Length and Age Trends of Chinook Salmon in the Nushagak River, Alaska, Related to Commercial and Recreational Fishery Selection and Exploitation

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Abstract
Long-term trends in fish age and size at maturation provide important insights into population stability as they are affected by changes in growing conditions. Fishery exploitation and selection can also induce such trends. It is important to identify the causes of changing life history patterns because they affect population dynamics and productivity. Average body sizes or ages of many western North American populations of Chinook salmon Oncorhynchus tshawytscha, including the Nushagak River population in Bristol Bay, Alaska, have declined over the past several decades. This population is caught in commercial, recreational, and subsistence fisheries and therefore represents an opportunity to compare fishery exploitation and selection and to examine their possible effects. We compiled data and examined trends in size and age at maturation between 1981 and 2009, and we then quantified commercial and recreational fishery exploitation and selection rates. The average age and lengths at most ages of maturing fish decreased over time. The commercial fishery caught the majority (73%) of the harvested fish annually compared with the recreational (9%) and subsistence fisheries (18%). Size selection by the commercial fishery was highly variable over time, but overall, smaller-than-average fish were caught, inconsistent with the declining trends in age and size of returning fish. In contrast, the recreational fishery and presumably the subsistence fishery regularly removed larger-than-average fish, consistent with the trends. However, the opposing selection by the commercial fishery suggests that the trends in age and size at maturation are unlikely to have been caused solely by fishery selection. Rather, the trends are probably also related to environmental changes affecting fish growth. Still, regulations that decrease either the allowable size of harvested Chinook salmon or the allowable number of large fish may help to decrease the size selectivity of the Nushagak River recreational and subsistence fisheries.

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 (e.g., age and size at maturation) of exploited fish populations are also important for conservation and management, allowing managers to anticipate population growth rates and stability. Ricker (1981) discussed the importance of tracking the 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 recently increased (Cooke and Cowx 2006; Lewin et al. 2006; Arlinghaus et al. 2009).

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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 harvest and selectivity between recreational and commercial fisheries (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 effects of angling on fish populations and their ecosystems have been less extensively researched compared with commercial fisheries (Lewin et al. 2006), and consideration of the 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 studies have successfully quantified long-term fishery selection on heritable traits (but see Sinclair et al. 2002; Carlson et al. 2007); the required data, including the size or age composition of the fish that are not caught (Quinn 2006), are often difficult to obtain. Data from recreational fisheries are rarer than data from commercial fisheries owing to the difficulties and high cost 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 and Quinn 2009; Kendall et al. 2009). All salmon migrating into freshwater are maturing adults, so they can be counted and life history data (e.g., age, sex, and length [ASL]) can be collected, which facilitates direct comparisons between fish that are caught and those that escape to spawn. For the most part, pink salmon *O. gorbuscha*, sockeye salmon *O. nerka*, and chum salmon *O. keta* are exploited only as maturing adults on their homeward migration, and recreational fisheries for these species are minor in comparison with commercial fisheries. In contrast, Chinook salmon *O. tshawytscha* present special challenges because they are exploited in both commercial and recreational fisheries and because their duration of marine residence and coastal distribution make some populations vulnerable as both immature and maturing fish. The Chinook salmon achieves a larger size at maturation and is less numerous than other Pacific salmon (Quinn 2005); this species is typically the most prized in recreational fisheries and is the 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 Chinook salmon of the Nushagak River, Bristol Bay, Alaska (Figure 1); this discrete population of wild fish is subject to harvest by both commercial and recreational fisheries. The Nushagak River supports one of the largest runs of wild Chinook salmon in the world (Clark et al. 2006).

We quantified trends in age and size, both heritable traits (Carlson and Seamons 2008), and related them to calculated fishery exploitation and selection of Nushagak River Chinook salmon. Chinook salmon in Bristol Bay have been subjected to an intense commercial gill-net fishery since the late 1800s (Bue 1986; Link et al. 2003; Kendall et al. 2009) and have been caught in significant numbers by recreational fishers since the late 1970s (Nelson 1987). The Alaska Department of Fish and Game (ADFG) manages the Bristol Bay salmon fisheries to achieve and maintain sustained production (Clark 2005). Our specific goals were to determine (1) whether there has been a decline in body size over time in the Nushagak River Chinook salmon population; (2) whether the decline reflects a change in age at maturation, length at the age of maturation, or both; (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 in which some aspect of growth is influenced by environmental conditions.

**METHODS**

*Study site and data collection.*—Bristol Bay supports one of the most abundant and diverse sockeye salmon runs in the world (Hilborn et al. 2003) and also has significant Chinook salmon populations, the largest of which spawns in the Nushagak River (Figure 1). An economically important commercial gill-net 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 River 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 that is adjacent to ideal fishing locations in the Nushagak River is privately held, which has to some degree limited the number of commercial lodges that host sport fishers (Jason E. Dye, ADFG, personal communication). 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 1992 adoption of the Nushagak–Mulchatna Chinook Salmon Management Plan, 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 Chinook salmon are returning to the Nushagak River at younger ages than in previous years (Brookover et al. 1997).

Commercial catch and escapement daily count data and individual ASL data describing Nushagak River Chinook salmon have been collected by ADFG in most years since 1966. Fish are caught by commercial fishers in the Nushagak Fishing District (hereafter, Nushagak District; Figure 1). Directed commercial Chinook salmon fisheries have been allowed annually since 2002 in early to mid-June; a minimum gill-net mesh size of 191 mm (7.5 in) is imposed so that Chinook salmon are targeted instead of the smaller-bodied sockeye salmon. During years in which there are 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 a temporary maximum gill-net mesh size of 140 mm (5.5 in) has been specified to reduce exploitation. At commercial fish processing plants, total catches are estimated, samples are measured for length and weight, scales are collected for age determination, and the sex of each fish is recorded. A sonar device enumerates upstream-migrating Chinook salmon that have escaped the commercial fisheries about 65 km upriver from the mouth of the Nushagak River (Figure 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 on the lower Nushagak River and middle Mulchatna River upstream of the Nushagak District commercial fishery (Figure 1); therefore, fish that are vulnerable to recreational harvest are those that have escaped the commercial fishery. Recreational fishing regulations between 1980 and 1997 mandated that sport fishers could keep up to five Chinook salmon daily, only two of which could be greater than 711 mm (28 in) total length (TL). In 1997, regulations were modified to allow (on a daily basis) either (1) one fish between 508 and 711 mm (20–28 in) and one fish greater than 711 mm or (2) two fish between 508 and 711 mm; a yearly limit of four 508-mm or larger Chinook salmon was also imposed. In 2003, regulations were changed again to allow up to five Chinook salmon less than 508 mm (<20 in; predominantly jacks, or males that spend only 1 year at sea) to be retained each day. Recreational harvest count data have been collected annually since 1977, although individual fish length and age data obtained in creel surveys by ADFG have been collected in fewer years (1986, 1987, 1991, 1994, 2001, and 2007). Creel surveys have assessed sportfishing effort and harvest, and most have been roving surveys conducted in mid-June to mid-July, corresponding to the peak of the recreational fishing season (Minard 1987; Minard and Brookover 1988; Dunaway and
Bingham 1992; Dunaway and Fleischman 1995; Cappiello and Dye 2006; Jason E. Dye, unpublished data). No data on size or age of fish caught by the subsistence fishery are available.

**Length and age characterization.**—We used ASL data to characterize the annual age, length, and length at age of Nushagak River Chinook salmon commercial fishery catch and escapement, treating male and female fish separately. Over 99% of Nushagak River Chinook salmon spend 1 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 gill nets. Because fish of different ages, sizes, and sexes may enter the fishery and escape upriver at different times and because 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, we used daily ASL data 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 of a given age that were caught by commercial gear or that escaped, we multiplied the total catch or escapement by the proportion of fish of the given age-group on a daily basis. This analysis assumes that on average, fish of all sizes and age-groups have equal contact with the fishery (i.e., equal opportunity to get caught) in a given year and that differential fishing mortality is due to the effects of the gill-net fishery rather than some other attribute, such as migration route.

Annual creel surveys (Minard 1987; Minard and Brookover 1988; Dunaway and Bingham 1992; Dunaway and Fleischman 1995; Cappiello and Dye 2006; Jason E. Dye, unpublished data) reported the total number of male or female fish sampled from each age-group and also reported the average length (with SD) for each category. To characterize the length distribution of recreationally caught fish for a given year, we assumed that fish of a given sex and ocean age were described by a normal distribution based on the mean length and SD given in the creel surveys. This assumption was justified because commercially caught Chinook salmon, for which 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 the estimated number of recreationally caught fish within each length bin from the commercial escapement to obtain the number and length distribution of the recreational fishery escapement for a given year. The mean length of fish from the recreational fishery escapement was then estimated from this distribution and was used for calculation of selection metrics.

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

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

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

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

For a given cohort, this value would increase for each ocean age-group as more fish mature and would be equal to 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, were caught by the recreational fishery, or 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 or recreational) on a yearly ($y$) basis ($P_{s,a,f,y}$),

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

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 and 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 (SDIF$_{s,a,y}$) and standardized selection differentials (SSDIF$_{s,a,y}$) for each sex and each fishery with all ages combined (equations 4 and 5). Although commercial fishery selection could be estimated for most years between 1981 and 2009, data used to calculate selection metrics for the recreational fishery were only available for 1986, 1987, 1991, 1994, 2001, and
2007. We first calculated the mean length of fish in the total prefishery run in a given season for each sex and each fishery \((L_{R,f,y})\). Second, we calculated the mean length of males or females that escaped the fishery and thus had a chance to spawn in that season \((L_{E,f,y})\). The SDIF is the difference in mean length between fish in the prefishery run and fish in the escapement (Law and Rowell 1993). Thus, SDIFs represent the overall difference in the average length of the population before and after a potentially selective event (i.e., fishery harvest) and are calculated as

\[
\text{SDIF}_{s,f,y} = \bar{L}_{E,s,f,y} - \bar{L}_{R,s,f,y}.
\]

To standardize the SDIF, we divided the calculated difference by the SD of the length of fish in the run \((S_{R})\), which allows for comparison among years and also facilitates comparison with other studies:

\[
\text{SSDIF}_{s,f,y} = \frac{\bar{L}_{E,s,f,y} - \bar{L}_{R,s,f,y}}{S_{R,s,f,y}}.
\]

Selection differentials and SSDIFs were calculated separately for the commercial and recreational fisheries. We also calculated the average annual combined SDIF and SSDIF of the commercial and recreational fisheries by adding together the means of all available annual SDIFs and SSDIFs from each fishery. Because SDIFs and SSDIFs measure the net effect of each year’s fishery on that cohort, they implicitly incorporate interannual and intra-annual variability in fishery management regulations and run sizes. In fact, such effects shape the SDIFs and SSDIFs (Kendall et al. 2009). This allows comparisons among years of selection resulting from such regulations and changes in abundance. Thus, it is not necessary to weight SDIFs and SSDIFs 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 Nushagak River Chinook salmon between 1981 and 2009 with the patterns of fishery exploitation and selection to see whether they were correlated. Because age and size at maturation are heritable traits in Chinook salmon (Carlson and Seamos 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 (i.e., response = heritability \times 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 (\(t\)-test: females: \(F = 34.2, \text{df} = 25, P < 0.001\); males: \(F = 12.7, \text{df} = 25, P = 0.001\); Figure 2A, B). These patterns were driven by significant changes
FIGURE 3. Length and age at maturity of Chinook salmon returning to the Nushagak River, Alaska, annually between 1981 and 2009: (A) proportion of females in the total run of ocean age 2 (black diamonds, solid black trend line), ocean age 3 (gray squares, solid gray trend line), and ocean age 4 (open circles, dashed black trend line); (B) proportion of males in the total run of ocean ages 2–4; (C) mean length (mm) of females in the total run of ocean ages 2–4; (D) mean length of males in the total run of ocean ages 2–4; (E) proportion of all females in each brood year (1978–1994) that were mature at ocean ages 2–4; and (F) proportion of all males in each brood year (1978–1994) that were mature at ocean ages 2–4.

in age composition and length of maturing fish at various ocean ages. The average ocean age of each sex also decreased significantly over time (linear regression: females: $F = 27.7$, df = 24, $P < 0.001$; males: $F = 17.7$, df = 24, $P < 0.001$; Figure 2B, C). These trends were driven primarily by the significant temporal decrease in the proportion of ocean age-4 fish in the total run and the increase in the proportion of ocean age-2 fish (linear regression: $P \leq 0.005$ for ocean ages 2 and 4 [both sexes]; $P > 0.05$ for ocean age 3 [both sexes]; Figure 3C, D). Additionally, despite the high allowance for ocean age-1 fish (jacks) by the recreational fishery, these fish were rarely caught. For both sexes, ocean age-2 fish did not change significantly in length over time, but ocean age-3 and ocean age-4 fish became shorter between 1981 and 2009 (linear regression: females, ocean age 3: $F = 10.8$, df = 24, $P = 0.003$; females, ocean age 4: $F = 8.0$, df = 25, $P = 0.009$; males, ocean age 3: $F = 4.2$, df = 24, $P = 0.05$; males, ocean age 4: $F = 24.1$, df = 25, $P < 0.001$; Figure 3A, B). Thus, between 1981 and 2009, Nushagak River Chinook salmon of both sexes decreased in length, age, and length at most ages. Finally, for both males and females, the proportion of all fish in a given cohort that were mature at each ocean age increased over time, although most were not significant at the $\alpha$ level of 0.05 (linear regression: females, ocean age 4: $F = 4.916$, df = 15, $P = 0.04$; Figure 3E, F).

Nushagak River Chinook salmon harvests were first recorded in 1966; between 1966 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 to a high of 356,190 in 1982 (Figure 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 escaped to spawn have also varied greatly over time, although the commercial catch has typically exceeded the recreational and subsistence fisheries’ catch (Figure 4B). On average, from 1977 to 2009, 35% of the total run was caught by the commercial fishery, 4% was caught by the recreational fishery, 8% was caught by subsistence users, and 53% escaped to spawn. We also examined the proportions of fish that were available to the commercial, recreational, and subsistence fisheries and that were caught each year (Figure 5). On average, 35% of the Chinook salmon returning to the Nushagak River were caught by the commercial fishery annually; of the fish that escaped the commercial fishery, 7% were caught in the recreational fishery and 15% were caught in the subsistence fishery. Except in 1 year (1990), the commercial fishery always exerted a higher exploitation rate than the recreational fishery, although exploitation rates were similar in some recent years when commercial fishing decreased and recreational fishing increased.

The SDIFs (Figure 6) and SSDIFs showed similar patterns as they were derived from the same values; SDIFs show the actual length difference between the total run and the escaped fish, and SSDIFs are standardized and therefore are unitless. The commercial fishery SDIFs and SSDIFs varied greatly in direction and magnitude, and in a given year they often differed between males and females. Between 1981 and 2009, the average commercial fishery SSDIF was 0.06 for females (SD = 0.22; average SDIF = 6.6 mm, SD = 25.1 mm) compared with 0.01 for males (SD = 0.24; average SDIF = 3.1 mm, SD = 35.8 mm). Thus, the fishery took smaller-than-average Chinook salmon and larger fish escaped. On the other hand, the annual recreational fishery SDIFs and SSDIFs were consistently negative and smaller in magnitude than those of the commercial fishery. The average
recreational fishery SSDIFs (based on the 5 years with available length-specific data) were $-0.09$ for females (SD = 0.05; average SDIF = $-8.6$ mm, SD = 5.7 mm) and $-0.03$ for males (SD = 0.01; average SDIF = $-3.6$ mm, SD = 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 selection by the commercial fishery varied between catching...
larger-than-average and smaller-than-average Chinook salmon whereas the recreational fishery consistently harvested larger-than-average fish, the average SDIFs and SSDIFs for the recreational fishery were greater in magnitude than those of the commercial fishery. Both fisheries exhibited stronger size selection of females than males when averaged across all years, although not necessarily in every year.

**DISCUSSION**

We successfully quantified long-term trends in age and size at maturation of Chinook salmon from the Nushagak River. We showed that the age and length of both females and males returning to the river decreased between 1981 and 2009. This pattern was driven by significant decreases in the number of older (and thus larger) fish and declines in the lengths of ocean age-3 and ocean age-4 fish of both sexes. The proportion of fish that were mature at ocean ages 2–4 increased significantly during the period of record, suggesting that Nushagak River Chinook salmon are returning at younger ages. Specifically, most fish in the more recent cohorts were mature by ocean age 4, whereas in earlier cohorts most fish were mature by ocean age 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, over 20 years of size selection data from the commercial fishery, and 5 years of size selection data from the recreational fishery. Although the run size of Nushagak River Chinook salmon and the proportion of the run harvested by each fishery varied between 1977 and 2009, the commercial fishery consistently took a higher proportion (average harvest rate = 35%) than the recreational fishery or subsistence fishery (average harvest rates = 7% and 15%, respectively). Also, even though the selective nature of the commercial fishery varied greatly over time as larger and smaller fish were harvested in greater numbers in different years, the recreational fishery consistently caught larger-than-average fish between 1981 and 2009. Both fisheries, averaged over time, exhibited greater selection on females than on males. Data on the size and age composition of the fish captured by subsistence users were not available, so selection by that fishery could not be directly calculated. There are no mesh size or net type regulations for subsistence fishing gear targeting Nushagak.
River Chinook salmon, but most people are likely to use Chinook salmon gill nets with 19-cm (7.5-in) or larger mesh (Tim Sands, ADFG, personal communication). These gill nets—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 in the commercial fishery was not correlated with the trends in fish age and size over time, selection by the recreational fishery was. Between 1981 and 2009, lengths at all ages declined by an average of 3.1 mm/year for females and by an average of 2.6 mm/year for males. The combined average annual SDIFs for the commercial and recreational fisheries between 1981 and 2009 were −2.0 mm for females and −0.5 mm for males (female SSDIF = −0.03; male SSDIF = −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 subsistence fishery harvest of larger-than-average Chinook salmon, and thus older fish, may have contributed. Other factors can also be assessed for possible contributions to the observed trait changes: these factors include ocean and freshwater conditions (Pyper and Peterman 1999; Wells et al. 2007, 2008), ocean harvest of immature fish (Hard et al. 2008), potential interceptions by the fishery for walleye pollock Theragra chalcogramma (NPFMC 2009), competition with hatchery-released salmon (Cooney and Brodeur 1998; Ruggerone et al. 2003, 2010), and changes in abundances of subpopulations that differ in maturation metrics.

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 was seen for Nushagak River fish, and can result in larger-bodied fish, which were not seen (Wells et al. 2007, 2008). Additionally, warming of the freshwater environment could result in larger smolts, thereby 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 the age of maturation. Second, many populations of Chinook salmon are vulnerable to capture as immature fish in coastal waters from California 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 bycatch in fisheries for other nonsalmonid fishes, such as walleye pollock, are difficult to estimate, so it is challenging to determine the extent to which 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, 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 Nushagak River Chinook salmon subpopulations that differ in age and size at maturation could also contribute to the observed patterns. Genetic analysis and other analyses of Nushagak River Chinook salmon subpopulation dynamics could contribute to our understanding of this mechanism. Our findings can be extrapolated to other salmon populations in which maturing 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 the age of maturation for Nushagak River Chinook salmon cannot be entirely explained by commercial and recreational fishery selection. The commercial fishery can be highly selective in a given year, but overall it spares the larger and older fish, which are valuable in natural populations (Birkeland and Dayton 2005; Law 2007; Hsieh et al. 2010) because of the higher reproductive potential (e.g., greater fecundity and larger eggs) of these fish (Beacham and Murray 1993; Quinn 2005) and their ability to dig deeper redds (Steen and Quinn 1999). Although 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 extreme, 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 Merila 2007; Quinn et al. 2009). Maturation reaction norms between length at maturation and age at maturation (as in Stearns and Koella 1986, their Figures 5 and 6) 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 will favor faster growth and younger, smaller adults (Hard et al. 2008), as was observed for Nushagak River Chinook salmon. Thus, regulations that decrease the allowable size of harvested fish or the allowable number of large fish may decrease the size selectivity of the recreational and subsistence fisheries and their potential contributions to the decline in age and length of returning Chinook salmon. Results of a stochastic, individual-based model of selective fishing for Chinook salmon in the Yukon River, Alaska (Bromaghin et al. 2008), concurred with this suggestion. Bromaghin et al. (2008) found that management strategies for reversing the effects of selective exploitation are more effective when exploitation
rates and selectivity for large individuals are concurrently reduced.

Factors that may confound our results include delayed mortality of fish after disentanglement from gill nets in the commercial fishery and catch-and-release mortality associated with the recreational fishery. Gill-net disentanglement mortality was greater for smaller-than-average sockeye salmon (positive SDIFs; Baker et al. 2011). If gill-net disentanglement mortality also affects smaller-than-average Chinook salmon, it may operate synergistically with commercial fishery mortality such that larger-than-average fish would be more likely to survive the fishery. Hooking mortality for Chinook salmon examined elsewhere averaged 7.6% (Kenai River, Alaska; Bendock and Alexandersdottir 1993) and 12.2% (Willamette River, Oregon; Lindsay et al. 2004). Hooking mortality was most strongly dependent on the hook location, but fish length was also a significant factor. Specifically, hooking mortality for Kenai River Chinook salmon was highest for small males and lower for large males and females of all lengths (Bendock and Alexandersdottir 1993). This result suggests that hooking mortality could amplify mortality of 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 to some degree.

Selection patterns in the Nushagak River Chinook salmon fishery are expected to be related to annual variation in total run sizes, gill-net 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 probably been more consistently size selective than the commercial fishery because of gear regulations. Commercial fishery regulations stipulating maximum gill-net mesh sizes or fishery closure in early June during the peak of Chinook salmon migration through Nushagak Bay prevented the capture of large individuals in most years. In addition, the predominance of sockeye salmon rather than Chinook salmon in Bristol Bay has probably contributed to different patterns of selectivity by the commercial and recreational fisheries. Sockeye salmon outnumber Chinook salmon in the Nushagak District, where the catch ratio in the commercial fisheries averaged 43:1 from 1980 to 2009. Although Chinook salmon are generally more valuable than sockeye salmon, fishers profit overall by harvesting more sockeye salmon; thus, fishers will often use nets with smaller mesh sizes to target sockeye salmon rather than use larger mesh sizes that would catch Chinook salmon but fewer sockeye salmon. Thus, the much greater size of the sockeye salmon population may reduce the harvest of large Chinook salmon.

Our findings both concur with and contradict stereotypes about the selective nature of commercial versus recreational fisheries (Cooke and Cowx 2006; Lewin et al. 2006) and the few comparative studies available. In general, the recreational fishery in the Nushagak River harvests fewer Chinook salmon than its commercial counterpart, which has also been demonstrated for other recreational fisheries (Murray-Jones and Steffe 2000; Rangel and Erzini 2007). Additionally, in any given year the Nushagak River commercial fishery is typically more selective than the recreational fishery, but averaged over time the recreational fishery is more selective as it more consistently selects for larger fish. In comparison, Murray-Jones and Steffe (2000) reported that in the fishery for Australian surf clams Donax deltoides, commercial fishers and recreational fishers who collected clams for bait were similarly size selective, whereas the recreational fishers who collected the clams for food were less size selective than the other two groups.

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