

Critical Size and Period for Pacific Salmon: A Review and Response to Beacham et al. (2018)

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For Pacific salmon, their early marine residence and first winter at sea are hypothesized as “Critical Periods” where mortality within a cohort can be large. Sogard (1997) suggests that mortality acts on a cohort in three possible ways: 1) indiscriminately—there is the same probability of mortality for all individuals (i.e., larval life history stage); 2) randomly—mortality is inconsistent or unpredictable; and 3) non-random—traits within a cohort reduce “relative” risk of mortality. For juvenile salmon, mortality is hypothesized to be “non-random” where the traits used to define “critical periods” include size and lipid storage that juveniles attain during their first summer at sea. These traits are a reflection of the marine ecosystems that the juvenile salmon experience. This concept of a critical period (summer growth and energy storage) has also recently been developed for young of the year pollock and Pacific cod within the Bering Sea (Hunt et al. 2011; Coyle et al. 2011; Heintz et al. 2013; Farley et al. 2015).

Beacham et al. (2018) assume size-selective mortality is a “knife-edge” process, where fish that do not reach an “absolute” critical size die. They simulated two size frequencies under this assumption and then compared statistics from the simulated size frequencies to previous work that used empirical data. In natural marine systems, fish do not exhibit a knife-edge mortality. Instead, there is a decreasing probability of size-related mortality as fish become larger. For example, Howard et al. (2016) illustrate (Fig. 1) the probability of size-selective mortality in relation to juvenile Yukon River Chinook Salmon weight. Weight is a proxy to energy density (lipid), which is a key biological trait when assessing the health of a population prior to their first winter at sea. Fish scale to fish length, fish length to fish weight, and fish weight to fish energy density relationships are all described via statistical relationship with error distributions. Thus, even if there was a single critical energy density value (i.e., a knife edge mortality) instead of a range of weights (energy densities) as demonstrated by Howard et al. (2016), we would still expect to see a broader distribution of scale circuli and fish lengths associated with these densities, rather than a knife edge mortality as suggested by Beacham et al. (this volume).

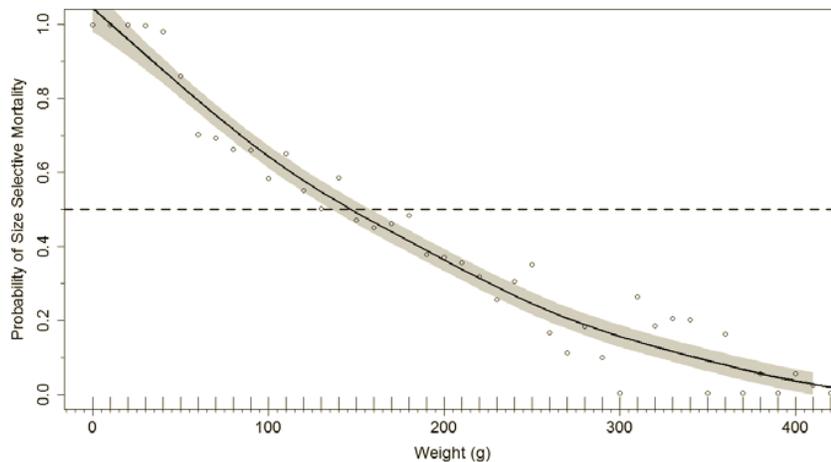


Fig. 1. (Fig. 7 from Howard et al. 2016) Generalized additive model (thick solid black line) fit to size selective mortality (SSM) probabilities of juvenile Yukon River Chinook Salmon based on differences between actual juvenile weights and the average of simulated back-calculated weights of adults during the second critical period (summer growth prior to the first winter at sea). The horizontal dashed 0.5 probability line identifies the reference point of neutral selection of the GAM model; a selective disadvantage is expected for weights smaller than this point, a selective advantage is expected for weights larger than this point. Shaded area represents GAM model confidence intervals.

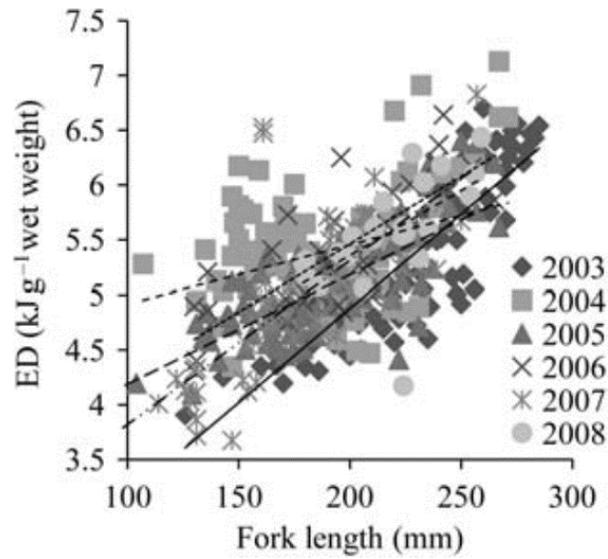


Fig. 2. (Fig. 3 from Farley et al. 2011) Scatterplot displaying the relationship between energy density (ED; kJ g⁻¹ wet weight) and fork length (mm) for juvenile sockeye salmon collected during autumn 2003–2008 in the eastern Bering Sea. Linear lines for each year were fit to the data to illustrate differences in the relationship between ED and fork length for juvenile salmon among years.

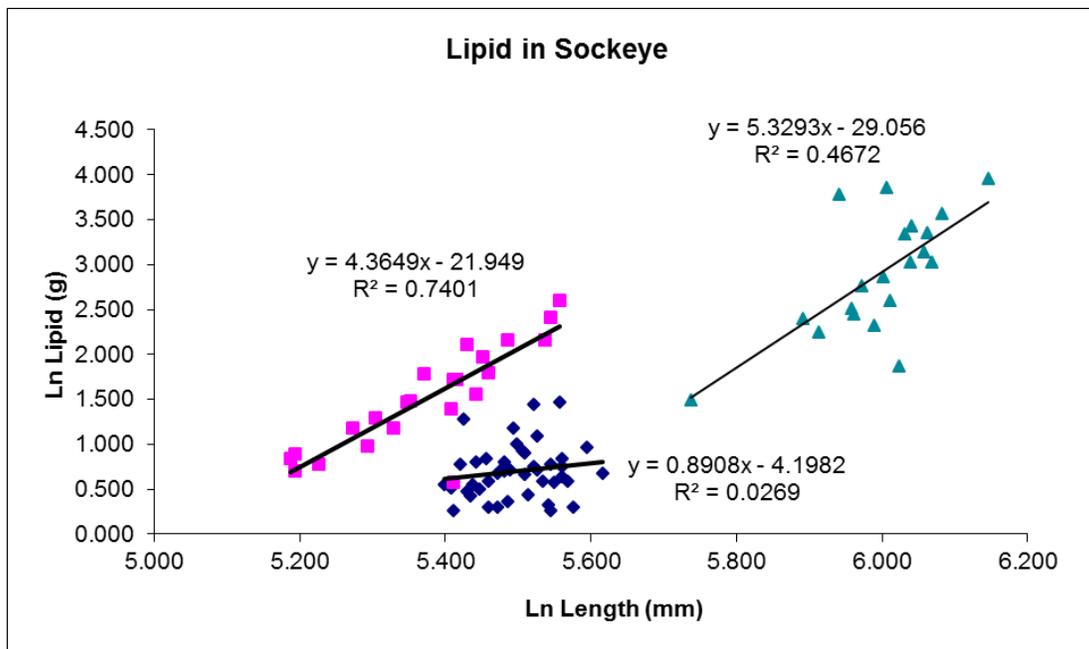


Fig. 3. (based on Fig. 5 from Farley et al. 2011) The relationship between the natural log of fork length and lipid for juvenile (squares), ocean age-1 (diamonds), and ocean age-2 plus (triangles) collected during autumn 2008 (juveniles) in the eastern Bering Sea and winter 2009 (age-1 and age 2+) in the North Pacific Ocean.

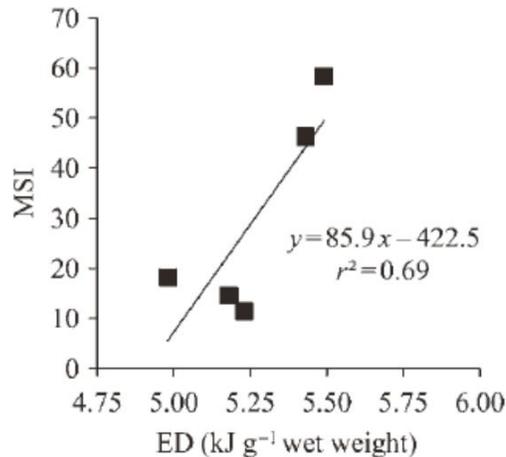


Fig. 4. (Fig. 6 from Farley et al. 2011) The relationship between the marine survival index (MSI) and energy density (ED; kJ g⁻¹ wet weight) for juvenile salmon caught during autumn of 2003–2007 in the eastern Bering Sea.

The role of juvenile salmon size and mortality is dynamic and complex: ecosystem processes like temperature regime, ontogenetic timing, prey dynamics and predator dynamics are expected to interact with size-selective mortality processes in a variety of ways, at multiple time scales and at different magnitudes. Farley et al. (2011) found that energy (lipid) is related to the length of fishes; however, this relationship can vary (in both intercept and slope) depending on ecosystem dynamics during summer months. Sometimes a smaller fish can have more lipid during one year than a fish of similar size during other years (Fig. 2 from Farley et al. 2011) and the path to high or low lipid states during summer for fish is likely a function of temperature and prey quality and quantity. Therefore, size-dependent mortality can vary depending on quality and quantity of prey, suggesting that critical-size (as it relates to energy reserves) can also vary. Farley et al. (2011) also note that the relationship between energy and size shifts during the first winter at sea for juvenile to age-1 Bristol Bay sockeye salmon (Fig. 3). The seasonal signatures for lipid and protein suggest that ocean age-1 sockeye salmon are not starving, but instead the larger fish are likely utilizing energy stores to minimize predation. Energy density that juvenile sockeye salmon accumulate during summer is also strongly related to their marine survival (Fig. 4).

The time frame defining a critical period when size-selective mortality may be most influential should also be expected to be dynamic, complex, and stock-specific. Farley et al. (2007) used survey data to estimate the abundance of juvenile Prince William Sound (PWS) hatchery pink salmon during August. They then compared this estimate to the number of PWS hatchery pink salmon released and the number of PWS hatchery adult pink salmon that returned the following year. They found that the highest marine mortality occurred prior to the August survey (93%), but there was still substantial marine mortality after the survey (26%) illustrating the magnitude of mortality during the two critical periods (first 40 days at sea and winter) for juvenile pink salmon. Moss et al. (2005) found that surviving adults were significantly larger than juveniles at the same circulus for 5 different circuli comparisons using scales collected from juvenile and adult PWS hatchery pink salmon. These size frequency comparisons provide evidence that juvenile pink salmon undergo significant size-selective mortality after the first growing season. Beacham et al. (2018) focused only on circuli 15 (Fig. 5) and suggest that the distribution patterns between juveniles and adults for this circuli comparison do not conform to their hypothesis regarding size-selective mortality. They suggest that Moss et al. (2005) likely missed the larger cohorts in the populations of hatchery pink salmon, thereby overstating the significance of selective processes over winter. While this is a possibility, it is also a possibility that a restricted approach to defining the timing of a critical period may underestimate natural processes. It is also highly likely that the survey missed the smaller cohorts within the population, thereby understating the significance of selective processes over winter.

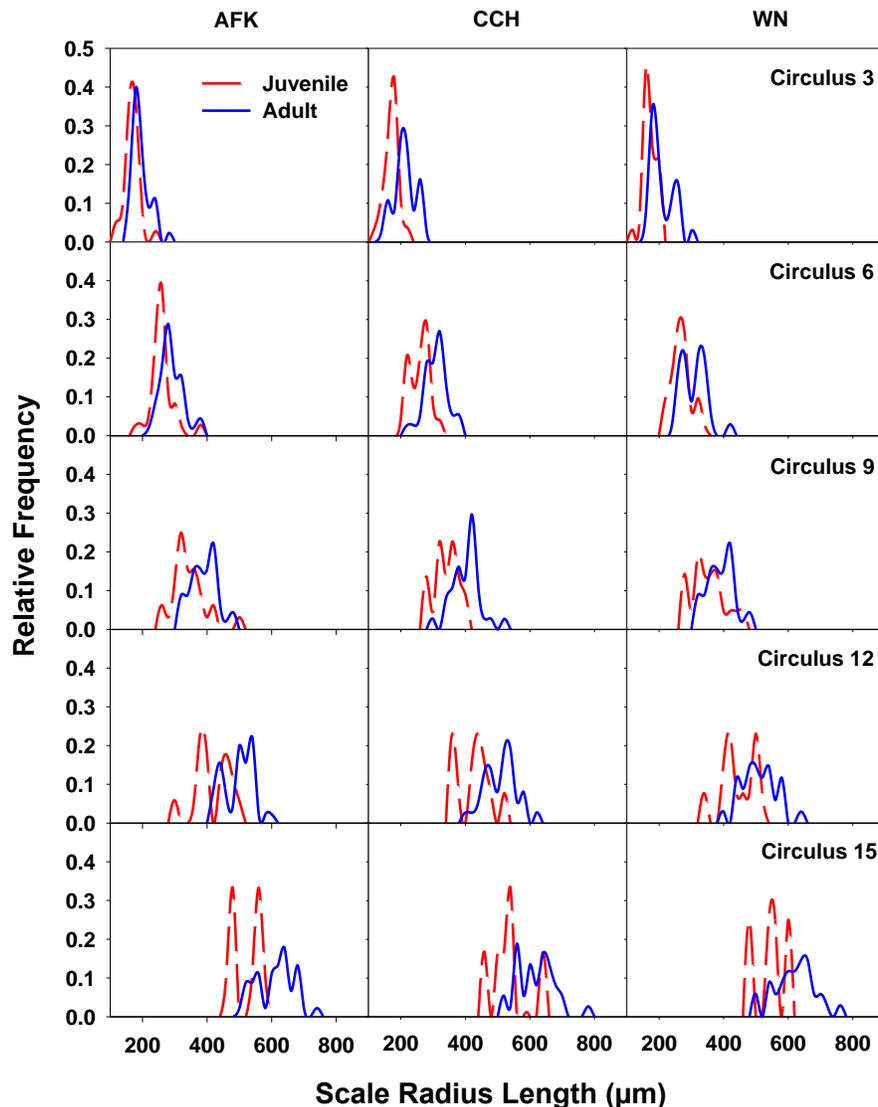


Fig. 5. (Fig. 2 from Moss et al. 2005) Relative frequencies of scale radius length to circuli 3, 6, 9, 12, and 15 for hatchery pink salmon juveniles (dotted lines) and individuals of that cohort returning the following year as mature adults (solid lines) released by Armin F. Koernig (AFK), Cannery Creek (CC), and Wally Noerenberg (WN) hatcheries in 2001 (brood year 2000).

Conclusion

Beacham et al. (2018) assume mortality for fishes within natural populations is a knife edge function. Their illustration is one that is unlikely to occur in nature and is inconsistent with the descriptions of size-selective mortality in the literature they cite. The critical-size literature cited attempts to describe the increased likelihood of survival for those individuals that meet the energetic needs for over-winter survival and a size that reduces predation risk. Therefore, their interpretation of size-selection based on skewness and kurtosis for a population experiencing “knife edge” mortality is not a valid comparison to our empirical data distributions.

Simulations can be used to support alternative hypotheses for many ecological studies. However, several assumptions used in the Beacham et al. (this volume) simulations lead to an over-simplified attempt to undermine the conclusions drawn from empirical data. The empirical data allows for the inter-play between size and energy density, and they allow for inter-annual variability in the natural environment. Such biological and environmental stochasticity is ignored in the simulations.

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