In the small streams the dearth of males is often further exaggerated by the more intense predation rate by bears on males compared to females (Quinn and Buck 2001).

The shift towards a more female-biased sex ratio will likely relax selection on males, providing reproductive opportunities to some males that might otherwise be unable to compete for access to females. In salmon, these are typically smaller and younger males, not selected as mates by females (Foote 1989) and dominated by larger males in competition (Quinn et al. 2001a). Indeed, these smaller males are more likely to escape the fisheries, and are also less vulnerable to predation by bears in small streams (Quinn and Buck 2001). Size at maturation is heritable in salmonids (Carlson and Seamons 2008), so as the reproductive success of smaller males increases, the size of individuals in future generations may decrease. In salmon species with non-anadromous males, these “precocious parr” may also enjoy greater reproductive opportunities if anadromous males are less numerous (e.g., Jones and Hutchings 2001). With the relaxed selection on male size in populations with skewed sex ratios, reproductive success may change. Male salmonids in general exhibit greater variation in reproductive success (as indicated, for example, by DNA parentage analysis) than do females (Serbezov et al. 2010), but this may not be the case in populations that are dominated by females. Genetic parentage assignment in two Wood River system spawning populations with highly skewed sex ratios demonstrated higher variability in reproductive success in females than in males, and also suggested that selection on body size was affected by sex ratios (L. Hauser, School of Aquatic and Fishery Sciences, University of Washington, unpublished data).

Other than sex-directed fisheries and those targeting hermaphroditic species, our study is one of the few to empirically examine how size-selective fishing could affect sex ratios and thus sexual selection and breeding dynamics of wild populations. Most studies examining the evolutionary effects of selective fishing have focused on changes in age, size, and correlated traits over time (Jørgensen et al. 2007; Kuparinen and Merilä 2007; Hutchings and Fraser 2008; Allendorf and Hard 2009; Darimont et al. 2009; but see Fenberg and Roy 2008), and we argue that such studies should also document sex ratios and examine the potential for sex-selection. The larger body of literature on sex-selective harvest of terrestrial wildlife and its implications (Ginsberg and Milner-Gulland 1994; Milner et al. 2007) can serve as a guide. For example, sex ratios of large terrestrial mammals have been linked to population demographics and life history traits (Saether et al. 2003; Holand et al. 2006; Milner et al. 2007). In populations with skewed sex ratios and increased reproductive success of younger males, females may hesitate to breed, which can delay offspring birth dates, decrease body mass development, reduce birth synchrony, and alter offspring sex ratios.

Because skewed sex ratios can affect breeding dynamics and sexual selection, with the potential for both ecological and evolutionary consequences, understanding the effects of selective fishing on sex ratios may help to explain changes in structure and sustainability of harvested wild fish populations. Studies on size-selective fishing should assess the SSD of exploited populations, evaluate if and how the fishing gear used is size-selective, and then consider how the sexual dimorphism could interact with selective fishing to result in skewed sex ratios. Managers should consider gear types and other strategies that harvest fish less selectively, and when selective fishing is in place management plans should explicitly consider sex-specific age and maturation patterns such as those for striped bass (Richards and Rago 1999) and gag, *Mycteroperca microlepis* (Heppell et al. 2006).

We note that variation in migration timing of salmon and other fishes can strongly affect exploitation rate, depending on how the fishery is managed, and that timing can vary among spawning populations, between males and females, and as a function of size or age within populations (Quinn et al. 2009). These patterns can all interact with fishery size-selection to influence overall selection, including effects on sex ratios of spawning populations. For example, a fishery’s harvest rate can vary within a given season due to management strategies. Fixed escapement management, applied to many salmon fisheries including Bristol Bay, often results in higher fishery exploitation rates later in the season once the escapement goal has been met (Quinn et al. 2007).

Sockeye salmon in Bristol Bay have thrived over the past century (Hilborn et al. 2003b) so sex ratio biases of spawning fish and other forms of selection have not undermined population productivity. Nevertheless, skewed sex ratios can affect sexual selection and alter patterns of behavior and reproductive success among individuals (Mathisen 1962). Such effects may not be immediately revealed by standard fishery production data but they are still important ecological and evolutionary processes.

Table 4.1. Average proportion of sockeye salmon that were male in the total run, catch, and escapement of each of the five Bristol Bay fishing districts between 1963 and 2009 with 95% confidence intervals.

	Average proportion male		
Fishing district	**Total run**	**Catch**	**Escapement**
Nushagak	0.47 ± 0.012	0.48 ± 0.018	0.44 ± 0.015
Naknek-Kvichak	0.47 ± 0.014	0.48 ± 0.018	0.46 ± 0.015
Togiak	0.47 ± 0.016	0.46 ± 0.021	0.48 ± 0.018
Egegik	0.47 ± 0.014	0.48 ± 0.017	0.45 ± 0.020
Ugashik	0.50 ± 0.017	0.52 ± 0.025	0.47 ± 0.022

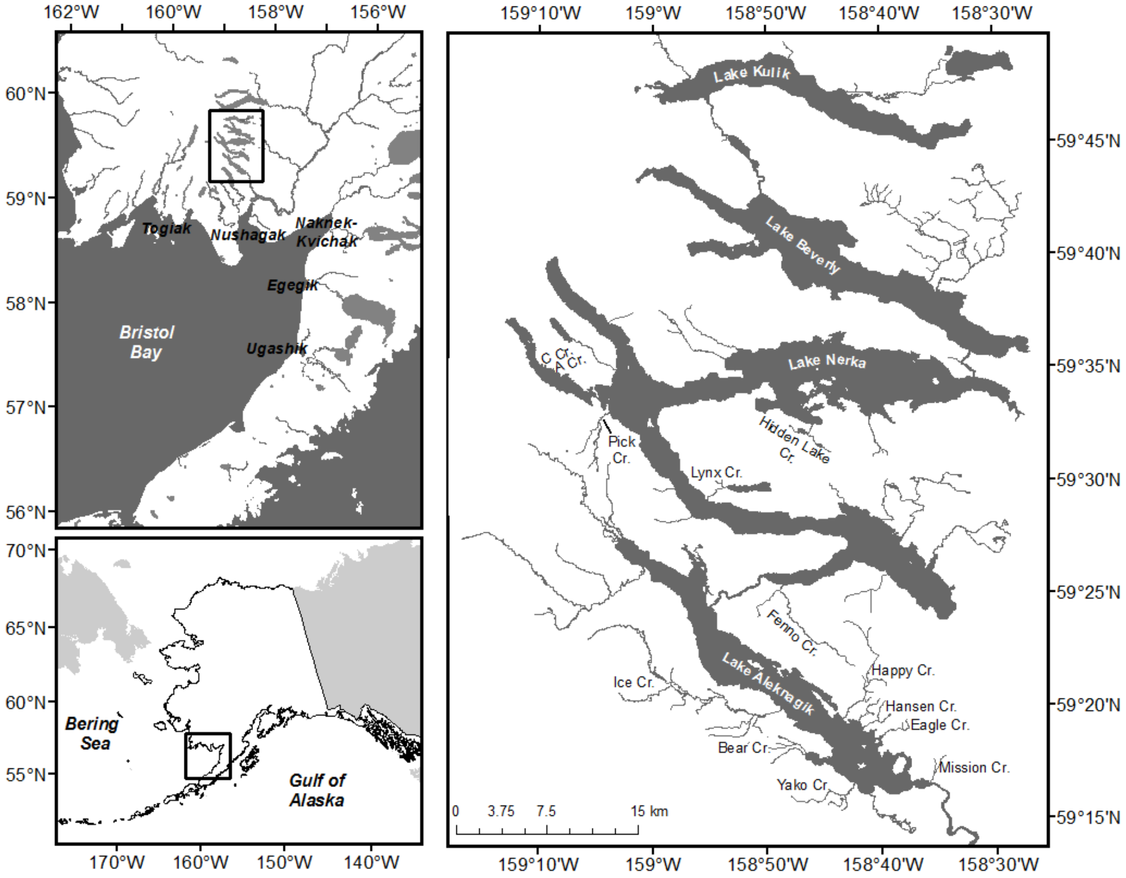


Fig. 4.1. Map of Bristol Bay, located in southwest Alaska, the five fishing districts, and the Wood River system lakes showing the 13 study streams.

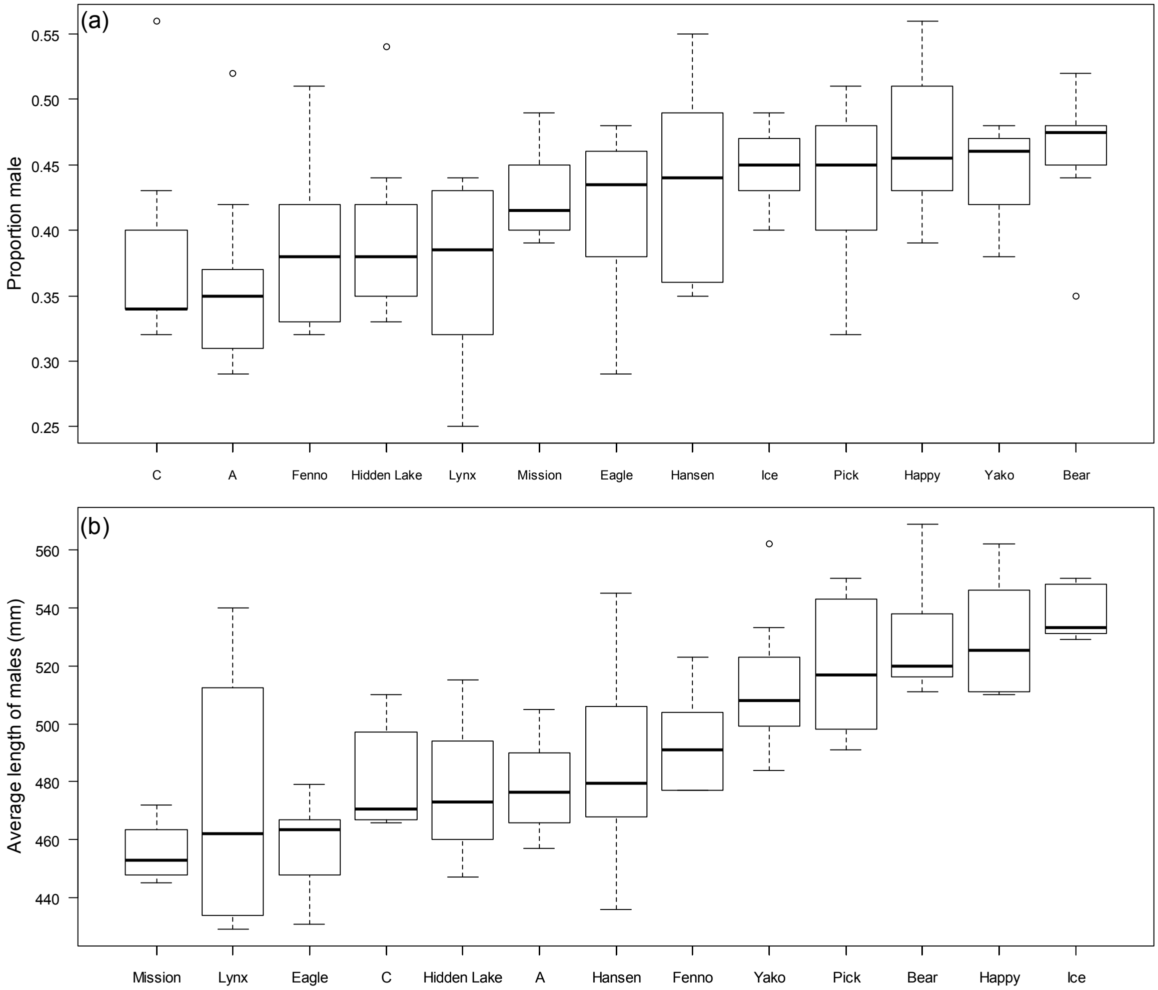


Fig. 4.2. Boxplots of the annual (a) proportion of sockeye salmon that were male and (b) average length of males for sockeye salmon spawning in each of 13 streams in the Wood River system of Bristol Bay, Alaska between 2000 and 2009. Populations are arranged from lowest to highest for each attribute.

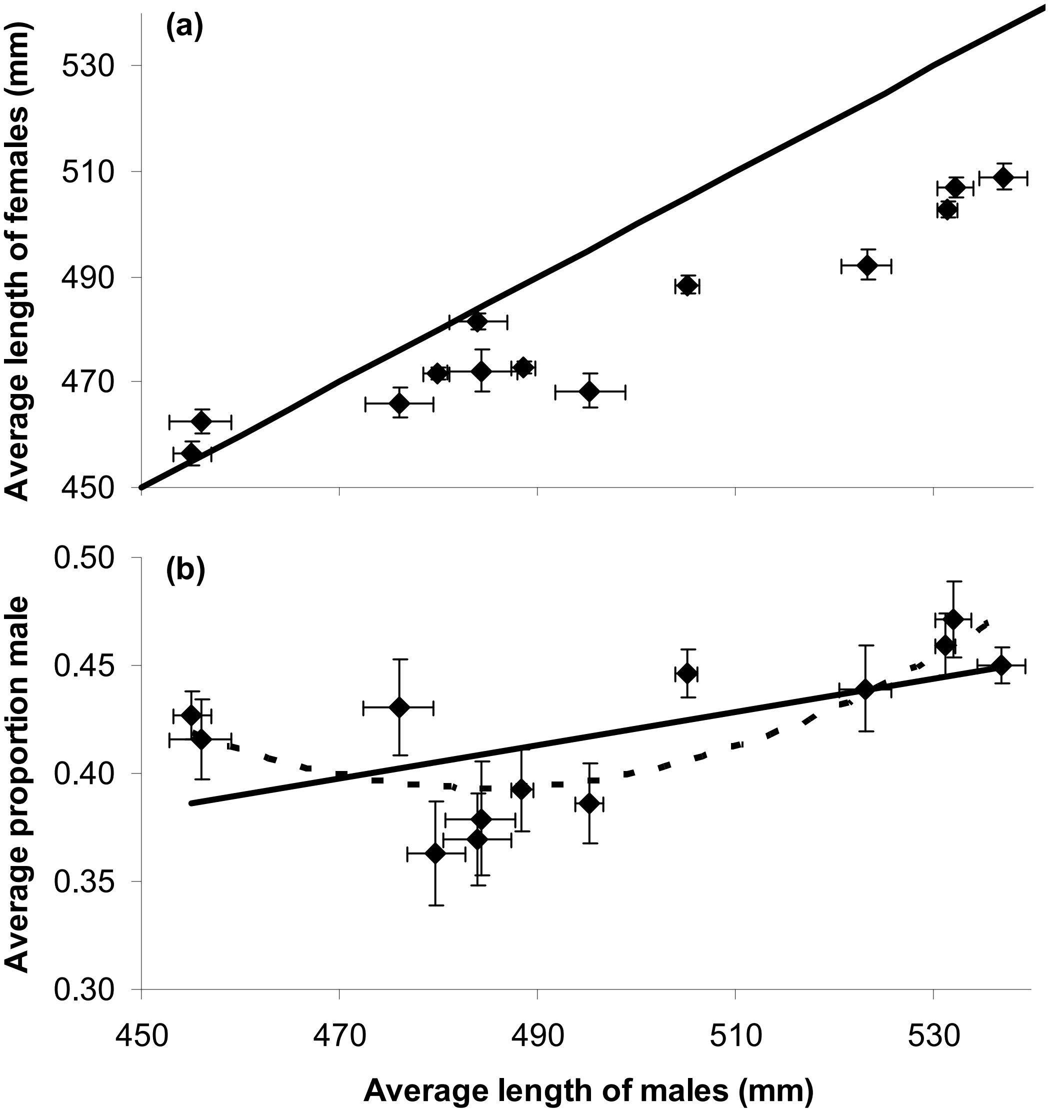
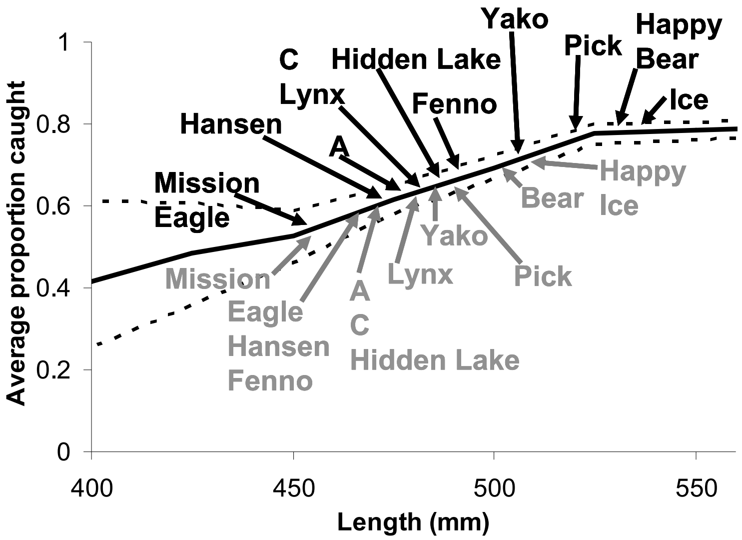


Fig. 4.3. The relationship between (a) the average length of male and female sockeye salmon and (b) average length of male sockeye salmon and the average proportion of males spawning in 13 streams in the Wood River system of Bristol Bay, Alaska between 2000 and 2009. Error bars represent standard error values. In (a) the solid line indicates a 1:1 relationship. Data points above the line represent populations where on average females are longer than males, and points below the line represent populations where males are longer than females. In (b) the solid line represents a first-order polynomial function ($R^2 = 0.35$) and the dashed line is a second-order polynomial ($R^2 = 0.65$).



Stream	Average proportion male
A	0.36
Lynx	0.37
C	0.38
Fenno	0.39
Hidden Lake	0.39
Eagle	0.42
Mission	0.43
Hansen	0.43
Pick	0.44
Yako	0.45
Ice	0.45
Bear	0.46
Happy	0.47

Fig. 4.4. Mean Nushagak District fishery selectivity curve, truncated after 560 mm, showing the average proportion of sockeye salmon of different lengths caught by the Nushagak District fishery of Bristol Bay, Alaska between 2000 and 2009, along with the average length of male and female fish in different stream-spawning populations over this time period. The dashed lines represent the 95% confidence intervals of the proportion of fish caught by length. Black and grey letters and arrows refer to males and females, respectively. Also given is the average proportion of males in each population between 2000 and 2009.

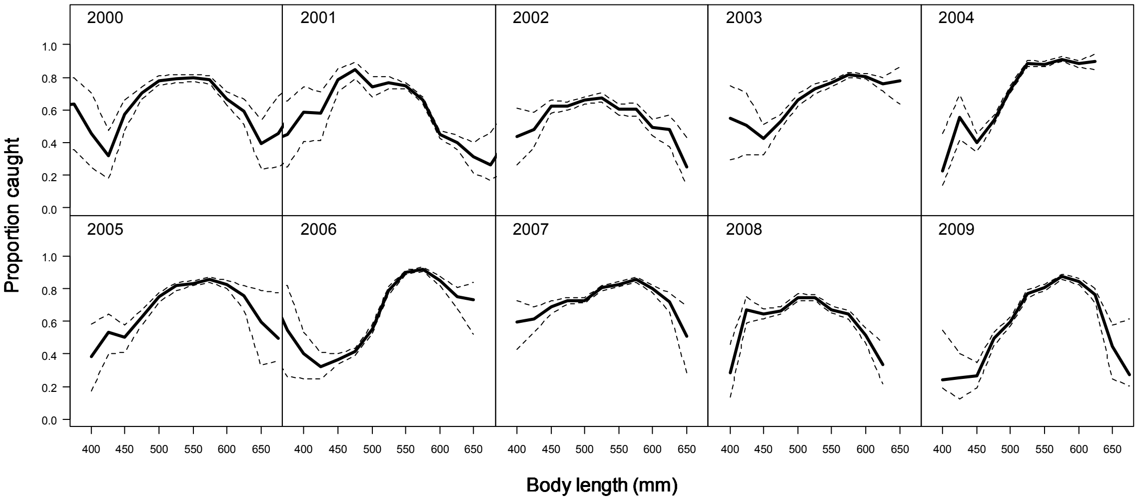


Fig. 4.5. Proportion of sockeye salmon of different lengths caught by the Nushagak District fishery of Bristol Bay, Alaska in 2000 through 2009 (updated from Kendall et al. 2009). The dashed lines represent the 95% confidence intervals of the proportion of fish caught by length.

Chapter Five: Evolution of age and size at maturation of Alaskan sockeye salmon under size-selective harvest

Introduction

Age and size at maturation help determine the success of an individual's reproduction and thus its fitness (Mangel 1996), and are also important in the dynamics of populations. Individuals may mature at younger ages and smaller sizes to avoid additional mortality, such as predation, during continued growth time, but may have lower fecundity than their larger or older counterparts. Such trade-offs are often influenced by the environment in which individuals spawn. Locally adapted populations reproducing in different habitats encounter varying environmental conditions (Reznick et al. 1990; Blair et al. 1993) and predation rates (Reznick et al. 1996; Carlson et al. 2007a) and thus exhibit different patterns of age and size at maturation (Quinn et al. 2001b). Life history traits including age and size at maturation can change rapidly in exploited populations because they are exposed to novel regimes of mortality. Harvest mortality rates can be significantly higher than those of natural mortality (Mertz and Myers 1998), and exploitation is frequently size-selective, removing larger individuals more often than smaller ones (McGraw 2001; Sinclair et al. 2002; Coltman et al. 2003; Carlson et al. 2007b; Darimont et al. 2009; Kendall et al. 2009; Kendall and Quinn In press). Natural differences in age and size at maturation among populations determine the extent to which the populations are affected by size-selective exploitation, so populations may differ in response to selection. Scientists and managers are interested in understanding trait changes and the factors that influence them (Jørgensen et al. 2007).

Life history trait changes in exploited populations can be adaptive, allowing the populations to persist under continued harvest (Fenberg and Roy 2008), or maladaptive if individuals are pushed too far from the range of phenotypes needed for persistence (Conover 2000). In fishes, shifts in the size or age distribution towards smaller or younger individuals have been associated with decreased fecundity (Walsh et al. 2006), increased sexual dimorphism (Wolak et al. 2010), lowered reproductive rates (Venturelli et al. 2009), decreased reproductive potential (Marteinsdottir and Begg 2002; Hutchings 2005), loss of yield (Law and Grey 1989; Conover and Munch 2002), increased variability in abundance (Hsieh et al. 2006, Anderson et al. 2008), and even fishery collapses (Olsen et al. 2004).

Tracking changes in length at age at maturation over time promotes greater understanding of population dynamics and sustainable management. Three general ways to understand age and length at maturation patterns among populations or over time include examination of populations' average length and age at maturation, regression of maturation status (yes or no) against length and age (maturity ogives), and regression of fish that have become mature in a given year (yes or no) against length and age (probabilistic maturation reaction norms [PMRNs]). The average length and age at maturation can be heavily influenced by demographic changes, including changes in growth and mortality, and processes that affect mature and immature fish differently are not accounted for, including changes in growth over time. Maturity ogives and PMRNs are less confounded by demographic processes because they incorporate yearly growth and mortality of individuals in their calculation so as to separate the effects of these processes from other, genetic influences on age and size at maturation (Heino et al. 2002a; Dieckmann and Heino 2007; Heino and Dieckmann 2008). However, maturity ogives do not describe the process of maturation, only the state of being mature. For semelparous species, maturity ogives and PMRNs are the same, but they differ for iteroparous ones.

Norms of reaction show the magnitude of phenotypic plasticity for a given trait—the ranges of potential phenotypes, such as different ages and sizes at maturation, that a given genotype could develop if an individual is exposed to different environmental conditions (Stearns and Koella 1986; Hutchings 2011). PMRNs are bivariate reaction norms and describe the phenotypic maturation schedule of individuals within a given population, showing the probability of a fish becoming mature in the next season as a function of its size and age (Heino et al. 2002a). Specifically, for a given growth and mortality rate, PMRNs show the probability of fish maturing at a specified age and length. Patterns of length at age at maturation of individuals vary over time either because environmental conditions change, affecting growth and mortality, or because of genetic changes, including responses to size-selective harvest, both of which can be visualized using PMRNs (Dieckmann and Heino 2007). By comparing changes in PMRNs over time with changes in length at age and age at maturation, we can better understand the eco-evolutionary dynamics (Carlson et al. 2011; Schoener 2011) affecting these important life history traits and thus better manage the populations when environmental conditions change or with continued size-selective harvest. We can also better understand differences in the maturation length threshold among individual locally adapted populations (Dieckmann and Heino 2007).

PMRNs help to disentangle, to some degree (Heino and Dieckmann 2008; Morita et al. 2009; Kuparinen et al. 2011), phenotypic plasticity of life history traits caused by environmental changes affecting growth and mortality from microevolutionary trait changes associated with size-selective fishing. Phenotypic plasticity (i.e, non-genetic change) refers to environmentally-influenced phenotypic variation in a given trait (Roff 1997). The expression of phenotypic plasticity requires that an individual can sense cues, and thus that cues are available, which signify environmental variation (Scheiner 1993). Plastic changes, such as growth rates, are temporary as they are not passed on to subsequent generations, whereas evolutionary responses alter genotype frequencies (Kuparinen and Merilä 2007). The expression of phenotypic plasticity in age and size at maturation, due to variation in growth and mortality caused by environmental effects, is represented as movement along the reaction norm over time.

Microevolution (i.e., genetic adaptation) comes about when a phenotypic response in a given trait is caused by a selection pressure, such as exploitation or environmental change. The trait under selection must be heritable (Falconer and Mackay 1996). Microevolutionary changes result in different gene expression across generations, which are visualized as changes in the shape or position of a population’s PMRN over time (Olsen et al. 2004; Grift et al. 2007; Mollet et al. 2007; Pardoe et al. 2009). The nature of hunting and fishing suggests that this force may bring about genetic changes (Law 2000;

Allendorf and Hard 2009). However, environmental effects can also lead to evolutionary changes in life history and other traits (Reznick and Endler 1982; Quinn and Adams 1996; Grant and Grant 2002; Carlson et al. 2007a; Crozier et al. 2011). Thus, both human exploitation and environmental factors can lead to rapid microevolution in wild populations, whereas in many cases hunting and fishing do not present the necessary cues to lead to the expression of phenotypic plasticity. When trait changes are observed, it is valuable to understand if microevolution has played a role in addition to phenotypic plasticity; traits changes associated with phenotypic plasticity have greater potential to be reversed, and on shorter time scales, than microevolutionary ones (Hutchings and Reynolds 2004; Kuparinen and Merilä 2007).

Scientists and managers have recognized that length and age at maturation in Pacific salmon (*Oncorhynchus spp.*) have changed over the last half-decade (Ricker 1981; Bigler et al. 1996). These traits are heritable (Carlson and Seamons 2008), and studies examining the size-selective nature of fishery selection on Pacific salmon have shown that larger than average fish have been caught in most, but not all, years (e.g., Kendall et al. 2009; Kendall and Quinn In press). Genetic changes resulting from such size-selective fishing may be associated with decreasing age and size at maturation in some exploited populations (Ricker 1981; Fukuwaka and Morita 2008). Age and size at maturation of Pacific salmon are influenced by an intricate combination of both genetic and environmental factors that are difficult to quantify (Rogers 1987; Pyper and Peterman 1999). Thus, Pacific salmon are also likely responding to changes in growing conditions and expressing phenotypes for smaller size and older ages at maturation (Morita et al. 2005). Age and size at maturation trends of sockeye salmon (*O. nerka*) fluctuate with environmental conditions including density and temperature in freshwater temperature (Quinn et al. 2009), density of other salmon at sea including hatchery fish (Bigler et al. 1996; Cooney and Brodeur 1998; Ruggerone et al. 2003; Ruggerone et al. 2010), sea-surface temperatures (Cox and Hinch 1997; Pyper and Peterman 1999), and changes in species distributions (Hinch et al. 1995). Analysis of size and age trends in many salmon populations is complicated by mixtures of wild and hatchery fish, as the latter experience different growth rates prior to release, and by interceptions of immature fish, thus affecting the observed distribution of ages at maturity.

Sockeye salmon of Bristol Bay, Alaska are an ideal model to evaluate shifts in maturation length thresholds over time and among populations, and whether size-selective fishing can contribute to microevolutionary changes in these thresholds. Bristol Bay is home to one of the largest and most diverse sockeye salmon runs in the world, there are no hatcheries, the salmon spawn in environments largely unaffected by humans (Hilborn et al. 2003a), and a commercial gillnet fishery, known to be size-selective, has exploited a large percentage of fish for over 100 years (Bue 1986; Kendall et al. 2009; Kendall and Quinn In press). Sockeye salmon spawn in a variety of habitats including streams and rivers of varying sizes and beaches. Age and size at maturation vary consistently among spawning populations (Rogers 1987; Blair et al. 1993), making the populations differentially vulnerable to size-selective fishing (Kendall and Quinn 2009).

In this study we estimated PMRNs for length at ocean age 2 at maturation of five locally adapted sockeye salmon (*Oncorhynchus nerka*) spawning populations of Iliamna Lake from 41cohorts (brood year) since 1960 and four spawning populations of the Wood River lakes from 14 cohorts since 1958. Few studies have calculated PMRNs for semelparous species such as salmon (but see Morita et al. 2005; Morita and Fukuwaka 2006; 2007; Kendall et al. 2010; Kinnison et al. 2011), and only Kinnison et al.'s study has examined PMRNs of multiple naturally spawning, locally adapted populations. We assessed patterns of PMRNs over time and among spawning populations. We also compared size-selective fishing mortality with the estimated PMRNs for each spawning population. We hypothesized that PMRNs would vary among the spawning populations and that fisheries-induced evolution would be consistent with changes in PMRNs. However, we also predicted that environmental conditions have affected age and size at maturation patterns in these fish.

Methods

Study site

Our research focused on sockeye salmon spawning in Iliamna Lake and the Wood River lakes, specifically Aleknagik and Nerka, of Bristol Bay in southwest Alaska (Fig. 5.1). These lakes are home to dozens of genetically and ecologically distinct populations. These fish spend one or two years rearing in lakes before migrating to sea, where they typically spend two or three (rarely one or four) more years, returning in June-July and spawning in July-September (Quinn et al. 2009). Size at age vary considerably among spawning populations due to local adaptation (Blair et al. 1993; Quinn et al. 2001b), and this variation affects vulnerability to size-selective fishing mortality (Kendall and Quinn 2009). Iliamna Lake sockeye salmon are fished in the Naknek-Kvichak district as they return to freshwater whereas Wood River lakes sockeye salmon are fished in the Nushagak district. Both fisheries have used set and drift gillnets to catch sockeye salmon since the late 1800s (Bue 1986). The recent 25 year (1985-2009) average total run size to the Naknek-Kvichak district was 14.5 million fish and that of the Nushagak fishing district was 7.2 million fish. Size-selection by these fisheries has varied over time; both larger and smaller than average fish are caught annually. But in most years since 1963 (93% for males and 91% for females for the Naknek-Kvichak fishery; 62% and 89% for males and females, respectively, in the Nushagak fishery) larger than average fish have been caught, leaving smaller fish to escape to the spawning grounds (Kendall et al. 2009; Kendall and Quinn In press).

Data have been collected on these sockeye salmon on two scales since the early 1960s. On a larger scale, personnel from the Alaska Department of Fish and Game (ADFG) have estimated the Naknek-Kvichak and Nushagak fisheries' catch and escapement (i.e., fish that are not caught and go on to spawn) counts and collected age, sex, and length (ASL) data on individual fish on a daily basis throughout the fishing and escapement periods. Catches are calculated by dividing the total weight of fish delivered to processing plants by the average weight of individual fish. At the processing plants, a sample of the catch is measured for length (mid-eye to fork of tail), scales are collected to be read in the lab to determine fish age, and the sex of each fish is recorded. Upstream migrating fish that have escaped the fishery are counted visually using a counting tower or with a sonar system on each of the rivers (Kvichak and Wood). Gear designed to catch the entire range of fish sizes in a non-selective manner is used to collect a sample of the escapement for ASL data. The catch and escapement together comprise the total run. Sockeye salmon do not feed or grow during the final stages of migration so the lengths in the catch and escapement can be directly compared.

On a finer scale, University of Washington (UW) personnel have collected ASL data on the spawning grounds of Iliamna Lake from approximately ten populations during most years since the early 1960s and on the spawning grounds of the Wood River lakes from 1960-1965 and then between 1990-2009 from approximately 15 populations. In general, 110 males and females from each spawning population were sampled during the peak of the spawning season and measured for length (mid-eye to hypural plate, converted to mid-eye to fork of tail based on a regression developed for these populations), and from which otoliths were collected to age the fish. We chose five spawning populations for our analysis from Iliamna Lake (Chinkelyes Creek, Gibraltar Creek, Copper River, Knutson Bay beach, and Woody Island beaches) and four spawning populations from the Wood River lakes (Agulowak River, Hansen Creek, Happy Creek, and Ice Creek; Fig. 5.1 and Table 5.1). These populations had the most complete records and represented the range of spawning sites used by the sockeye salmon in the lakes, including smaller streams to larger rivers and both mainland and island beaches, and the range of body sizes and age compositions seen.

Analyses

To estimate changes in length at age at maturation over time, we first estimated and plotted the average length at age (ocean ages 2 and 3) of sockeye salmon in the nine spawning populations for all years with available data. We examined differences over time using linear models and tested for variation in length among populations using ANOVAs. We also examined age composition temporally, and specifically the proportion of fish of ocean ages 2 and 3. We calculated and plotted these proportions for each spawning population over time. Second, we calculated population-specific PMRNs for Iliamna Lake sockeye salmon from 41 cohorts since 1960 of sexes and ocean age classes. From the Wood River lakes populations, we estimated PMRNs over 14 cohorts from 1958-1962 and 1994-2004.

During the PMRN calculation, the number and length distribution of immature fish must be compared with those of mature fish at a given age and in a given cohort (Heino et al. 2002a). However, length at age distributions of immature salmon are unknown because the fish are only measured at maturity, as they return to freshwater to spawn. Therefore, we reconstructed the unobserved length distributions of these immature fish similar to established methods (Heino et al. 2002b; Morita et al. 2005; Fukuwaka and Morita 2008).

Immature count and length reconstruction

We back-calculated the number and length of immature sockeye salmon in a given cohort based on the length distribution of mature fish observed in the Iliamna and Wood River lakes spawning populations. Immature fish would be shorter and more numerous than the fish that returned to spawn due to growth and mortality in the ocean (Ricker 1976; Ruggerone et al. 2005), fishing mortality by the Japanese high seas fisheries (Harris 1987; Myers et al. 1993), and terminal fishing mortality in the Naknek-Kvichak and Nushagak districts (Kendall et al. 2009; Kendall and Quinn In press). As part of this process, we used annual data on the number and average length of sockeye salmon smolts leaving Iliamna Lake and the Wood River lakes and their length distributions, collected by ADFG and detailed in annual reports (e.g., Crawford et al. 1992; Crawford and Fair 2003).

Length reconstruction was completed separately for each spawning population and by cohort. We took the lengths of mature fish measured on the spawning grounds and back-projected the length of the fish when they were immature, one and two years before they matured, thus estimating lengths after the fish had spent one and two years in the ocean. Salmon marine growth is not linear; Burgner (1991) reported that the increase in body length was convex over time and that length increased most during the first year at sea. Thus, we used equation 1 to back-calculate the immature length (mid-eye to fork of tail) one year before maturation (l'; for sockeye salmon maturing at ocean ages 2 or 3) and two years before maturation (l''; only for fish maturing at ocean age 3) for fish in a given cohort (*c*) that matured at a given freshwater age (*g*; either 1 or 2) and ocean age (*a*; either 2 or 3).

(1a) $$l'_{c,g,a} = l_{c,g,a} - \frac{(l_{c,g,a} - h_{g,c})}{a} * f_{g,a,t-1}$$

(1b) $$l''_{c,g,a} = l'_{c,g,a} - \frac{(l'_{c,g,a} - h_{g,c})}{a-1} * f_{g,a,t-2}$$

In this equation $h_{g,c}$ is the average smolt length in a particular cohort for fish of a given freshwater and ocean age, $l_{c,g,a}$ is the mature fish length by cohort, freshwater age, and ocean age, $f_{g,a,t-1}$ is a growth factor specific to freshwater and ocean age and represents the proportion of growth associated with the year prior to maturation (from age 1 to 2 for ocean age 2 fish and from age 2 to 3 for ocean age 3 fish), and $f_{g,a,t-2}$ is a growth factor specific to freshwater and ocean age and represents the proportion of growth associated with two years prior to maturation (from age 1 to 2). The use of the average smolt length is justified given little variation in smolt lengths of a given freshwater age in a given cohort; Farley et al. (2007) reported that differences in smolt length among years and within age classes and river systems was < 9%. Growth factors were calculated empirically using data from Ruggerone et al. (2005), who reported scale measurements and fork lengths of sockeye salmon of different ages throughout their marine residence. The percent of growth during each year of marine residence was calculated and represented annual growth factors. The growth factor for freshwater age 1, ocean age 2 (abbreviated as 'age 1.2') sockeye was estimated to be 1.04 in their first year in the ocean and 0.96 for their second year. For age 2.2 fish, growth factors were 1.05 and 0.95. Growth factors for age 1.3 fish were 1.07, 1.00, and 0.93, and those for age 2.3 fish were 1.08, 1.00, and 0.92. Other growth factors given by Lander and Tanonaka (1964), Lander et al. (1966), and French et al. (1976) were used in the sensitivity analyses of the PMRNs, which ranged from 1.18-1.46 and 0.54-0.82 for the first and second years in the ocean, respectively, for ocean age 2 fish and 1.69-1.88, 0.4-0.6, and 0.68-0.89 for the first, second, and third year in the ocean, respectively, for ocean age 3 fish.

Next we estimated the number of immature fish one and two years before they matured by adjusting the number of mature fish measured in each spawning population to account for mortality, including natural, high-seas fishing, and inshore fishing mortality. The Japanese high seas fishing mortality was included in the overall offshore rates, which therefore were a combination of high seas fishing and natural mortality. We were not interested in the timing of mortality within a year but its annual sum. We estimated cohort-specific offshore annual instantaneous mortality rates ($M_c yr^{-1}$) for the penultimate and ultimate year that salmon were in the ocean as

$$(2) \qquad M_c yr^{-1} = |\ln(1-(0.1 * e^{-\frac{B_c}{D_c}})|,$$

where B_c was the total number of adults returning for each cohort and D_c was the total number of smolts in that cohort. Furnell and Brett (1986) concluded that approximately 90% of marine natural mortality if sockeye salmon occurs in the first four months in the ocean, so thus we estimated $M_c yr^{-1}$ values corresponding to 10% of total interval marine mortality for a given cohort. These values ranged from 0.048-0.11. In years for which total smolt counts were not available, we used the average instantaneous mortality rate estimates of adjacent years. A range of instantaneous marine mortality rates for sockeye salmon estimated by Fredin (1965), Ricker (1976), and Furnell and Brett (1986) were used in the sensitivity analyses. We chose to use only values that were unbiased based on Ricker's (1976) review and specific to the penultimate and ultimate year of a sockeye salmon's life in the ocean. Fredin (1965) reported an annual M value for the penultimate year in the ocean of 0.22 yr^{-1} for ocean age 3 fish, Ricker (1976) gave annual M values for the final year in the ocean of 0.14 yr^{-1}, 0.23 yr^{-1}, and 0.24 yr^{-1} (depending on the population and ocean age), and Furnell and Brett (1986) listed annual M values for the penultimate year of 0.12 yr^{-1} and for the ultimate year of 0.048 yr^{-1} and 0.096 yr^{-1} (lower for older fish).

Inshore fishing mortality by the Naknek-Kvichak and Nushagak fishing districts were calculated as the yearly (y) proportion of fish caught (u), by 10 mm length bins, as in Kendall et al. (2009). Specifically, each year's proportion caught value was estimated as the number of fish caught (X), by length bin, divided by the number of fish in the total run (catch plus escapement; E) of that length.

$$u_{l,y} = \frac{X_{l,y}}{X_{l,y} + E_{l,y}} \tag{3}$$

These proportions were calculated for all fish of both sexes and all ocean ages because fish are caught based on length rather than sex or age and ranged from 0.005 to 0.98.

We estimated the number of immature individuals (i) by length (l' and l''), freshwater age (g), ocean age (a), sex (s), cohort (c), and spawning population (p) one year (y) prior to their maturation (for sockeye salmon maturing at ocean ages 2 or 3) using equation 4a and two years prior (for fish maturing at ocean age 3) using equation 4b.

$$i_{l',g,a-1,c,y-1,s,p} = \frac{n_{l,g,a,c,y,s,p}}{(1-u_{l,y})e^{-(M_c)}} \tag{4a}$$

$$i_{l'',g,a-2,c,y-2,s,p} = \frac{i_{l',g,a-1,c,y-1,s,p}}{e^{-(M_c)}} \tag{4b}$$

The mature fish (n) were counted and measured directly on the spawning grounds. For Iliamna Lake the total number of mature fish for all populations, cohorts, and sexes was 15,720 and the total number of back-calculated immature fish was 23,570 and for the Wood River lakes the total numbers of mature and immature fish were 4,133 and 11,098, respectively.

After completion of these calculations, the numbers of immature fish in the same cohort were added together and the associated immature length distributions were combined to get the complete count and length at age distribution for the immature fish of the cohort. Each length distribution was examined to confirm that it was realistic, that was not bimodal, and that immature fish were on average smaller than mature ones (Heino et al. 2002b).

PMRN estimation

PMRNs were calculated for sex-cohort-spawning population groupings of ocean age 2 that had ten or more length at age data points available for both mature and immature fish (so that small samples sizes would not skew the results). Insufficient numbers of mature ocean age 1 fish were available to calculate PMRNs for this group. Condition and growth rate can also be included in the calculation of PMRNs to help explain maturation (Morita and Fukuwaka 2006; Grift et al. 2007; Mollet et al. 2007; Uusi-Heikkilä et al. 2011), but could not be calculated from our available data.

The probability of a fish maturing (o) was calculated from the individual mature ($n_{l,g,a,c,y,s,p}$) and immature ($i_{l',g,a-1,c,y-1,s,p}$ and $i_{l'',g,a-2,c,y-2,s,p}$) fish data using logistic regression with binomial error distribution, as maturation is a binary response variable (0 or 1; Heino et al. 2002a). We used the generalized linear model (GLM) framework in the program R (R Development Core Team 2009). Different GLMs were used to estimate o (Table 5.2), represented by equations 5a-f, based on length (continuous variable), population (categorical), cohort (categorical), and sex (categorical). We also used models 5a-f that included two-way interactions between the predictor variables (we did not include three- or four-way interactions due to the difficulty of interpreting them).

(5a) $\text{logit}(o) \sim \beta_0 + \beta_1 l + \beta_c$

(5b) $\text{logit}(o) \sim \beta_0 + \beta_1 l + \beta_c + \beta_s$

(5c) $\text{logit}(o) \sim \beta_0 + \beta_1 l + \beta_p$

(5d) $\text{logit}(o) \sim \beta_0 + \beta_1 l + \beta_p + \beta_s$

(5e) $\text{logit}(o) \sim \beta_0 + \beta_1 l + \beta_p + \beta_c$

(5f) $\text{logit}(o) \sim \beta_0 + \beta_1 l + \beta_p + \beta_c + \beta_s$

We selected the best models using calculated AIC_c values (AIC with a correction for finite sample sizes; Burnham and Anderson 2002). Lower AIC_c values indicate support for models providing a balance between better fits to the data and not being over-parameterized. Utilizing the best model, we estimated the PMRN, including the length at which the probability of maturing was 50% (L_{P50}; the midpoint) and the maturation envelope, represented at its edges as the length at which the probability of maturing is 25% (L_{P25}) and 75% (L_{P75}). Values were estimated for fish of each ocean age on a cohort, sex, and spawning population basis. Equations 6a-c are the estimators associated with equation 5f above.

$$L_{P50_{a,c,s,p}} = -\frac{\beta_0 + \beta_c + \beta_s + \beta_p}{\beta_l} \tag{6a}$$

$$L_{P25_{a,c,s,p}} = \log(1/3) - \frac{\beta_0 + \beta_c + \beta_s + \beta_p}{\beta_l} \tag{6b}$$

$$L_{P75_{a,c,s,p}} = \log(3) - \frac{\beta_0 + \beta_c + \beta_s + \beta_p}{\beta_l} \tag{6c}$$

Variation in PMRNs over time was evaluated by assessing the significance of the coefficients for the year terms in the GLMs and by regressing L_{P50} values against cohort (here as a continuous variable) to examine trends over time. To evaluate differences in L_{P50} values among spawning populations and between males and females we examined the significance of the population terms in the GLMs.

We estimated the PMRN uncertainty by bootstrapping the original data 1000 times. Specifically, for each cohort and spawning population, by sex, freshwater age, and ocean age, we sampled with replacement the length data 1000 times, used these data to re-estimate the immature length and counts, and recalculated the L_{P50} value. We presented the 2.5th and 97.5th quantiles of these bootstraps as the 95% confidence intervals for the L_{P50} values. Given the uncertainty of various parameters in the calculation of sockeye salmon PMRNs, especially marine growth and mortality, we also performed a sensitivity analysis. As noted above, various marine growth factors and mortality values were used to recalculate the PMRNs to see how sensitive the L_{p50} estimates were to the different variables. Specifically, these included four marine instantaneous mortality values, 0.05, 0.1, 0.2, and 0. 3 yr^{-1}, and four growth factors combinations, listed in Table 5.3.

Comparisons of L_{P50} trends with fishing mortality and environmental trends

We calculated two metrics describing the fishing mortality and size-selectivity experienced by fish in each population over time and evaluated their correlation with PMRN trends. We first estimated each population's annual exploitation ratio using methods detailed in Kendall and Quinn (2009). Briefly, we used the estimated fishing mortality ratios (equation 3; $u_{l,y}$) along with the number of fish counted on the spawning grounds for each population (post fishing; $N_{l,p,y}^{post}$) to quantify the yearly pre-fishery length distribution of fish in each spawning population ($N_{l,p,y}^{pre}$). This was done by dividing the number of fish observed in each spawning population (post-fishery) of a given length bin by an expansion factor incorporating the proportion caught (equation 7).

$$(7) \qquad N_{l,p,y}^{pre} = \frac{N_{l,p,y}^{post}}{1-u_{l,y}}$$

We used these population-specific pre-fishery length distributions, along with the spawning ground distributions, to quantify yearly Naknek-Kvichak and Nushagak fishery exploitation ratios on individual spawning populations. This was measured as the proportion of sockeye salmon caught by the fishery from a given population in a given year ($V_{p,y}$).

$$(8) \qquad V_{p,y} = 1 - \frac{\sum_{l} N_{l,p,y}^{post}}{\sum_{l} N_{l,p,y}^{pre}}$$

Second, we estimated population-specific fishery size-selectivity (Kendall and Quinn 2009) by calculating length-based standardized selection differentials (SSDs) by year ($SSD_{p,y}$) (equation 9), which describe the difference in average length of fish in a given population after fishing ($\bar{L}_{p,y}^{post}$) vs. those in the population before fishing occurred ($\bar{L}_{p,y}^{pre}$). Negative values mean that larger fish than average were removed by the fishery and positive values mean that smaller fish were caught. These values were standardized by dividing them by the standard deviation of length of fish before fishing ($\sigma_{p,y}^{pre}$), allowing comparison among years (Law and Rowell 1993).

$$(9) \qquad SSD_{p,y} = \frac{\overline{L}_{p,y}^{post} - \overline{L}_{p,y}^{pre}}{\sigma_{p,y}^{pre}}$$

We examined correlations between each population's L_{P50} trends and population-specific fishing exploitation rates ($V_{p,y}$) and SSDs. L_{P50} trends correlated with fishing rates may indicate evolutionary changes in maturation schedules in addition to those associated with phenotypic plasticity (Heino and Dieckmann 2008; Pardoe et al. 2009).

Results

The average lengths at ocean ages 2 and 3 of male and female sockeye salmon spawning in Iliamna Lake and the Wood River lakes of Bristol Bay, Alaska have decreased over time (Fig. 5.2). While the slopes of average length of fish for all Iliamna and Wood River lakes ocean age-sex-spawning population groups were negative, they were significantly different than zero for ten of the 20 Iliamna Lake groups (Gibraltar Creek ocean age 3 males and females, Gibraltar Creek age 2 males, Woody Island beaches ocean age 2 males and females, Woody Island age 3 females, Copper River ocean age 3 males and females, Chinkelyes Creek ocean age 3 males, and Knutson Bay beach ocean age 2 females) and all of the Wood River lakes groups (linear models, $p < 0.004$ using Šidák correction for multiple comparisons). Average length at age also differed between males and females in most spawning populations, including all but one of the Iliamna Lake age-populations pairs and all but one of the Wood River lakes pairs (ANOVAs, $p < 0.005$ using Šidák correction).

Populations differed in the age composition (Table 5.1 and see Blair et al. 1993; Quinn et al. 2001b; Kendall and Quinn 2009), and in populations with older fish, fish also tended to be larger at a given age. While the slopes of linear regressions plotting age composition over time for different populations were a range of negative and positive values, no statistically significant trends in age composition were detected for fish of either sex in any Iliamna or Wood River lakes populations (ANOVAs, $p > 0.01$ required by the Šidák correction).

Counts and lengths of immature fish at ocean age 2 were estimated for each spawning population and cohort using the back-calculation methods. Immature lengths were smaller than mature lengths for each ocean age, though the combined immature and mature fish length distributions at age were generally bimodal (Fig. 5.3a). These length at age distributions changed more with different marine growth factors included in the sensitivity analysis than with the different marine mortality rates. The combined immature and mature fish length distributions at age were unimodal for growth factor combinations 3 and 4 (Fig. 5.3b).

Results from the generalized linear model used to estimate the probability of maturation, and thus the PMRNs, suggested that length, population, cohort, and sex were all important factors in predicting maturation (Table 5.2). The best-fit model showed that p-values associated with many, but not all, cohorts were < 0.05, emphasizing variation in maturation length thresholds over time. Also, regression models showed that the length at which the probability of maturing was 50% (L_{P50}) of ocean age 2 fish decreased over time for males and females in all populations from both Iliamna and the Wood River lakes (Fig. 5.4). These changes were statistically significant among Iliamna Lake fish for females in Gibraltar Creek, Knutson Bay beaches, and Woody Island beaches (linear models, $p < 0.01$ using Šidák correction), and for males in Knutson Bay beaches and Woody Island beaches ($p < 0.01$ using Šidák correction). For Wood River lake populations, L_{P50} values decreased significantly over time for females in three populations, Hansen, Happy, and Ice creeks (linear model, slope $p < 0.01$ using Šidák correction), and for males in all populations ($p < 0.004$). The best-fit GLM also showed that p-values associated with most populations were < 0.05, emphasizing the variation in maturation length thresholds among populations, and that females differed significant in maturation length thresholds than males ($p < 0.000001$ for both Iliamna and Wood River lakes).

Reaction norm envelopes, representing the difference between the length at which the probability of maturation was 25% (L_{P25}) and 75% (L_{P75}) were very narrow, ~ 2.2 mm wide for all populations and cohorts, suggesting a sharp maturation length threshold.

PMRNs shifted more for populations in the Wood River lakes than in Iliamna Lake. In Iliamna Lake, L_{P50} values (determined by linear extrapolation) for female (Fig. 5.4a) and male (Fig. 5.4b) sockeye salmon spawning on Woody Island beaches decreased by 21 mm (from 432 to 411 mm) and 29 mm (from 459 to 430 mm), respectively, between the 1960 and 2004 cohorts. For Knutson Bay beach spawners L_{P50} values for females and males decreased 7 and 24 mm, respectively. Finally, Gibraltar Creek L_{P50} values for females decreased by 20 mm (from 453 to 433 mm). For Wood River lakes populations, L_{P50} values shifted by 73 mm (480 to 407 mm) for female sockeye salmon (Fig. 5.4c) and 75 mm (795 to 420 mm) for males (Fig. 5.4d) in Hansen Creek between the 1958 and 2004 cohorts. L_{P50} values of Happy Creek females and males decreased by 47 and 71 mm, respectively, and L_{P50} values for males from Ice Creek decreased by 59 mm and those of females decreased by 53 mm. Finally, Agulowak River male L_{P50} values decreased 55 mm (508 to 453 mm).

Sockeye salmon spawning populations with smaller fish at a given ocean age had smaller L_{P50} values than populations whose fish were longer at a given age (regression of average length of ocean age 2 fish and L_{P50} values: slope $p < 0.0001$ and $R^2 = 0.49$ for Iliamna Lake populations; slope $p < 0.0001$ and $R^2 = 0.93$ for Wood River lakes populations). Because spawning habitat shapes average fish size (Blair et al. 1993; Quinn et al. 2001b), L_{P50} values were similar among populations spawning in similar habitats; small stream-spawning populations had smaller L_{P50} values, L_{P50} values increased for fish spawning in larger streams, and river and mainland beach spawners had the largest L_{P50} values. Island beach spawners are known to be shorter at a given age than fish in other Iliamna Lake spawning populations and had corresponding smaller L_{P50} values.

L_{P50} values changed little across the range of ocean instantaneous mortality rates used in the sensitivity analysis (Table 5.4). Specifically, L_{P50} values decreased by 0-1.7 mm for Iliamna Lake spawning populations and 0-2.1 mm for Wood River lakes populations. The change varied among populations and between males and females. However, even when the ocean mortality rate of 0.3 was used, there were no differences in the PMRN findings; they decreased over time for all populations and there were no differences in the significance of these changes from the original mortality values used. However, L_{P50} values differed considerably with different marine growth factors used to estimate immature fish lengths. Specifically, L_{P50} values decreased for all populations and all growth factor combinations by 2.8-38.7 mm for Iliamna Lake populations and 2.8-45.4 mm for Wood River lakes populations. Using growth factor combination 4 (Table 5.3), we found considerable differences in the statistical significance of L_{P50} declines for Iliamna Lake populations but not Wood river lakes populations. Specifically, for Iliamna Lake fish significant declines were only seen for 2 sex-spawning populations groups using growth factor combination 4, whereas originally this was seen for five groups. Also, only one population was found to have declined significantly using both the original and combination 4 growth factors. For the Wood River lakes populations, the decline in L_{P50} values for one population (Happy Creek males) was no longer statistically significant but no changes were found for the other sex-population groups using growth factor 4 values. The declines in L_{P50} values differed among the spawning populations when the various ocean mortality rates and growth factors were used. Finally, the width of the PMRN envelope also did not change with different ocean mortality rates or growth factors.

Exploitation rate and size-selective fishing varied over time, limiting the power to detect significant differences in these metrics among populations. Overall, though, average SSDs were negative for all nine Iliamna and Wood River lakes spawning populations (one-sided t-test, $p < 0.0001$ for both Iliamna and Wood River lakes populations), consistent with the overall decreases in the PMRNs across all populations. We also found that exploitation rates were higher (Wood River lakes average = 0.60 for all populations and cohorts, Iliamna Lake average = 0.45; t-test, $p < 0.00001$) and SSDs were more negative for the Wood River lakes populations than for the Iliamna Lake populations (Wood River lakes average = -0.25, Iliamna Lake average = -0.14; t-test, p =

0.00003). Consistent with these differences, L_{P50} values decreased more for Wood River populations than for Iliamna populations.

The Iliamna Lake populations did not vary significantly in estimated exploitation rates or SSDs and thus, not surprisingly, these features were not linked to differences in maturation length thresholds. For the Wood River lakes spawning populations, though, size-selective fishing may have influenced changes in maturation length thresholds over time more than overall exploitation. Specifically, we found larger declines in L_{P50} values for sockeye salmon from Hansen Creek than those from the Agulowak River. In an earlier study Kendall and Quinn (2009) reported, and here we confirmed, that since the early 1960s more fish from large-bodied populations (Agulowak River and Ice Creek) were caught by the fishery than from shorter-bodied populations (e.g., Hansen Creek). On the other hand, Kendall and Quinn (2009) also found that SSDs were most frequently negative and greater in magnitude for Hansen Creek and other small-bodied populations than populations with larger fish. These SSD findings aligned more closely with the PMRN trends (greater decreases in smaller-bodied populations than larger-bodied) than the exploitation rates, and these findings are congruent with greater microevolutionary changes towards a lower maturation length threshold by the populations whose larger than average fish were harvested.

Discussion

Sockeye salmon from numerous spawning populations of Bristol Bay, Alaska have become significantly shorter at a given age since the early 1960s. For males and females of ocean age 2 and 3 from a total of nine populations in Iliamna Lake the Wood River lakes, all 36 age-sex-spawning population groups have become shorter, 26 statistically significantly so. The significant decreases in length at age ranged from 22 to 37 mm for Iliamna Lake populations between the 1960 and 2004 cohorts and from 62 to 106 mm for Wood River lakes populations between the 1958 and 2004 cohorts. Length at maturation is an important life history trait linked to fecundity (Mangel 1996), so such decreases have the potential to impact the sustainability of these fish. On the other hand, age composition has not changed for these populations over time; specifically, the number of fish spending three years in the ocean has not changed significantly. Morita et al. (2005) concluded that decreases in Pacific salmon size at maturation, concurrent with increases in age, are likely an adaptive response to reduced growth rate. However, we found that factors in addition to changes in growth have contributed to age and size at maturation shifts in Bristol Bay sockeye salmon, and PMRN results showed that these factors were likely related to size-selective fishing.

In this study we applied the PMRN methodology for the first time to multiple spawning populations of an exploited fish stock. We successfully estimated PMRNs, or maturation length thresholds, for Iliamna and Wood River lakes sockeye salmon spawning populations using five decades of age, sex, and length data from fish collected on the spawning grounds to back-calculate the number and length of immature fish in the ocean. PMRNs differed among many, but not all, cohorts and decreased over time for all spawning populations. The length at which the probability of maturing was 50% (L_{P50}) decreased significantly over time in five of ten Iliamna Lake sex-spawning population groups and in seven of eight Wood River lakes sex-population groups. The significant decreases in L_{P50} values ranged from 7 to 29 mm for Iliamna Lake populations between the 1960 and 2004 cohorts and from 47 to 76 mm for Wood River lakes populations between the 1958 and 2004 cohorts. This suggests that for given growth and mortality rates, Iliamna Lake and Wood River lakes sockeye salmon in many spawning populations tend to mature at smaller sizes than in the past. We also found significant differences in maturation length thresholds among most spawning populations and between males and females. Finally, spawning populations whose fish were smaller at a given age were found to have lower maturation length thresholds (smaller L_{P50} values) and populations with larger fish had higher thresholds.

Bristol Bay sockeye salmon have experienced heavy but variable size-selective harvest by gillnet fisheries since the late 1800s (Bue 1986; Kendall et al. 2009; Kendall and Quinn In press). Average standardized selection differentials (SSDs) have been significantly negative for all Iliamna and Wood River lakes spawning populations, implying that larger than average fish have been removed, leaving smaller individuals to spawn. The decreases in L_{P50} values over time are strongly correlated with this size-selective fishing. However, decreases in L_{P50} values were not significant for all spawning populations, and this may be due to the large variation in fishery selection over time. Although in most years larger than average fish have been caught, in some years smaller fish have been preferentially harvested and the magnitude of the selection has ranged greatly over time. Fewer Iliamna Lake spawning populations showed changes in maturation length thresholds than Wood River lakes fish, and these fish experienced lower exploitation rates and less size-selectivity than Wood River lakes fish. Overall, our findings support the hypothesis that changes in length at age at maturation exhibited by some spawning populations were microevolutionary adaptations to size-selective exploitation and thus represent fisheries-induced evolution. However, changes in maturation length thresholds in some populations were not detected, perhaps due to variation in the size-selective exploitation, the exploitation being less size-selective, or lower exploitation rates. In addition, it is possible that the changes took place but were masked by insufficient or unrepresentative sampling.

PMRN estimates are only valid if variability in growth and maturation can be attributable mainly to environmental variation rather than genetic differences (Dieckmann and Heino 2007). For this reason, we estimated PMRNs separately for each spawning population. The Iliamna and Wood River lakes spawning populations are genetically distinct (Lin 2008; Gomez-Uchida et al. 2011) and exhibit distinct life history patterns including age and size at maturation (Rogers 1987; Blair et al. 1993; Quinn et al. 2001b). Together, these findings suggest that the PMRN is a population-specific attribute reflecting genetic differences among populations, which was also shown for Columbia River sockeye salmon populations of the United States and Canada (Kendall et al. 2010). By visualizing the PMRNs for each population over time, we can see that these thresholds vary among populations and have changed temporally.

We did not find statistically significant changes in age composition in Iliamna and Wood River lakes sockeye salmon. Decreases in the maturation length threshold suggest that if growing conditions had remained the same over time, we would have seen the fish maturing at younger ages in recent years. Because such shifts in the age composition have not been realized, we conclude that additional factors have contributed to length and age at maturation in the fish, likely including environmental changes resulting in decreased growth. With slower growth in the ocean, fewer sockeye salmon would have reached the maturation length threshold at younger ages and the age composition may not have changed. Additionally, changes in variation in the length of fish at a given ocean age over time could have contributed to decreased length at age but not age at maturation.

Both freshwater and ocean environmental conditions are well-known to directly and indirectly affect sockeye salmon growth and thus age and size at maturation. For Iliamna and Wood River lakes sockeye salmon, changes in growth as a result of such environmental variation have likely interacted with changing PMRNs and resulted in the maturation schedules and length and age compositions seen on the spawning grounds. An increasing number of studies have shown that both phenotypic plasticity, resulting from changing environmental conditions, and adaptive evolution, due to size-selective fishing and other forces, can contribute to life history trait changes (Bigler et al. 1996; Dieckmann and Heino 2007; Gienapp et al. 2007; Kuparinen and Merilä 2007; Fukuwaka and Morita 2008; Crozier et al. 2011), and our study supports the interaction of these effects in shaping age and size at maturation.

The sensitivity analysis showed that our PMRN findings were generally insensitive to marine mortality rate variation but that maturation length thresholds did vary with different marine growth factors used to estimate immature length distributions. Even with the most different growth factors, the slopes for PMRNs for all spawning populations still decreased, but differences in the significance of these declines were noted. These differences were greater for Iliamna Lake spawning populations, where fewer, and different, populations were found to have significant declines in PMRNs. Still, the general patterns remained the same across the different values used in the sensitivity analysis. Specifically, PMRNs were found to decrease significantly over time in some, but not all, spawning populations, and these declines were more frequently noted for the more heavily fished Wood River system spawning populations than for Iliamna Lake populations. Further research to estimate marine growth factors observed in Bristol Bay sockeye salmon with greater precision and confidence could help to clarify population-specific L_{P50} trends.

The degree to which shifts in PMRNs can indicate microevolution remains somewhat uncertain; the methodology has been criticized for not disentangling genetic and environmental effects affecting maturation other than through size at age (Kraak 2007; Marshall and McAdam 2007; Thorpe 2007; Wright 2007; Kinnison et al. 2011; Uusi-Heikkilä et al. 2011), and studies have shown that environmental factors can affect PMRNs directly, not just through growth (Morita et al. 2009; Kuparinen et al. 2011). While PMRNs tease apart phenotypic plasticity and microevolution to some degree, the method is a purely phenotypic approach and therefore cannot demonstrate genetic change directly (Hard et al. 2008). Kinnison et al. (2011) found that the main evolutionary change among spawning populations experiencing different environmental conditions was in growth rate rather than maturation length threshold. Though PMRNs are not a perfect tool, they can help to track changes in important life history traits, examine differences among populations, and better understand the contribution of harvest to microevolutionary changes in exploited populations. The genetic data needed to create animal models (Kruuk 2004) and conclusively show genetic evolution in exploited populations are very difficult, if not impossible, to collect at this time for large wild populations such as Bristol Bay sockeye salmon and thus other methodologies are needed to help scientists and mangers understand life history trait shifts and the factors behind them.

We attempted to account for as many factors influencing growth and mortality of Iliamna and Wood River lakes sockeye salmon as our data allowed while calculating the PMRNs. One factor we were not able to incorporate was size-specific mortality by the Japanese high seas gillnet fisheries. These fleets caught thousands of Bristol Bay sockeye salmon in the open ocean from the mid-1950s to 1991 (Ossiander 1965; Myers et al. 1993). North Pacific high seas fisheries treaty revisions in 1977-78 resulted in a sharp decline of North American sockeye salmon, including those from Bristol Bay, caught by the Japanese high seas fishery (Harris 1987). No specific length or age data on high seas catches were available for us to include in our analyses, but this fishery likely caught more ocean age 3 fish because they spent more years in the ocean and their distribution was further west. However, we may estimate that because size-selective gillnets were used (Fukuwaka and Morita 2008) selective fishing similar to that of the Naknek-Kvichak and Nushagak nearshore gillnet fisheries resulted. However, fishing mortality on the high seas can have different consequences than that on the breeding grounds (Law 2000; Hard et al. 2008; Eldridge et al. 2010).

Fishery managers should be wary of genetic changes associated with size-selective harvest (Allendorf and Hard 2009). Managers need to know about the potential for genetic changes to take place in exploited populations and understand the consequences of such changes. Fishery managers can use information about changes in age and size at maturation to adjust fishing strategies in the short and long term; they may want to reduce exploitation rates or change gillnet mesh size regulations to catch fewer large fish (Kendall et al. 2009; Kendall and Quinn In press). Reversing trends towards smaller sizes at age may be difficult; while removing the selective pressure on large fish may slow or stop the changes in maturation size, selection towards the original genotype in the absence of fishing may be weaker than selection caused by intensive fishing (Law and Grey 1989; Law 2000; Fukuwaka and Morita 2008; Conover et al. 2009). However, we also found less evidence of microevolutionary changes in maturation length thresholds for some Bristol Bay sockeye salmon spawning populations, which may be associated with lower overall exploitation rates and/or temporal variation in size-selective fishing. Overall, we should be aware of the combined consequences of environmental changes that alter growth rates and size-selective fishing that alters maturation length thresholds on salmon age and length at maturation patterns. We also need to understand that locally adapted populations often have different maturation length thresholds, so these populations should be managed as unique entities and transfer of individuals between populations, such as for stocking purposes, should be done with full information and with caution (Ayllon et al. 2006). Armed with this information, scientists and managers can work together to successfully manage exploited fish stocks with different population structures into the future.

Table 5.1. Spawning site characteristics, average length of mature ocean age 2 sockeye salmon, and proportion of fish of ocean age 2 in five Iliamna Lake and four Wood River lakes spawning populations sampled between 1962 and 2009 (Demory et al. 1964; Marriott et al. 1964). Beaches are extensive and thus width is not especially meaningful so not given.

Lake	Population	Habitat type	Avg. spawning site width (m)	Avg. length ocean age 2 fish (mm)	% ocean age 2 fish
Iliamna	Copper River	intermediate river	21	490	59
	Gibraltar Creek	intermediate river	15	495	52
	Chinkelyes Creek	large river	29	504	68
	Woody Island beaches	island beach	-	483	69
	Knutson Bay beaches	mainland beach	-	507	74
Wood River	Hansen Creek	small stream	2	481	77
	Happy Creek	intermediate stream	3	501	53
	Ice Creek	large stream	15	516	33
	Agulowak River	large river	60	525	29

Table 5.2. Models used to predict maturation of Iliamna Lake and Wood River lakes sockeye salmon, and thus estimate PMRNs, along with their ΔAIC_c values (the difference between each model's AIC_c value and that of the model with the lowest value).

	Iliamna Lake		**Wood River Lakes**	
Variables in model	**# parameters**	**ΔAICc**	**# parameters**	**ΔAICc**
Length + cohort	43	1950	15	758
Length * cohort	84	1845	28	730
Length + sex	3	2954	3	4428
Length * sex	4	2645	4	4265
Length + cohort + sex	44	1177	16	402
Length + population	6	2995	5	2760
Length * population	10	2946	8	2760
Length + population + sex	7	2067	6	2524
Length + population + cohort	47	1281	18	400
Length + population * cohort	211	835	57	316
Length * population + cohort	51	1244	21	357
Length + population + cohort + sex	48	540	19	102
Length * population + cohort + sex	52	497	22	87
Length + population * cohort + sex	212	243	58	46
Length + population + cohort * sex	89	463	32	102
Length * population + cohort * sex	93	399	35	83
Length + population * cohort * sex	421	193	113	68
Length * cohort + population * sex	93	424	35	70
Length * cohort + population + sex	89	473	32	74
Length + cohort * population + sex	212	243	58	46
Length * sex + cohort * population	213	0	59	0
Length * sex + cohort + population	49	305	20	58
Length + sex * population + cohort	52	498	22	88

Table 5.3. Marine growth factors used to calculate PMRNs for Bristol Bay, Alaska sockeye salmon in the sensitivity analysis.

Growth factors number	Year 0-1, ocean age 2	Year 1-2, ocean age 2	Year 0-1, ocean age 3	Year 1-2, ocean age 3	Year 2-3, ocean age 3
1	1.5	0.5	1.7	0.4	0.9
2	1.6	0.4	1.7	0.6	0.7
3	1.7	0.3	1.8	0.5	0.7
4	1.8	0.2	1.9	0.45	0.65

Table 5.4. The range of L_{P50} values estimated for Iliamna Lake and Wood River lakes sockeye salmon in the sensitivity analysis based on different marine mortality values (0.05, 0.1, 0.2, and 0.3) and marine growth factors (listed in Table 5.3).

Lake	Differing factor	Average difference in L_{P50} value (mm)				
		Chinkelyes Creek	Copper River	Gibraltar Creek	Knutson Bay beach	Woody Island beaches
Iliamna		**males**				
	Ocean mortality rate = 0.05	0.1	0.4	0.2	0.2	0.2
	Ocean mortality rate = 0.1	-0.2	-0.1	-0.1	0.0	-0.1
	Ocean mortality rate = 0.2	-0.5	-0.9	-0.8	-0.3	-0.4
	Ocean mortality rate = 0.3	-0.9	-1.7	-1.3	-0.9	-0.6
	Growth factors 1	-3.5	-3.8	-4.7	-3.9	-2.9
	Growth factors 2	-23.8	-27.1	-31.6	-26.5	-19.8
	Growth factors 3	-23.8	-27.1	-31.6	-26.5	-19.8
	Growth factors 4	-27.9	-33.2	-38.7	-31.2	-24.0
		females				
	Ocean mortality rate = 0.05	0.2	0.1	0.1	0.1	0.1
	Ocean mortality rate = 0.1	0.0	0.0	0.0	0.0	0.0
	Ocean mortality rate = 0.2	-0.2	-0.4	-0.4	-0.4	-0.3
	Ocean mortality rate = 0.3	-0.4	-0.8	-0.5	-0.7	-0.4
	Growth factors 1	-3.2	-3.0	-3.5	-3.2	-2.8
	Growth factors 2	-24.7	-23.7	-25.2	-22.6	-20.7
	Growth factors 3	-24.7	-23.7	-25.2	-22.6	-20.7
	Growth factors 4	-30.0	-28.9	-31.0	-27.1	-24.4
		Agulowak River	**Hansen Creek**	**Happy Creek**	**Ice Creek**	
Wood River		**males**				
	Ocean mortality rate = 0.05	0.0	0.2	0.1	0.1	
	Ocean mortality rate = 0.1	0.0	0.0	0.0	0.0	
	Ocean mortality rate = 0.2	-0.2	-0.4	-2.0	-0.4	
	Ocean mortality rate = 0.3	-0.4	-1.0	-2.1	-0.6	
	Growth factors 1	-4.0	-3.3	-4.3	-5.3	
	Growth factors 2	-29.1	-20.8	-31.6	-36.2	
	Growth factors 3	-29.1	-20.8	-31.6	-36.2	
	Growth factors 4	-36.4	-24.6	-39.0	-45.4	
		females				
	Ocean mortality rate = 0.05	0.0	0.1	0.1	0.0	
	Ocean mortality rate = 0.1	0.0	0.0	0.0	0.0	
	Ocean mortality rate = 0.2	0.0	-0.2	-0.6	-0.1	
	Ocean mortality rate = 0.3	0.0	-0.3	-0.7	-0.2	
	Growth factors 1	-2.8	-4.1	-3.7	-3.5	
	Growth factors 2	-35.7	-24.4	-26.4	-27.9	
	Growth factors 3	-35.7	-24.4	-26.4	-27.9	
	Growth factors 4	-42.8	-28.2	-32.7	-34.7	

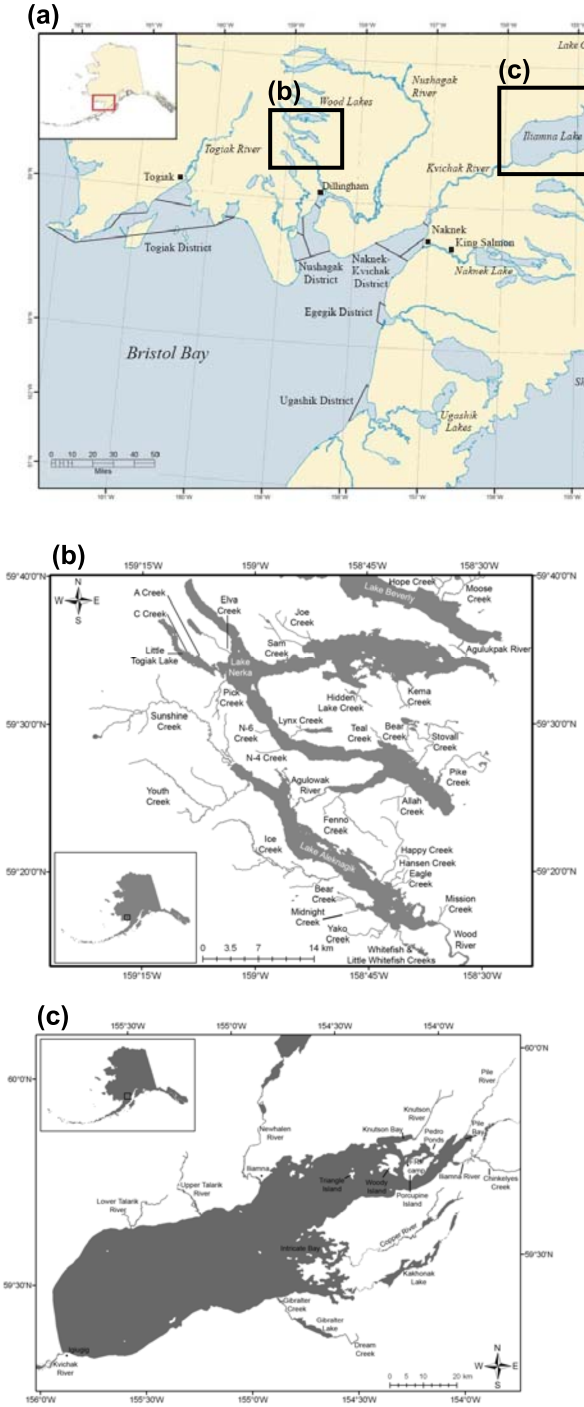


Fig. 5.1. Maps of Bristol Bay, Alaska (a) showing the location of the spawning populations whose PMRNs were estimated in this study. Iliamna Lake (b) sockeye salmon are exploited by the Naknek-Kvichak fishery while Wood River lakes (c) fish are targeted by the Nushagak fishery.

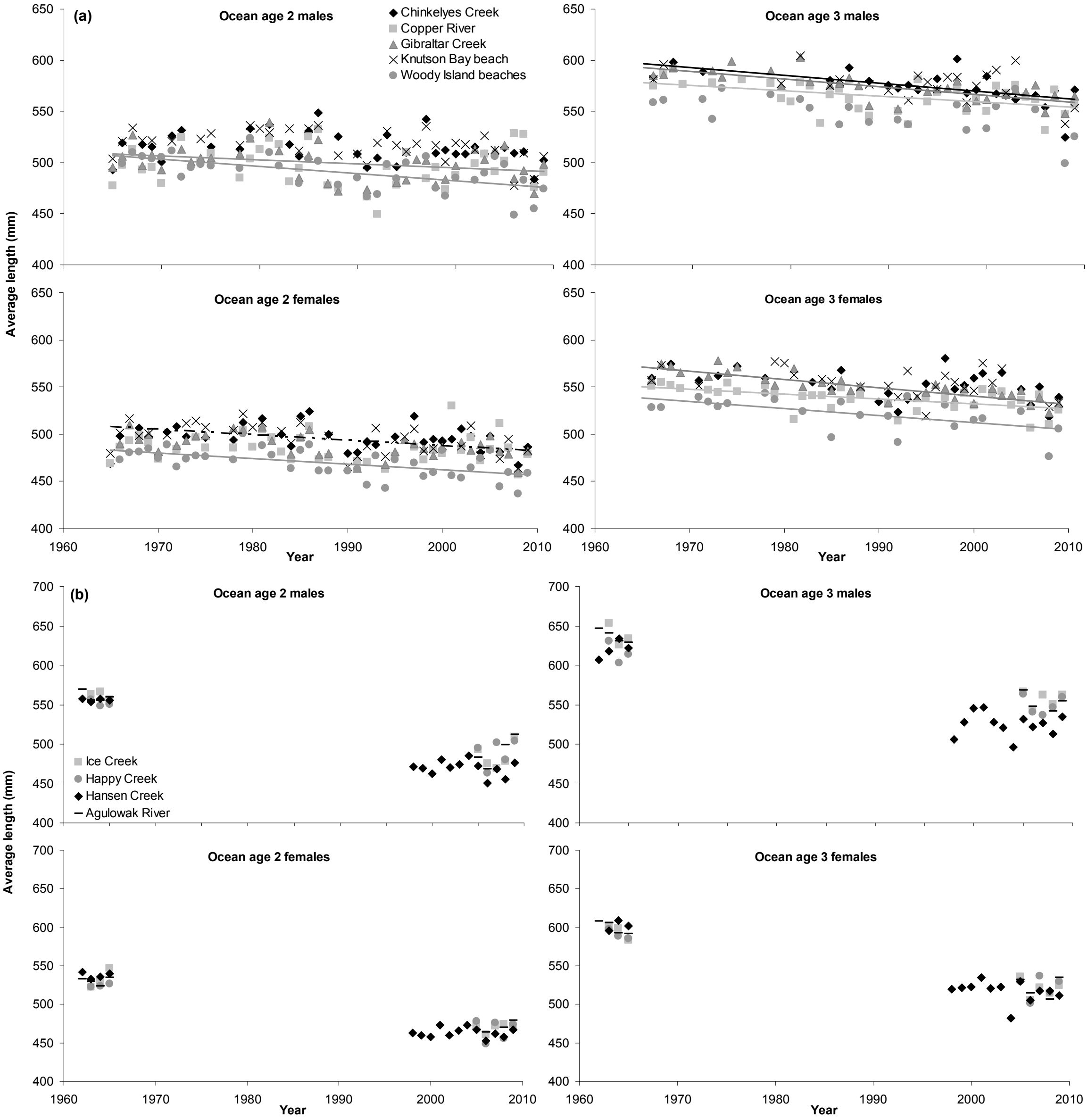


Fig. 5.2. Average length at ocean ages 2 and 3 of male and female sockeye salmon in five Iliamna Lake and four Wood River lakes spawning populations. For the Iliamna Lake populations, trend lines are given for the populations with slope values found to be significantly different than 0 (Gibraltar Creek ocean age 3 males and females, Woody Island beaches ocean age 2 males and females, Copper River ocean age 3 females, Chinkelyes Creek ocean age 3 males, and Knutson Bay beach ocean age 2 females). For the Wood river lakes populations, trend lines are not given because the average length was found to decrease significantly over time for every population-sex-age group.

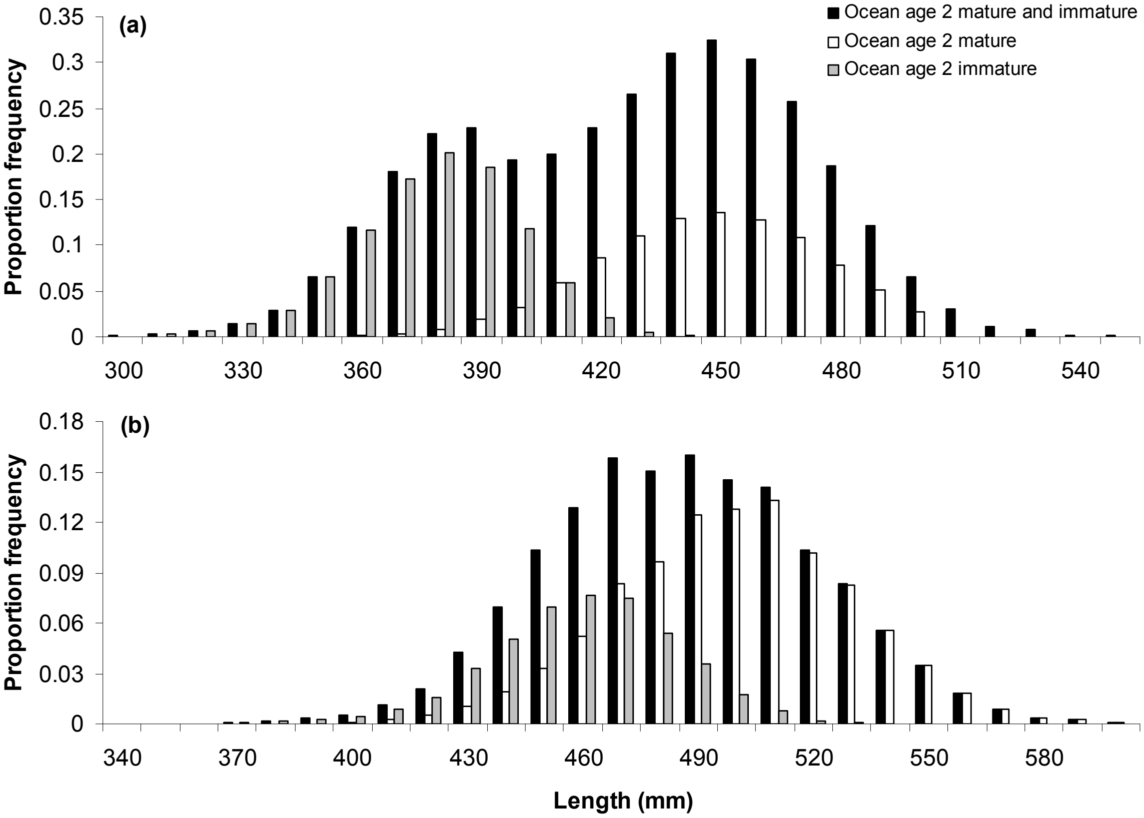


Fig. 5.3. Length frequency histograms of immature, mature, and combined Iliamna Lake sockeye salmon of ocean age 2 for all cohorts and populations for (a) the original length at age data and (b) length at age data produced in the sensitivity analysis (growth factors number 4 of 1.8 and 0.2 for ocean age 2 and 1.9, 0.45, and 0.65 for ocean age 3).

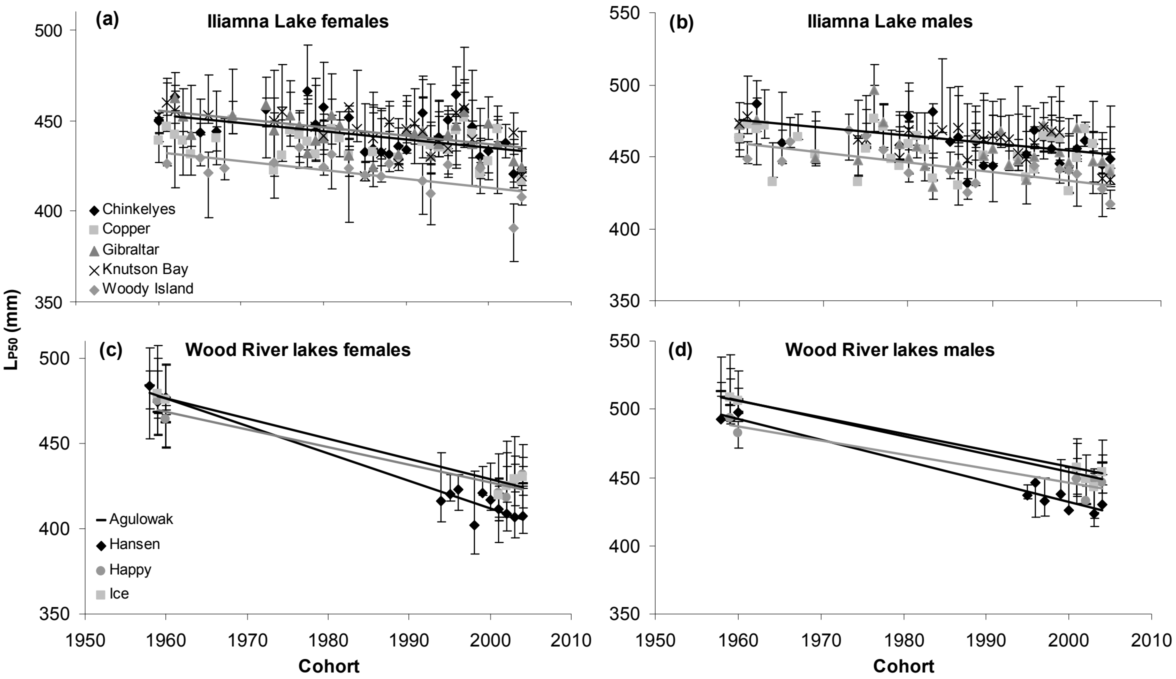


Fig. 5.4. PMRNs, represented by L_{P50} values, for ocean age 2 sockeye salmon of Bristol Bay, Alaska. Panel (a) shows estimates for females and (b) males spawning in Iliamna Lake from cohorts ranging from 1960-2004. Panel (c) is PMRN estimates for females and (d) males spawning in the Wood River lakes from cohorts including 1958-1960 and 1994-2004. Error bars of the L_{P50} values are 95% confident intervals estimated from bootstrap analysis. Best-fit lines are for the populations where PMRNs decreased statistically significantly over time ($p < 0.01$ using Šidák correction), including Gibraltar Creek females, Knutson Bay beach females, and Gibraltar Creek males from Iliamna Lake and both males and females from Hansen, Ice, and Happy creeks and males from the Agulowak River in Wood River lakes.

General Conclusions

This research provides some of the most detailed analyses available of multi-decadal size-selective fishing on wild Pacific salmon populations, long term trends in length, age, and length-at-age at maturation of these fish, and if and how such fishing can contribute to microevolutionary changes in the life history traits. These findings provide fishery managers and scientists with information to promote sustainable exploitation into the future.

The results of the first chapter of this dissertation indicate the importance of recognizing local adaptation and genetic differences among individual sockeye salmon spawning populations. Based on data from a common garden study and from fish spawning in the wild, Columbia River sockeye salmon populations were found to exhibit different patterns of age and size at smolt transformation and maturation. Effective conservation and management requires the identification of population differences within species (Waples 1991; Neville et al. 2007). I found that age and size at maturation in sockeye salmon are under some genetic control, so these traits have the potential to be influenced by size-selective fishing. Shifts in environmental conditions, such as climate change, are likely to affect smolt size and maturation patterns in different ways, potentially strengthening local adaptation or homogenizing populations. My results also strengthen the findings that introduction of individuals to a new habitat, supplementation of current populations, and population transplantations will be more successful when life history trait variability is considered.

Second, I documented that between 1981 and 2009 the average age and lengths at most ages of maturing Chinook salmon in one population in Alaska decreased over time. Most Chinook salmon were caught each year by the commercial fishery, which produced highly variable size selection over time but generally catches smaller than average fish. In contrast, the recreational fishery was found to be steadily size-selective, removing larger fish, consistent with observed declines in length and age of these fish. The opposing selection by the commercial fishery suggests that the trends of decreasing age and size at maturation are unlikely to have been caused solely by fishery selection; they are probably also related to environmental changes affecting fish growth. This finding is likely common to other cases of size-selective fishing; both fishing and environmental changes contribute to changes in life history traits over time, with the specific contribution of each factor varying across fisheries. Still, regulations that decrease either the allowable size of harvested fish or the allowable number of large fish may help to decrease fishery size selectivity and thus microevolutionary changes towards smaller and younger fish over time.

Third, I found that despite differing characteristics among nine Alaskan commercial sockeye salmon fisheries, selection patterns showed many similarities: size-selectivity varied over time but on average larger fish were caught, leaving smaller fish to spawn. Selection was generally stronger on females than males, so larger than average female sockeye salmon were removed more often than were larger males. The fisheries were less size-selective in years with lower exploitation rates, when fish in the total run were larger than average, when fishing seasons were shorter, and when a smaller percentage of days were fished. Thus, fishery selection was influenced by factors under and beyond management control. Such findings may be applicable to similar fisheries that lack the data necessary to quantify size selection. A long term perspective has enabled a more complete picture of selection, revealing different patterns than short term studies have in the past (Burgner 1964; Bue 1986; Hamon et al. 2000). The observed harvest of larger-than-average fish is consistent with the hypothesis that fishery selection can contribute to decreasing age and size at maturation trends over time, but the variability in size selection suggests weaker overall directional pressure than is often assumed in evolutionary models.

Fourth, I quantified sex-selective fishing on Alaskan sockeye salmon related to size-selective harvest. This study filled a gap in the literature; few studies have empirically documented skewed sex ratios in exploited fish with only moderate sexual size dimorphism (SSD), which is generally found in sockeye salmon. We found that more males are caught than females in most fisheries assessed, resulting in female-biased sex ratios in the escapement and on the spawning grounds. Sex ratios varied among spawning populations from 36-47% male; populations with fish of intermediate sizes experienced the greatest sex ratio biases due to the combination of larger SSD and different harvest rates between the sexes associated with the fishery selectivity curve shape. There is concern about skewed sex ratios in natural populations; studies have documented changes in competition and behavior on the spawning grounds when males are less numerous (Mathisen 1962). In such cases selection on male traits associated with mate choice by females or intra-sexual competition may be relaxed, which could result in altered demographic and evolutionary pressures. Studies examining size-selective fishing should also evaluate if such fisheries are sex selective to improve overall fisheries management and maintain healthy spawning stocks.

Finally, I documented trends in age, length, and length at age of sockeye salmon in a range of spawning populations in Alaska. I found that the age composition of fish in individual spawning populations has not changed, but fish in most, but not all, populations have become shorter at age at maturation over time. I used a novel method, probabilistic maturation reaction norms, to quantify differences in maturation length thresholds among populations over time and to determine whether fishery selection likely contributed to microevolutionary changes in maturation length of these fish. Understanding the influences of phenotypic plasticity and genetic change in life history trait change is a very important topic in evolutionary ecology (Dieckmann and Heino 2007; Allendorf and Hard 2009). Life history trait changes caused by phenotypic plasticity can be more quickly reversed than genetic changes that result from selective exploitation. Maturation length thresholds have decreased over time for most, but not all, sockeye salmon spawning populations, consistent with the strong but variable size-selective harvest that has tended to remove larger than average fish from these populations. Environmental changes in the ocean resulting in decreased growth rates combined with adaptive microevolution leading to decreased maturation length thresholds have likely combined to produce the observed length and age at maturation patterns. Populations experiencing temporal variation in size-selective fishing, less size selection, and lower rates of exploitation have shown lower rates of life history changes over time. Quantification of fishery exploitation and selection on age and size at maturation over long time periods is essential to understand evolutionary consequences on stock demographics and sustainable fishery management (Kuparinen and Merilä 2007; Law 2007). With this knowledge, managers and scientists can track further changes in age and size at maturation and incorporate evolutionary considerations for sustainable exploitation of wild salmon populations.

Future work should examine patterns of fishery size and sex selection on a finer time scale, such as weekly instead of annually. Variation in migration timing of salmon and other fishes can strongly affect exploitation rate, depending on how the fishery is managed, and that timing can vary among spawning populations, between males and females, and as a function of size or age within populations (Quinn et al. 2009). These processes can all interact with fishery size- and sex-selection patterns. To further understand the contributions of microevolutionary changes as a result of size-selective fishing and phenotypic plasticity to life history trait trends, the animal model (Kruuk 2004), quantitative genetic models (Swain et al. 2007; Crozier et al. 2011), and other eco-evolutionary models can be employed. Finally, assessments of the combined effects of fishery and natural selection may prove valuable to fully understand salmon population dynamics, demography, and life history trait evolution (Carlson et al. 2007b; Edeline et al. 2007).

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