Effects of Freshwater and Marine Growth Rates on Early Maturity in Male Coho and Chinook Salmon

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Abstract.—In many populations of salmonid fishes, a fraction of the males mature at a younger age than the females; these males are termed jacks if they have migrated to sea and precocious parr if they matured in freshwater. We examined detailed data on the University of Washington hatchery populations of coho salmon *Oncorhynchus kisutch* and Chinook salmon *O. tshawytscha* for more than 30 years to test whether rapid growth in freshwater or at sea increases the probability of early maturity in males. The average size of Chinook salmon smolts (2.6–20.9 g) increased over the years in question. The proportion of males maturing as jacks increased with smolt size but not with the potential for growth at sea. The size of the smolts (but not growth potential at sea) was positively correlated with the proportion of the jacks maturing after only one summer at sea (so-called minijacks) rather than two summers. In coho salmon, average smolt size (6.1–22.4 g) did not vary consistently with time. There was a slight tendency for cohorts with larger smolts to produce more jacks, but marine growth potential was negatively related to the proportion of jacks. For neither species did marine environmental variables influence the proportion of jacks. Taken together, these results support the hypothesis that size prior to seawater entry has the predominate effect on the probability of early maturation and that the growth potential at sea has a neutral or even inhibitory effect on early maturity.

The diadromous life cycle exhibited by some migratory fishes reflects the discrete growing conditions and regimes of mortality in freshwater and marine environments (Gross et al. 1988). In general, growth at high latitudes is faster at sea than in freshwater, and the reverse is true at lower latitudes. This inequality has ramifications for the life history patterns of populations and individuals undertaking the migration or remaining in freshwater for their entire lives (Gross 1987). The difference in potential for growth in marine and freshwater systems is common among diadromous fishes but has been most extensively studied in salmonids.

In salmonids, growth rate influences both survival in a given environment and the age at which individuals undergo two critical life history transitions: (1) smolt transformation and migration to the ocean for feeding and (2) maturation and return migration to freshwater for reproduction. In general, rapid growth and large size are associated with an early transition to the other habitat whereas slower growth is associated with a delay of migration for an additional year or more (Thorpe 1989). For example, fertilization of lakes with in-organic nutrients to stimulate phytoplankton and zooplankton accelerated the growth of sockeye salmon *Oncorhynchus nerka* and increased the proportion of fish leaving the lake as smolts after 1 rather than 2 years. Conversely, increased density of sockeye salmon was associated with slow growth and an increased proportion of fish leaving the lake after 2 years (Koenings and Burkett 1987). Likewise, the age at which Atlantic salmon *Salmo salar* migrate to sea is inversely related to growth (Thorpe 1989; Hutchings and Jones 1998). In parallel to the relationship between growth and migration to sea, rapid growth at sea is generally associated with reduced age at maturity. It has long been known that the fastest-growing individuals within a population tend to mature at a given year and the slower-growing individuals to mature in subsequent years (e.g., Parker and Larkin 1959; LaLanne 1971). These trends are not unique to salmonids. It is quite common to find a negative relationship between the age at which various life history transitions occur and the growth conditions under which individuals develop (Day and Rowe 2002).

In many salmonid species, a fraction of the males return from the ocean to spawn at a younger age than do the females of the population. The proportion of these ''jacks'' is often related to the size or release date of the smolts (e.g., Bilton et al. 1982; Brannon et al. 1982), implying that there

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is an environmental control over this life history pattern. Jacks are smaller than older mature males and try to fertilize eggs by sneaking tactics rather than by fighting (Gross 1985). However, two lines of evidence indicate genetic control over age at maturity, including the tendency to mature as jacks. First, the production of jacks is greater in families sired by jacks than in families sired by older adults (e.g., Iwamoto et al. 1984; Hard et al. 1985; but see Unwin et al. 1999). Estimates of the heritability of age at maturity vary from 0.05 to 0.62, depending on the population (Silverstein and Hershberger 1992; Hankin et al. 1993; Heath et al. 1994, 2002). Second, there is substantial variation in the proportion of jacks among populations (e.g., Chinook salmon *O. tshawytscha*: Hard et al. 1985; coho salmon *O. kisutch*: Young 1999; sockeye salmon: Healey et al. 2000; Quinn et al. 2001). Thus, the evidence for the relative roles of genotype and environmental induction of early maturity is mixed.

During the latter part of the 20th century, interest in the growth and life history of salmonids was heightened by evidence of declining body size in many populations of Pacific salmon *Oncorhynchus* spp. (Ricker 1980; Helle and Hoffman 1995, 1998; Weitkamp et al. 1995; Bigler et al. 1996). There are several possible explanations for these changes in body size, and they are not mutually exclusive (Ricker 1980). The explanations include selective effects of fishing on the phenotypes being measured; genetic selection for size or age at maturity; the loss of large-bodied populations; and shifts in age composition related to changes in growing conditions at sea (either ocean productivity or density-dependent competition for food). Changes in growing conditions at sea might have compensatory effects on size and age at maturity if rapid growth leads to earlier maturity or slower growth delays maturity. In addition to the natural ecological processes affecting growth at sea, there may be effects related to the hatchery production of salmon. The growth rates of juvenile salmon in hatcheries exceed those in most wild populations because the hatchery fish are given large quantities of nutritious food and may also be reared at elevated temperatures.

The purpose of this study was to investigate the influence of growth in freshwater and marine environments on the age at maturity of male coho and Chinook salmon propagated at the University of Washington's hatchery over the last 30–40 years. Growth rates, both in the hatchery and at sea, varied considerably over this period, enabling

us to test the hypothesis that age at maturity is negatively correlated with the growth rates of juvenile salmon in the hatchery. We also tested the hypothesis that good growing conditions at sea are associated with early maturity against the alternative that poor growing conditions stimulate the fish to mature rather than to remain at sea.

Methods

Our study was based on male coho and Chinook salmon at the University of Washington (UW) hatchery in Seattle. The hatchery is not associated with natural spawning populations. Rather, the populations were initiated in the late 1940s (Chinook salmon) and the late 1960s (coho salmon), primarily from the Green River system (Soos Creek hatchery) in Puget Sound (see Quinn et al. 2002 for further details). The Chinook salmon are an ocean-type population, migrating to sea in their first year of life. This is the characteristic life history pattern in lowland Puget Sound populations (Myers et al. 1998). In contrast, the juvenile coho salmon in the Puget Sound region almost invariably migrate to sea in their second year of life (Weitkamp et al. 1995). However, the epilimnion of Lake Washington (the UW hatchery's main water source) is intolerably warm for Pacific salmon in the summer. Therefore, both the coho and Chinook salmon are incubated and reared on a regime of elevated winter temperatures and accelerated feeding in spring so that they reach a size suitable for smolt transformation in their first spring (after about 5 months of growth). This is the natural life history pattern for the Chinook salmon but entails a shorter period in freshwater (and faster growth) than is typical for coho salmon. Adult Chinook salmon returned to the hatchery and were spawned from early October to early December and coho salmon from early November to mid-December (Quinn et al. 2002). Details about the treatment of fish and data collection are presented by Quinn et al. (2004). For both species, we use annual average smolt mass (g) for each cohort and species as an index of the growth rate in freshwater.

It was possible to assign ages to 9,651 male coho salmon and 25,449 male Chinook salmon based on tags or marks, but during most of the 1980s and the 1990s there were no marked fish and thus no fish of known age. Males of unknown age numbered 12,496 for coho salmon and 22,627 for Chinook salmon. Almost all of the coho salmon returned after one (10.8%, i.e., jacks) or two summers at sea (87.7%), the remaining 1.5% returning after three summers. Their size at maturity indi-
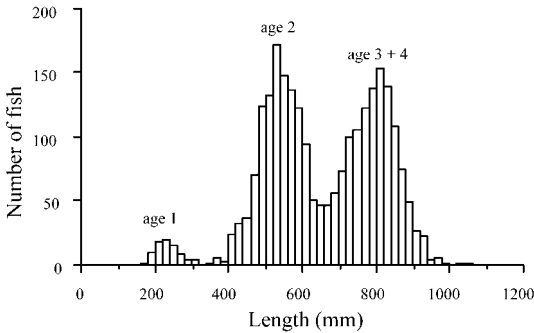
FIGURE 1.—Length frequencies of male Chinook salmon spawning in 1973; $n = 2{,}519$.

cated that the age-3 fish probably did not migrate to sea until a year after they were released rather than having spent an additional year at sea. Unmarked coho salmon were categorized as either jacks or age-2 fish because these two groups were clearly distinguishable from length-frequency analysis; because age-2 and the much scarcer age-3 fish were indistinguishable, all of the males that were not jacks were assumed to have spent 2 years at sea. Male Chinook salmon commonly returned after one (9.0%), two (39.4%), three (43.5%) or four summers at sea (7.8%), and only very rarely after five summers (0.3%). As females mature at ages 3, 4, and (rarely) 5 (Quinn et al. 2004), males aged 1 and 2 years can be considered jacks. To avoid confusion, we refer to the age-1 males (i.e., fish that spent only one summer at sea) as minijacks. Length-frequency analysis enabled us to distinguish the two youngest age-groups (i.e., the jacks and minijacks: Figure 1) with high precision, but the age-3 and older fish could not be reliably distinguished. We were therefore unable to examine traits associated with individual size at age during the period when the fish were not marked or tagged. However, we were able to estimate the age composition of the adults as a group in these years. Using the data for known-age males, we calculated the proportion of males within each 20-mm length bin in each age-group. This probability function was then applied to the size-frequency distribution of fish of unknown age to estimate their age composition as a group. Thus, length-at-age data were available for a subset of the years, but the age composition of the population as a whole was either calculated or estimated for all years.

The proportion of jacks was calculated for each smolt cohort as the number of jacks divided by the total number of returning fish from that smolt co-

hort. In using this index, we assumed that the exploitation rate did not vary among years. Only the larger fish of either species (not the jacks) are intercepted in the fisheries. To test whether variation in the exploitation rate would influence our conclusions, we obtained all of the data associated with the coded-wire-tagged Lake Washington watershed Chinook and coho salmon from the coded wire tag recovery database at the Regional Mark Processing Center managed by the Pacific States Marine Fisheries Commission. All return rates of coho and Chinook salmon were adjusted to the mean observed exploitation rate for each species. For coho salmon, exploitation rates increased strongly until about 1990 and then declined. For Chinook salmon, exploitation rates were low during the 1970s, increased during the 1980s, and decreased during the 1990s. The proportion of Chinook minijacks relative to the total number of jacks was estimated in the same way. All proportions were arcsine transformed to normalize the variance.

The maturation process strongly influences growth rate, and compensation between growth and age at maturation makes the size of males at a given age an unreliable index of growth at sea. Rather than using environmental factors that might correlate with growth in some indirect manner (e.g., sea surface temperature), we use the estimated annual marine growth rate for females (Quinn et al. 2004) as an index of the growth potential for the males of that cohort. For the Chinook salmon, we used estimates from known-age females returning at age 3. As virtually all of the female coho salmon returned at age 2, we used their growth as the index. The usual measures of growth rate, such as the specific growth rate ($[\log_e M_2 - \log_e M_1]$/time, where M_2 is fish size (g) at the time in question and M_1 is fish size at the start of the experiment) may be correlated with size at the start of the experiment. This was the case for our data and is probably due to an allometric relationship between growth efficiency and body mass. We therefore used a standardized mass-specific growth rate (Ω; Ostrovsky 1995) defined as follows:

$$\Omega = \frac{M_2^b - M_1^b}{b \cdot \text{time}} \cdot 100,$$

where b is the allometric mass exponent for the relation between growth rate and body mass. This exponent has not been estimated for coho or Chinook salmon. However, estimates obtained for

brown trout *Salmo trutta* (0.308) and Atlantic salmon (0.310) are very close (Elliott et al. 1995; Elliott and Hurley 1997), suggesting that this exponent is similar among all salmonids. In our analysis we set *b* equal to 0.31.

Further, we used information on various environmental variables that might be correlated with life history decisions to test for possible correlations with age at maturity within cohorts. Correlations between ocean conditions and size are often strongest for the first spring and summer, when the fish are entering the ocean and feeding on zooplankton (Fisher and Pearcy 1988; Hobday and Boehlert 2001; Koslow et al. 2002). Therefore, we used the conditions during May, June, and July of the year of release for our analysis. Data for ocean conditions were selected based on the ocean distribution of coded-wire-tagged coho and Chinook salmon from the UW hatchery (Quinn et al., unpublished data). Our measures of ocean conditions came from sources found on the World Wide Web. Pacific Decadal Oscillation (PDO) index values were obtained from Nathan Mantua (University of Washington; ftp://ftp.atmos.washington.edu/mantua/ pnw_impacts/INDICES/PDO.latest [all Web sites accessed in February–March 2002]). Average daily sea surface temperatures (SST) were obtained from four lighthouse stations (http://www.ios.bc.ca/ ios/osap/data/lighthouse/bcsop.htm): Neah Bay (48°22′N, 124°37′W), Race Rocks (48°11′N, 123°19′W), Amphitrite Point (48°33′N, 125°19′W), and Kains Island (50°16′N, 128°1′W). Mixed layer depth (MLD), a derivative of subsurface temperature structure, was obtained from the Joint Environmental Data Analysis Center at Scripps Institution of Oceanography (http://jedac.ucsd.edu/ DATA_Images/index.html); measurements from off the coast of Washington (48°N, 135°W and 48°N, 130°W) and British Columbia (50°N, 135°W and 50°N, 130°W) were used for this analysis. Sea level data from the University of Hawaii Sea Level Center (http://www.soest.Hawaii.edu/ kilonsky/uhslc.html) were obtained for Neah Bay, Washington, and Tofino, British Columbia. Average daily cross-shelf upwelling was obtained from the Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/products/ las.html) for Washington (48°N, 125°W) and British Columbia (51°N, 131°W). Most of these environmental variables are correlated. We therefore reduced the dimensionality of our environmental matrix using principal component analysis. The first four principal components explained 64.3% of the total variability in the data. Principal com-
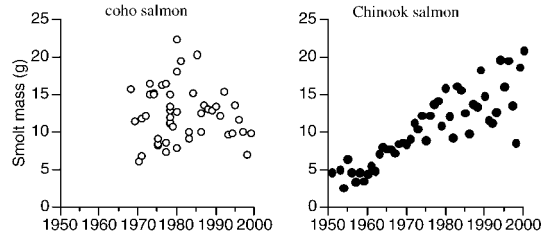

FIGURE 2.—Temporal variation in smolt size (g) of coho and Chinook salmon from the University of Washington hatchery.

ponent 1 (eigenvalue, 10.89), which consisted mainly of PDO and SST, explained 27.9%. Principal component 2 (eigenvalue, 5.46), on which the variation in mixed layer depth and upwelling intensity loaded most strongly, explained 14.0%. Principal component 3 (eigenvalue, 4.69), mostly comprising the variability in salinity, SST, and mixed layer depth, explained 12.0%. Principal component 4 (eigenvalue, 4.03), mainly an upwelling and salinity factor, explained 10.3% of the total variability in environmental conditions.

Results

Coho Salmon

There was considerable variation in coho salmon smolt size over the three decades but no significant time trend ($R^2 = 0.006$, $n = 52$, $P = 0.865$; Figure 2). In contrast, size at maturity declined strongly among the adult (i.e., age-2) coho salmon ($R^2 = 0.629$, $n = 31$, $P < 0.001$) but not the jacks ($R^2 = 0.092$, $n = 28$, $P = 0.641$; Figure 3). The proportion of coho salmon jacks varied strongly among cohorts (Figure 4). There were few jacks for the smolt cohorts from the mid-1960s to the mid-1970s; the number of jacks then increased to a peak with the 1993 cohort and subsequently declined.

Multiple regression analysis revealed a significant positive relationship between smolt size and the proportion of jacks ($F_{1,16} = 14.89$, $P = 0.001$) and a significant negative relationship between the proportion of jacks and marine growth ($F_{1,16} = 18.03$, $P < 0.001$). In simple linear regressions, marine growth potential explained 38.4% of the variation in the proportion of jacks ($n = 19$, $P = 0.005$) whereas smolt size ($\log_e$[mass]) explained 17.8% of the variation ($n = 24$, $P = 0.057$). Adjusting for the variability in the exploitation rates of large coho salmon among years did not change any of these results. Ocean conditions during the season of smolt migration could not explain any
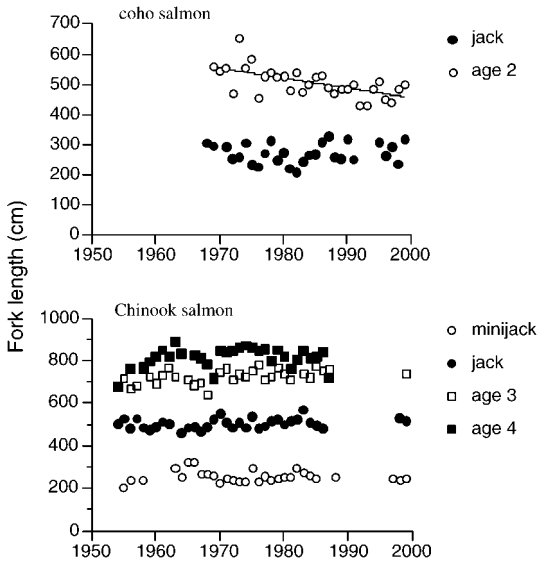
FIGURE 3.—Temporal variation in the average fork length (mm) of different age-classes of coho and Chinook salmon returning to the University of Washington hatchery.

Chinook Salmon

There was an almost 10-fold range in Chinook salmon smolt size and a significant trend toward larger smolts in more recent years ($R^2 = 0.737$, $n = 49$, $P < 0.001$; Figure 2). The average length of male UW Chinook salmon (all ages combined) declined over the entire period of record ($R^2 = 0.20$, $P < 0.002$). However, the mean length at age

either increased slightly (jacks: $R^2 = 0.093$, $n = 34$, $P = 0.082$; age-3 fish: $R^2 = 0.195$, $n = 33$, $P = 0.010$) or did not change with time (minijacks: $R^2 = 0.003$, $n = 30$, $P = 0.792$; age-4 fish: $R^2 = 0.049$, $n = 32$, $P = 0.226$; Figure 3). Thus the decrease in mean size of mature males was due to changes in age composition (Figure 5), not growth.

The proportion of jacks (ages 1 and 2 combined) of all returning males in a cohort increased markedly with time ($R^2 = 0.440$, $n = 48$, $P < 0.001$). In multiple regression analysis, neither smolt size nor marine growth opportunity was correlated with the proportion of jacks (smolt mass: $F_{1,12} = 3.01$, $P = 0.109$; growth: $F_{1,12} = 1.20$, $P = 0.296$). Further, the proportion of jacks was not correlated with either smolt size ($R^2 = 0.005$, $n = 27$, $P = 0.715$) or marine growth ($R^2 = 0.072$, $n = 15$, $P = 0.334$) when the factors were analyzed separately. Adjusting for the variability in the exploitation rates of large Chinook salmon among years did not change any of these results. Ocean conditions during smolt migration could not explain any of the remaining variability in the proportion of jacks.

The proportion of jacks returning as minijacks (age 1) was significantly correlated with smolt size but not the marine growth rate (multiple regression; smolt mass: $F_{1,21} = 12.33$, $P = 0.002$; growth: $F_{1,21} = 2.55$, $P = 0.126$). In single linear regression, smolt size explained 30.3% of the variation in the proportion of minijacks ($n = 49$, $P < 0.001$) whereas the marine growth rate was not correlated with the proportion of minijacks ($R^2 = 0.045$, $n = 24$, $P = 0.318$).

The ratio of age-3 to age-4 Chinook salmon did not change significantly with time ($R^2 = 0.008$, $n = 46$, $P = 0.334$), nor did it vary with growth
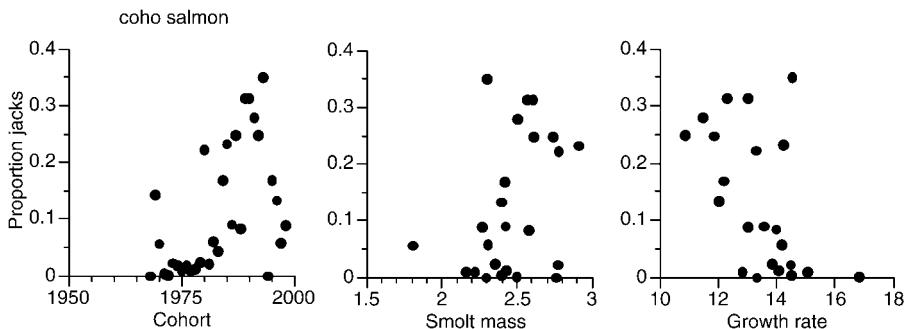
of the remaining variability in the proportion of jacks. Thus, despite poor growth at sea (as indicated by the decline in adult male length) and the absence of a time trend in smolt size, the proportion of jacks increased with time.

FIGURE 4.—Within-cohort variation in the number of jacks relative to the total number of returning male coho salmon (arcsine transformed), smolt mass (g; $\log_e$ transformed) over time, and marine growth potential (mass-specific growth rate [see text]; percent per gram of fish weight per year) over time.
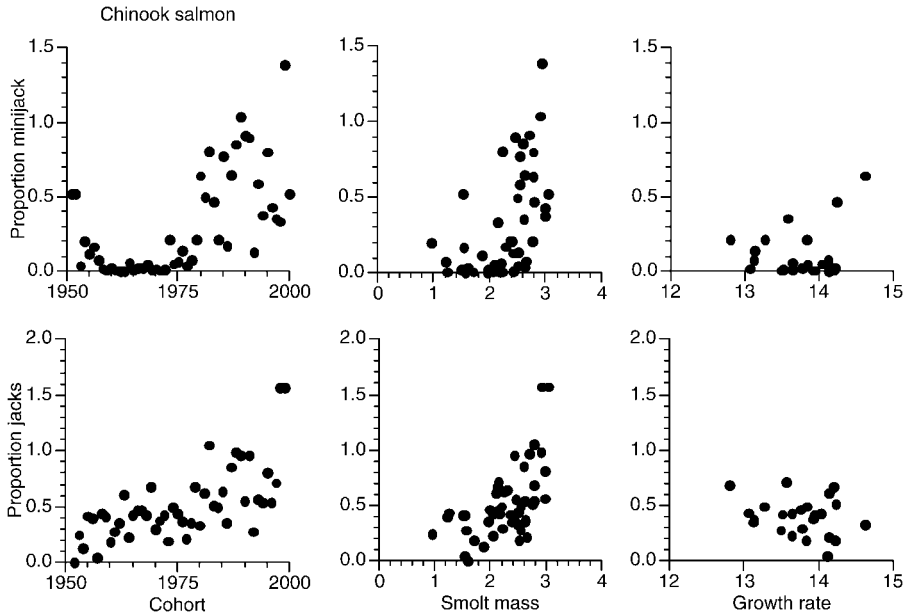
FIGURE 5.—Within-cohort variation in the number of jacks relative to the total number of returning male Chinook salmon (arcsine transformed; lower panels) and the number of minijacks relative to the total number of returning jacks (arcsine transformed; upper panels), smolt mass (g; $\log_e$ transformed) over time, and marine growth potential (mass-specific growth rate [see text]; percent per gram of fish weight per year) over time.

rate or smolt size (multiple regression; smolt mass: $F_{1,21} = 0.048$, $P = 0.829$; growth: $F_{1,21} = 0.13$, $P = 0.719$). The result was the same with single linear regressions (smolt size: $R^2 = 0.006$, $n = 45$, $P = 0.636$; growth rate: $R^2 = 0.001$, $n = 25$, $P = 0.905$).

Discussion

The proportion of male UW hatchery Chinook and coho salmon maturing at young ages (i.e., jacks) differed strongly among years during the approximately three decades of observations. The main conclusion from our analyses was that smolt size positively influenced the proportion of early-maturing coho and, to a lesser extent, Chinook salmon. Further, growth opportunity at sea influenced the maturation process of male coho salmon, high marine growth rates leading to increased age at maturity. Marine growth rate did not seem to influence the maturation decision in male Chinook salmon.

Early male maturity in salmonid fishes, once considered an aberration, is now recognized as an alternative life history pathway that is displayed to varying extents by different species and populations. There is considerable interest in the phenomenon from a theoretical perspective, as it may constitute a frequency-dependent, evolutionarily stable strategy (Gross 1985; Repka and Gross 1995; Gross and Repka 1998). From a practical standpoint, hatcheries and aquaculture operations commonly attempt to maximize growth rates but also regard jacks as wastage. Moreover, fisheries managers commonly use the number of jacks returning in a given year to help forecast the number of older fish returning the following year, based on the assumption that the proportion of jacks is relatively constant. Therefore, it is of great theoretical and practical interest to understand what factors lead to maturation as jacks for these species.

Understanding the balance between genetic and environmental factors in determining the likelihood that males will mature early is crucial in all such applications. Controlled-breeding studies have reported a significant genetic component to early maturity, based on the variation in family mean values (e.g., Unwin et al. 1999) or calculated heritability (e.g., Iwamoto et al. 1984; Silverstein and Hershberger 1992; Heath et al. 1994, 2002). Similarly, persistent differences in the proportion of jacks among populations with comparable opportunities for growth (Healey et al. 2000; Quinn et al. 2001) argue for genetic control. On the other hand, a large body of evidence indicates that early male maturation is related not only to size but also

to fat storage relatively early in life (e.g., Atlantic salmon: Simpson 1992; amago salmon *O. masou ishikawai*: Silverstein et al. 1997; Chinook salmon: Silverstein et al. 1998).

Our results point to a significant but not over-whelming environmental control and indicate that the effect is determined during the first spring of life (i.e., in freshwater). Average smolt size explained only 17.8% and 19.6% of the variation in the proportion of jacks in coho and Chinook salmon, respectively, and 30.3% of the variation in the proportion of minijacks among the Chinook salmon jacks. The growth opportunity at sea, as indicated by the observed growth by females of the same species and cohort, had no detectable influence on early male maturity in Chinook salmon and was negatively correlated with the proportion of coho salmon that matured as jacks. We observed a marked decline in the growth of male coho salmon (as well as in females; Quinn et al. 2004) over the period of record. Therefore, the increased proportion of jacks in recent years has occurred during a period with poor growth rates at sea. This contrasts with the observation that slower growth at sea was associated with advanced age at maturity (e.g., Japanese chum salmon *O. keta*: Kaeriyama 1998) and the experimental finding that restricted springtime feeding reduced the proportion of early-maturing Chinook salmon (Hopkins and Unwin 1997). Further, it contrasts with the more general theoretical principle that increased growth rates usually lead to earlier ages at life stage transitions such as smolt transformation and maturation (Alm 1959; Day and Rowe 2002).

The most plausible conclusion from these findings is that rapid growth early in life predisposes males to mature early but that later growing conditions have little effect. Indeed, in the case of coho salmon, slower growth at sea was associated with a higher proportion of jacks. However, these results must be interpreted from a larger and more complicated perspective. Many factors have operated during the past 30–50 years that might affect salmon life history patterns. First, the UW hatchery has assiduously avoided using jacks for spawning. While we cannot state that jacks have never been used, it has certainly been the policy to exclude them systematically. Thus, the high but varying production of jacks among coho salmon and the increasing proportion among Chinook salmon have occurred despite very strong genetic selection during breeding. Assuming the individuals that became jacks were the fast-growing members of the cohort, the hatchery has effectively been selecting for slow growth (at least in males).

The selection against jacks in the hatchery has not operated in a vacuum, however, as there are commercial and recreational fisheries operating on these populations. The coho salmon jacks are virtually all below the legal size limit in Washington's recreational fisheries (currently 40 cm). All of the Chinook salmon minijacks and most of the age-2 jacks have been below the legal size limit (currently 60 cm), though the limit has varied among years and areas. Moreover, the jack coho salmon and minijack Chinook salmon are virtually untouched by size-selective gill nets, which are regulated to catch adult Chinook salmon. The age-2 Chinook salmon jacks are about the same size as the adult coho salmon and so may be taken in some commercial fisheries. Thus, there has been selection in the fisheries to the advantage of smaller and younger fish. However, adjusting for the variation in the exploitation rate among years did not change any of our results. This indicates that our results are robust, although it does not preclude the possibility of genetic effects on these populations.

Many salmon populations, including both wild and hatchery fish over a wide geographic range, have shown declines in body size, probably from a complex mix of different factors. Declines in size seem to be influenced by environmental conditions, including (or at least correlated with) water temperature, and the intensity of exploitative competition with other salmon (e.g., Rogers and Ruggerone 1993; McKinnell 1995; Pyper and Peterman 1999). However, we did not find evidence for any environmental control over age at maturity other than that exerted directly through growth rate. Human activities have, however, exerted such complex (and often contradictory) regimes of selection that it is difficult to determine the relative magnitudes of different factors. All fisheries reduce adult competition on spawning grounds, and this may affect the relative fitness of different age-groups (Haugen and Vøllestad 2001; Ashley et al. 2003). Size-selective fisheries may favor small fish, and accelerated growing conditions in hatcheries may separate phenotypic expression from genotype. Although our results point to an important role for early growth, they should not be taken as contradicting the results of other studies because of the unique blend of natural and human selection that each population may experience.

Acknowledgments

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