

Session 4a: Age and size effects on reproductive behavior and breeding success (prepared by Barry Berejikian)

Summary

This session presented existing information on the effects of size and age on breeding success of male and female Pacific salmon. The objective was to improve understanding of natural mating processes that may contribute to a scientific basis for broodstock management and management of spawning populations above human-made barriers (weirs or dams). Berntson et al. summarized data from two Chinook salmon supplementation programs with ongoing pedigree studies designed to compare the RRS of hatchery and wild fish in natural rivers. The data from the Wenatchee River (Williamson et al. 2010) and Catherine Creek (Berntson et al. unpublished) were analyzed to compare the RRS males varying in age from age-2 to age-5. Younger males (ages 2 and 3; minijacks and jacks respectively) in both studies were less successful overall than older (ages 4 and 5) males, averaging approximately 50-60% RRS. Jacks in the Wenatchee River had higher RRS than would be predicted based on fish size alone. A few jacks in Catherine Creek had a much higher RRS than older males. This higher success suggests disruptive selection favoring older larger males and younger smaller males more so than intermediate-sized males. Disruptive selection on male body size should favor the persistence of variability in age-at-maturity over time in naturally spawning populations.

Schroder et al. reviewed relationships between size and age at maturation and offspring traits and production in naturally spawning female Pacific salmon. For these species there is a general belief that larger and older females will achieve higher fitness values than smaller and younger cohorts. This perception is based on several relationships. For example, larger females dig deeper nests which protect their eggs from scour, dislodgement by other females, and dewatering and desiccation. Furthermore, positive correlations between female weight and fecundity commonly occur in many salmonid species. Typically, female weight explains 40 to 60% of the variation in fecundity. Spending an additional year at sea often increases absolute fecundities by 10% or more, increases egg weight and may also increase the caloric value of the eggs produced by a female. Within the same age, female size may also be linked to egg size, although the amount of variation in egg weight that can be explained by maternal size when age is held constant is often 20% or less. Egg size is an important female parental investment as fry from large eggs are larger and have greater yolk reserves at emergence than those produced from smaller eggs. Consequently, fry originating from large eggs have a decreased risk of starvation and predation, have greater social dominance, a broader array of potential prey items available to them, and increased swimming speed and stamina. Size and age, however, have not been shown to affect the ability of females to deposit eggs, how attractive they are to males, how long they live after reaching maturation, or offspring production. Unpredictable environmental conditions at spawning and during freshwater rearing preclude the development of optimal stream-specific female sizes and ages. Instead, combinations of female sizes and ages appear to increase productivity. Consequently, the key for successful management is to provide a diversity of female sizes and ages on a spawning ground.

The breeding success and ultimate fitness of salmonid males has often been associated with their body size. Large males are in general more successful at producing offspring than relatively

small ones. In spring Chinook salmon, for example, slightly more than 30% of the variation in male breeding success could be explained by relative size. Work with chum salmon also showed that relative size affected which males had access to females when operational sex ratios (OSR) were greater than 1.2 males per female. Evolutionary theory predicts that alternative behavioral tactics and life history strategies will evolve when a portion of a population is excluded from resources that are closely associated with fitness. For example, relatively small or weak salmonid males will position themselves slightly downstream from a primary pair and attempt to fertilize eggs when a spawning occurs. When satellite males are able to participate in a spawning, they fertilize approximately 25% of the eggs. This behavioral tactic was observed to increase in a linear fashion as intra-sexual competition among males for females rose in spawning populations of chum salmon. Males may also use different life history strategies to fertilize eggs and produce offspring.

In the upper Yakima River, spring Chinook males adopt one of four different life history strategies. Large anadromous males mature at ages 4 and 5, smaller anadromous males mature at age 3 (jacks), and non-anadromous males reach maturation after just 6 to 7 months of freshwater life (sub-yearling precocious parr) or after 16 to 18 months of freshwater life (yearling precocious parr). The breeding success of jacks and precocious parr relative to large anadromous males was examined in an artificial stream. Jacks and yearling precocious parr had breeding success values that were about 25% of those achieved by the large anadromous males. Sub-yearling precocious parr were about 3% as effective at producing fry as the large anadromous males. These percentages remained fairly constant even though the proportion of large anadromous males in the populations examined varied from 48 to 88% and OSR values ranged from 1.4 to 2.4 males per female. Comparable work performed on Atlantic salmon suggests that even when just 1 to 2% of a population is comprised of large anadromous males they may fertilize up to 50% of the deposited eggs. These data suggest that when half or more of the males in natural breeding population represent the large anadromous strategy they are likely to fertilize 90% or so of the eggs deposited.

Berejikian et al. tested the hypothesis that mating success of jack and adult phenotypes is consistent with the negative frequency-dependent selection model and summarized existing information on jack male breeding success in Pacific salmon. As with other species, negative frequency-dependent selection during reproduction has long been proposed as an important mechanism in maintaining alternative male reproductive phenotypes in Pacific salmon. By holding male density constant and varying the frequency of adult and jack males in eight separate breeding groups, they found that adult male access to females, participation in spawning events and adult-to-fry reproductive success increased with their decreasing frequency in a breeding group. Jack males exhibited the same pattern (increasing success with decreasing frequency) although the relationships were not as strong as for adults. Overall, jack and adult males mated with a similar number of females but jacks sired only 20% of all offspring. Observational data and pedigree analyses of offspring produced from observed spawning events strongly suggested that adult males benefited from sperm precedence associated with their ability to court females and enter the nest first at the time of spawning. Offspring of jack males grew at a faster rate under quasi-natural conditions than offspring of adult males, providing the first evidence of paternal (genetic) effects on offspring growth rates and a potential mechanism (rapid growth to achieve maturation thresholds) for parent-offspring life history similarities.

Berejikian et al. also reviewed estimates of breeding success from the studies presented in this session and additional studies on coho salmon and sockeye salmon. The breeding success estimates for jack Chinook salmon are shown in Table 1. Data from coho and sockeye salmon, while more limited, suggest jack male breeding success is fairly consistent to that observed for Chinook salmon (i.e., relative jack male breeding success was approximately 0.40 to 0.50).

Uncertainty

The fairly consistent mean values for the relative reproductive success of jack males among the four studies suggest that the results may be generalizable to other populations. However, the total number of studies is still small and additional information should be forthcoming from pedigree studies evaluating the relative reproductive success of hatchery and wild Chinook salmon. Minijacks (age-2 stream-type Chinook salmon) were present in the spawning populations for three of the four studies, and in each study produced a portion of the offspring. In Schroder et al, jack males were less successful than in the other three studies and the minijacks produced as many progeny per individual as jack (age-3) males, suggesting that minijack breeding success may have come at the expense of jack males exhibiting similar (i.e., sneaking) mating tactics. The inconsistent and generally small number of minijacks in the breeding populations points to a need to better quantify their contribution to the next generation.

Future research or monitoring needs

The importance of age-at-maturity effects on breeding success depends largely on two questions. First, is heritability for age-at-maturity great enough for differences in alternative male phenotype reproductive success to exert significant control over the age structure of populations? In other words, if the genetic basis for male age-at-maturity is strong, changes in male spawner age composition may affect population age structure; if it is weak, then tight management of jack proportions in hatchery broodstocks and placement above weirs becomes less important. Estimates of heritability for age-at-maturity are scarce in Pacific salmon and better estimates are needed. Second, what are the paternal (i.e., genetic) effects of young, small (minijack and jack) males on female offspring growth, survival and associated reproductive capacity. It's unclear whether or how traits genetically linked to male age-at-maturity might affect female phenotypic traits. Age and size at maturity are positively correlated with fecundity, egg size, competitive ability, and nest depth and may ultimately affect the productivity of naturally spawning populations.

Recommendations

The RRS for jack males was 0.50 averaged over all of the 18 different breeding groups represented in the studies. This means that in naturally spawning populations, jack males produce on average one out of every three offspring. A meta-analysis of the 18 breeding groups examined indicated a significant positive relationship between the proportion of jacks in a population and the proportion of offspring produced from jacks; the slope of this line was 0.64 (significantly less than 1.0). Both of these metrics might be used as guidelines for broodstock management where the goal may be to mimic natural contributions of males of different ages and mating strategies. The suggestion of frequency-dependent selection, if it occurs in natural

populations (still to be tested) would suggest that jacks might be passed above weirs in their return proportions. In years where large numbers of jacks are present, their individual breeding success will likely decline, and in low jack return years, their per capita contribution should be greater. We'd caution against simply applying data from natural breeding success without considering other selective forces (e.g., size-selective fisheries).

Table 1. The relative breeding success (BS) of jack male Chinook salmon to that of older males in four studies. The number of breeding groups reflects independent spawning populations either in the same river in different years or separate stream channels over more than one year (Berejikian et al.). Relative breeding success was calculated as the mean number of offspring per spawner for jack males divided by the mean number of offspring per spawner for older males.

Study	Breeding groups	Jacks in population	Offspring from Jacks $f(\text{BS} \times \text{N})$		Relative Breeding Success	
	N	Range	Mean	Range	Mean	Range
Berejikian et al 2010	4	25 - 50%	20%	9 - 33%	0.56	0.15 - 1.00
Berntson et al. (unpublished)	5	10 - 14%	7%	2 - 13%	0.61	0.22 - 1.09
Williamson et al 2010	2	10 - 61%	27%	8 - 47%	0.45	0.18 - 0.71
Schroder et al 2011	7	7 - 13%	3%	1 - 5%	0.25	0.14 - 0.47
OVERALL	18	7 - 50%	14%	1 - 47%	0.50	0.14 - 1.09

Literature Cited

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