

Response to Comment on "Rapid Evolution of Egg Size in Captive Salmon" (II)

Heath *et al.* (1) reported extremely rapid evolution of egg size in a farmed population of chinook salmon and provided data showing egg size decline in two river populations that received aggressive supplementation. Beacham (2) provides additional data from the Department of Fisheries and Oceans, Canada, for those two populations (Quinsam River and Robertson Creek), as well as for one population not in the original paper (Big Qualicum River). Beacham challenges one of the primary conclusions in (1): that rapid evolution of egg size may be a concern for conservation programs. However, his statistical analysis has some serious limitations. We agree that standardization of egg size for changes in maternal body size is valuable for the assessment of changes in egg size over time. Because Heath *et al.* (1) found no significant change in mean population body size over time, they did not correct for body size. Beacham uses body size–egg size relationships across years to standardize egg size—a procedure described elsewhere (3), but not validated for use with this data. His use of an exponent of one ($b = 1.0$; slope) for nonsignificant egg size–body size relationships is incorrect; the correct value is $b = 0$ because there is no relationship between egg size and body size and, thus, E_s should equal E_o . We also question the rationale for using a marine regime–based analysis of standardized egg size because the time series data show no evidence for regime-related changes in body or egg size in these populations.

Interestingly, despite these concerns about standardization calculations, the Beacham data support the original hypothesis of Heath *et al.* in (1). We reanalyzed Beacham's standardized egg size and body size data using time series analysis, first smoothing the time series using Holt's exponential smoothing (4). The three populations showed a negative forecasting trend for standardized egg size, whereas only two of the populations (Big Qualicum and Quinsam River) showed a negative trend in body size. In fact, only the Quinsam River population showed a significant change in body size over time (regression analysis; $P < 0.001$), whereas all three populations showed significant declines in standardized egg size (regression analysis: Quinsam, $P = 0.059$; Robertson Creek, $P = 0.003$; Big Qualicum, $P = 0.03$). Most important, when applying a combined probability test [Fisher's meta-analysis (5)], standardized egg size shows a highly significant negative trend across all three populations ($P = 0.0003$). The meta-analysis was significant even after including regime as a controlling categorical variable ($P = 0.007$), indicating that there is a negative trend even in the face of the potential confounding effect of a marine regime shift during the series. Thus, Beacham's standardized egg size data further support the hypothesis presented in (1).

Beacham also provides egg size data from one other farmed population of chinook salmon, in which egg size did not decline over 10 years. However, Beacham does not provide

either body size or age at maturation for these fish, so possible reductions in egg size would be masked by increasing body size or age of the spawned fish. Furthermore, the Yellow Island Aquaculture Limited (YIAL) farmed population is quite different from the Sea Spring Salmon Farm Ltd. population. The YIAL offspring are reared to sexual maturity in one facility, and so the YIAL time series data are from a single population held in a common facility and are ideally suited for detecting selection effects.

The additional data and reanalysis from Beacham is welcome evidence that organizations charged with conservation of animal resources are addressing the questions raised by Heath *et al.* However, his data support rather than dispute the potential for genetically based egg size decline in supplemented populations.

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