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Comment on “Rapid Evolution of Egg Size in Captive Salmon” (I)

Heath *et al.* (1) estimated the intensity of selection and apparent rapid evolution of small eggs in a captive bred population of chinook salmon, and implicated the same process in the apparent decline in egg size of some heavily hatchery-supplemented natural populations. However, we believe that the change in egg size may have been greater than reported and that the evidence is inconclusive about the underlying cause (i.e., genetics, environment, or both). We identify several specific points that suggest a cautious approach toward the Heath *et al.* results.

Heath *et al.* (1) observed a 26% decrease in egg mass from the first generation (0.27 g) to the fifth generation (0.20 g) of captive (Yellow Island Aquaculture Limited; YIAL) females. However, the YIAL population was founded in 1985 by Robertson Creek females that had a mean egg volume of 0.47 cm³ [figure 3B in (1)], convertible to a fresh egg mass of 0.40 g (2). This 48% larger egg mass of founders than first-generation females cannot be explained solely by differences in female age and size. Adjusting for female age and size using an allometric slope for Vancouver Island chinook salmon populations (3), a similarly sized female (4.9 kg) from Robertson Creek in 1985 had a fresh egg mass of 0.32 g, some 19% larger than for their first-generation offspring (YIAL 1988). Moreover, independent data for Robertson Creek females from 1984 to 1986 (4) indicate that the size-adjusted fresh egg mass for a 4.9-kg female was about 0.35 g [combining the multiple regression in table 4 in (4) and the fecundity regression in (5)]. Thus, within the first generation of captive rearing, egg mass declined 15 to 23% (0.32 to 0.35 g, to 0.27 g)—similar to the total change over the next four generations. Furthermore, the Robertson Creek population had already incurred three generations of environmental and genetic effects of “supplemental” breeding by 1985 (4). Thus, the “natural” egg size of YIAL females (0.32 to 0.35 g) was likely at least 19 to 30% greater than previously assumed (0.27 g). These data imply a decline in maternal fitness and decrease in egg survival due to captive rearing that could be considerably greater than the reported 6% and 24%, respectively. This bolsters the conclusion of Heath *et al.* that culturing of fish can rapidly

move them away from the optimum for nature.

The above reanalysis identifies strong environmental determination of egg size, which was not recognized by Heath *et al.* (1). Salmonid egg size is plastic and responsive to maternal growth conditions (6–10). For example, egg size in Atlantic salmon has been shown to decline 12% within a single generation of “supplemental” breeding due to accelerated growth prior to seaward migration (7). A similar response is seen in captive-reared (farm) populations (11). Moreover, although the reciprocal hybridization study indicates that the YIAL and Big Qualicum populations differ genetically in egg size, it does not differentiate between the effects of captive rearing and differences in origin prior to captive rearing, nor does it account for potential body size differences among groups. As such, the study does not discount an environmental basis to the changes.

Similarly, the temporal decline in egg size within “supplemented” populations [figure 3B in (1)] may be more environmentally than genetically driven. First, the decline in Robertson Creek is nonlinear, occurring mainly within a single generation—consistent with an environmental basis. Second, temporal increases in the proportional contribution of supplemented fish (having fast juvenile growth and hence smaller eggs) due to increases in stocking effort, decreases in wild returns, or both, could explain the patterns. Third, although fish size was unchanged temporally, freshwater growth, age at sexual maturity, or both may have changed.

Body size measurements within “supplemented” populations may also not be representative of the small subsample of females measured for egg size. Without fully accounting for the allometric increase in egg size with female body size (4, 12, 13), changes observed may simply reflect changes in the size of females subsampled. Furthermore, broad geographic comparisons of supplemented and unsupplemented populations of coho salmon show no evidence of a decline in egg size (12, 13).

An overlooked expectation of selection due to captive breeding would be a flattening of the allometric relation between egg and body size. In the wild, variation in female phenotype (e.g., body size) likely in-

fluences offspring environment (through egg/offspring density and nest location, for example) and hence causes variation in the optimal egg size within populations (14–16). In hatcheries, offspring environment is independent of female phenotype (i.e., all eggs rear commonly), and thus the optimal egg size should be similar for all females.

These new insights neither refute nor diminish the significance that captive rearing can have on critical life history traits, but rather bring into question the underlying mechanism or mechanisms. Phenotypic plasticity may play an equally or more important role than evolutionary change in limiting the success of conservation by captive breeding.

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