

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

Fleming *et al.* (1) contend that the decline in egg size observed in the YIAL (Yellow Island Aquaculture Limited) population (2) is an underestimate of the true decline due to a large phenotypic shift in egg size in response to the YIAL hatchery environment. They further suggest that the observed decline in egg size in the supplemented populations may be due to some mechanism other than evolution in the hatchery and subsequent introduction of hatchery-adapted fish to nature.

We agree that our estimate of the decline in egg size observed at YIAL is conservative because we did not estimate the size of eggs at founding (YIAL was founded with fish from an unknown number of females from Stamp Creek, a tributary of the Robertson Creek). Salmonid egg sizes are very responsive to maternal growth conditions, and the switch from nature to a hatchery is expected to produce a shift in egg size as fish acclimate to the hatchery (phenotypic plasticity; see references in (1)). The significance of this plasticity was not explored in the original study (2), but is clearly of relevance to biologists interested in evaluating the effect of captive rearing on the phenotype, and thus performance, of animals intended for eventual release. Although the plasticity of key life history traits such as egg size is interesting and relevant, it does not detract from our observation of a substantial and consistent decline of egg size following founding of the YIAL population [figure 3 in (2)]. Fleming *et al.* specifically question whether the decline in egg size observed at YIAL, and in the supplemented populations, was due to genetically or environmentally based (i.e., phenotypic plasticity) causes. It is unlikely that such an environmental effect could produce the long-term consistent decline in egg size observed at YIAL because the YIAL rearing environment remained relatively uniform during the study period (the hatchery is supplied with ground water and the seapen site is in a very well mixed location; neither changed significantly during the study). Non-genetic shifts in phenotypic traits associated with acclimation of salmon to the hatchery environment are often large in the first gen-

eration (3, 4), but are not expected to continue across multiple generations (5). The decline in egg size was consistent throughout the entire study period, and it has been documented that at least some of the decline is genetically based (2).

Although the decline in egg size observed at YIAL is inconsistent with a phenotypically plastic response to the hatchery environment, Fleming *et al.* (1) correctly note that the decline in egg size of supplemented Robertson Creek fish is nonlinear, with most of the change occurring in the first generation. This is consistent with a large environmental change between the 1979 and 1983 estimates. Likewise, the long-term consistent decline in egg size observed in the supplemented Quinsam River population was nonlinear, with a significant amount of the decline in egg size observed between the 1993 and 1997 samples. Both of these patterns can be explained as an environmentally based shift in egg size. However, the observed declines in egg size are substantial, and mean egg sizes of hatchery-supplemented populations remain below the mean egg sizes at the start of the sample period, which indicates that the putative environmental factor that drove this change in egg size has not been reversed.

We emphasize that none of these issues detract from our main point: Minimizing juvenile mortality in the captive rearing environment relaxes selection on traits required for juvenile survival, allowing the evolution of traits that maximize adult reproduction (e.g., fecundity) at the expense of traits that affect juvenile survival in nature (e.g., egg size). Thus, captive rearing of animals for supplementation of natural populations can have large effects on the fitness of natural populations. Our data clearly demonstrate that fecundity has increased and egg size has decreased in hatchery-reared YIAL salmon. Although our data are not conclusive concerning the effect of population supplementation on the size of eggs laid by wild fish, the observed patterns in nature are consistent with expectations based on results from the YIAL hatchery. This correlation raises significant concern that supplementation of nat-

ural populations can reduce the fitness of wild fish, contrary to the objectives of the supplementation program.

Our results (2) have prompted criticism from the press (6–8) of captive salmon breeding and supplementation programs. We emphasize that captive rearing programs, whether for salmon or other organisms, are an essential component of our conservation toolbox. The proper interpretation of our salmon results (2) is that modern captive rearing methodologies can have previously unrecognized consequences for the make-up of natural populations. We enthusiastically agree with Fleming *et al.* (1) in their call for additional attention to the synergistic effects of phenotypic plasticity and genetic change on captive-reared animals, with the goal of improving captive rearing strategies. As global biodiversity declines, captive rearing programs will become an increasingly important tool for maintenance and reestablishment of natural populations. It is thus essential that we identify and thoroughly investigate the genetic and ecological consequences of population supplementation and make use of all available theoretical and empirical advances to improve the design of captive rearing programs.

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