North Pacific Anadromous Fish Commission
Technical Report No. 11:56–58, 2018

Validity of Inferring Size-selective Mortality in Pacific Salmon from Scale Circulus Spacing

Terry D. Beacham[1], **H. Andres Araujo**[1], **Strahan Tucker**[1], and **Marc Trudel**[1,2]

[1]*Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, B. C. Canada V9T 6N7*

[2]*Present address: Fisheries and Oceans Canada, St. Andrews Biological Station, 531 Brandy Cove Road, St. Andrews, NB, Canada E5B 2L9*

Keywords: critical size limit, critical period, Pacific salmon, size-selective mortality, scale circulus spacing

Beamish and Mahnken (2001) proposed that most natural mortality of Pacific salmon during the marine life history phase was size-dependent and occurs in two major episodes. The first phase of mortality was suggested to be predation based and occurs after the smolts enter the ocean, with other studies on salmonids typically reporting relatively high mortality after initial ocean entry (Parker 1968, Hartt 1980). The second phase of mortality was suggested to occur in the fall and winter of the first year in the ocean, when those individuals that have not attained a critical size die because they are unable to meet minimum metabolic requirements (Beamish and Mahnken 2001). Beamish et al. (2004) indicated that Pacific salmon had to achieve a sufficient size by the end of the first marine summer to be able to survive the metabolic demands during a period of energy deficit in the late fall and winter.

If evaluation of differences in frequency distributions of individuals with different scale circulus spacing is a valid way to infer size-selective mortality of juveniles, then a number of predictions can be made with respect to the distribution of individuals with different circulus spacing within the population. First, there should be a positive correlation between circulus spacing and body size both within and among sampling periods, as individuals with wider circulus spacing are imputed to be faster growing and thus larger. Next, if circulus spacing is a permanent record of growth, there should be a wide range of circulus spacing within the population of juveniles sampled during the first marine summer, but during the late fall and winter as hypothesized size-selective mortality occurs, individuals with narrow circulus spacing should disappear from the population as they were unable to attain the critical size necessary for survival during the first winter of ocean residence. There should be little identification of individuals later in the life cycle with circulus spacing unobserved during the first summer of rearing, merely a change in the relative frequencies of circulus spacing observed in the juvenile population during the first summer of rearing. Therefore, one should expect that the range of circulus spacing in the population should be greater during the first summer of marine rearing than later in the life cycle, and that the variance in circulus spacing within the population should be greater in the first summer than later in the life cycle.

Under the assumption that size-selective mortality would operate on the smaller members of the juvenile population, we investigated the expected distribution of the scale circulus index and the associated descriptive statistics of the distribution under expectations that failure to achieve a critical minimum would remove up to 80% of the existing population. As the projected juvenile mortality rate increased, the mean of the scale index of the remaining (adult) population increased, the range of the scale index declined, as did the standard deviation of the index. The skewness of the distribution of the index values of the remaining individuals increased positively, with higher values observed under more extensive mortality scenarios.

If size-selective mortality is operating on the smaller individuals in the juvenile population, then one should observe a shift in the frequency distribution of the scale index towards values associated with larger individuals. It is expected then that the scale circulus index of the adults should fall within the range of the index observed for the juveniles, but as juveniles with smaller values of the index are selectively removed from the population, then the range of the index observed in the adult population should be less than observed in the juveniles, and thus variance will be lower. There should also be higher positive values of skewness of the distribution in the adult population compared with the juvenile population.

Bond et al. (2008) compared the size distributions of hatchery-reared steelhead (*O. mykiss*) smolts sampled immediately before release with the back-calculated size at ocean entry of surviving adults from the same cohort. All adults in the sample displayed back-calculated fork lengths that were observed in the smolts upon release, and the back-calculated lengths were a subset of those observed in the smolts, with a shift in the frequency distribution of size towards values associated with larger individuals. These results illustrate what would be expected if the smaller individuals in the smolt population experienced size-selective mortality. We suggest that the key here was

https://doi.org/10.23849/npafctr11/56.58
All correspondence should be addressed to T. Beacham.
email: Terry.Beacham@dfo-mpo.gc.ca

that the juvenile samples were representative of the entire population, as the juveniles were sampled before hatchery release, and the returning adults must necessarily have been derived from the sampled juvenile population.

Some studies occur where the juvenile sample was obtained not from a hatchery prior to release of the juveniles, but instead was obtained by sampling juveniles after they had been rearing for a period of time in the ocean. Beamish et al. (2004) measured mean intercirculus spacing of the first 10 marine circuli of coho salmon in the Strait of Georgia in British Columbia, with juveniles sampled in September and November of their first year of ocean rearing (marine age 0). The results display the opposite results to those expected under a size-selective mortality environment directed at the smaller members of the population. The range and variance of the scale index values of the marine age-1 individuals were actually larger than those of the age-0 individuals, and skewness of the distribution actually declined, indicative of relatively more marine age-1 individuals with narrow circulus width spacing than would be expected.

Moss et al. (2005) measured distances from the scale focus to specific circulus for three hatchery populations of pink salmon in Prince William Sound, Alaska. Size-selective mortality was inferred by comparing the frequency and means of scale radius length classes at specific circulus for juveniles from the hatcheries sampled in July, August, and September in the year of release with that of adults that returned to the three hatcheries the following year. If substantial size-selective mortality were present between the juvenile and adult life history stages, then most adults in the sample should display circulus width values observed in the juvenile population, and the range and variance of the adult circulus spacing values should decline. It seems likely that the juveniles sampled were not representative of the whole population and underestimated the presence of the larger pink salmon that were resident in the ocean but unavailable to the summer and fall sampling regime, resulting in an overestimation of the impact of size-selective mortality on the populations.

A fundamental question to answer is how it is possible that adults derived from a juvenile population displayed values greater than the maximum observed in the juvenile population. One possible explanation is that the larger-sized individuals in the juvenile population were not available to be sampled when the initial distribution of the scale circulus values in the juvenile population was determined. The larger-sized individuals could have selectively moved from the geographic sampling area (Beacham et al. 2014, 2016, 2017), or they could have moved deeper in the water column making them unavailable to the sampling gear. It is possible that larger-sized juveniles were not available to be sampled as juveniles, but were available to be sampled as adults, resulting in observed scale circulus values outside of the range observed in juveniles. As outlined by Beacham et al. (2017), movement of larger-sized juvenile coho salmon likely from the Strait of Georgia did occur prior to the collection of first ocean year individuals by Beamish et al. (2004), and thus there was little support for the hypothesis that coho salmon experienced size-selective mortality and had to achieve a sufficient size (the "critical" size) by the end of the first marine summer or fall to be able to survive during the winter of their first year of ocean rearing.

Size-selective mortality is often invoked as an important driver of population dynamics of Pacific salmon (Beamish et al. 2004), so much so that the concept has been introduced of the necessity of obtaining a "critical size" by the fall of the first year of ocean rearing in order to ensure survival over the winter (Beamish and Mahnken 2001), a potential second "critical period" (Howard et al. 2016). There is no doubt that there can be substantial mortality of Pacific salmon during their first year of ocean residence. However, in order to invoke size selection as an important driver of this mortality, we suggest that it is necessary to demonstrate that size-selective mortality directed towards the smaller members of the population can account for a substantial portion of the observed mortality. With respect to size, a critical size implies that the individuals must attain this size or die; for a size to be defined as "critical," it must be demonstrated that the proportion of the population failing to attain this size by the specified period can account for the observed mortality. Studies that employ scale characteristics to infer size-selective mortality need to show that all scale index classes in the adult population were indeed present in the juvenile population, and that the adult scale classes were a subset of those present in the juvenile population.

REFERENCES

Beacham, T.D., R.J. Beamish, John R. Candy, Strahan Tucker, Jamal H. Moss, and Marc Trudel. 2014. Stock-specific size of juvenile Sockeye Salmon in British Columbia waters and in the Gulf of Alaska. Trans. Am. Fish. Soc. 143: 876–888.

Beacham, T.D., R.J. Beamish, Chrys M. Neville, John R. Candy, Colin Wallace, Strahan Tucker, and Marc Trudel. 2016. Stock-specific size and migration of juvenile Coho Salmon in British Columbia and southeastern Alaskan waters. Mar. Coast. Fish. 8: 292–314.

Beacham, T.D., Chrys M. Neville, John R. Candy, Strahan Tucker, and Marc Trudel. 2017. Is there evidence for biologically significant size-selective mortality of coho salmon during the first winter of marine residence? Trans. Am. Fish. Soc. 146: 395–407.

Beamish, R.J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog. Oceanogr. 49: 423–437.

Beamish, R.J., C. Mahnken, and C.M. Neville. 2004. Evidence that early marine growth is associated with lower marine survival of coho salmon. Trans. Am. Fish. Soc. 133:26–33.

Bond, M.H., S.A. Hayes, C.V. Hanson, and R.B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Can. J. Fish. Aquat. Sci. 65: 2242–2252.

Hartt, A.C. 1980. Juvenile salmonids in the ocean ecosystem: the critical first summer. pp. 25–57. In: W.J. McNeil and D.C. Himsworth (editors). Salmonid Ecosystems of the North Pacific. Oregon State Univ. Press, Corvallis, Oregon.

Howard, K.G., J. M. Murphy, L. I. Wilson, J. H. Moss, and E. V. Farley, Jr. 2016. Size-selective mortality of Chinook salmon in relation to body energy after the first summer in nearshore marine habitats. N. Pac. Anadr. Fish Comm. Bull. 6: 1–11. (Available at http://www.npafc.org)

Moss, J.H., D.A. Beauchamp, A.D. Cross, K.W. Myers, E.V. Farley Jr., J.M. Murphy, and J.H. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans. Am. Fish. Soc. 134:1313–1322.

Parker, R.R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25: 757–794.