

**ARE THERE INHERENT BEHAVIOURAL DIFFERENCES  
BETWEEN WILD AND CULTURED JUVENILE SALMON?**

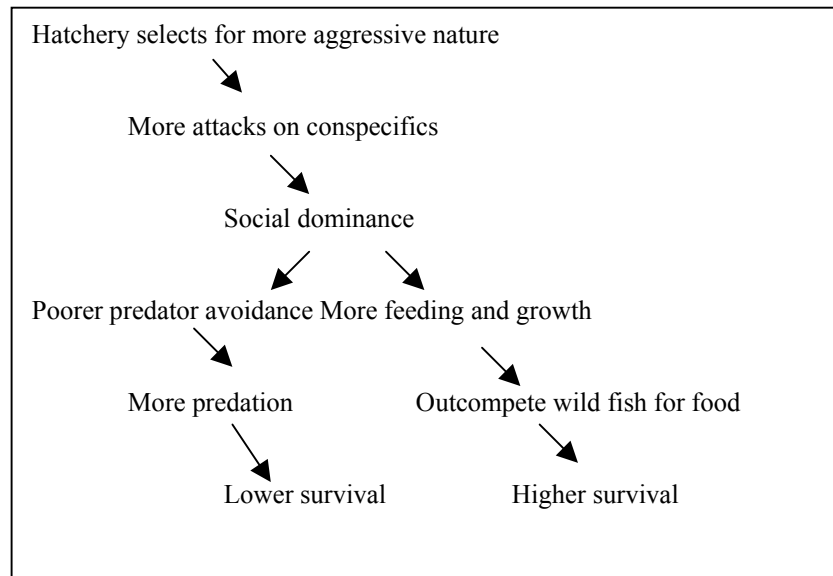
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**Introduction**

The culture of salmon and other fish under controlled conditions, followed by release or escape of juveniles into the wild has caused much discussion about the potential detrimental impact on existing wild salmon populations (Lichatowich 1999). If growing salmon in a controlled environment causes irreversible changes from the suite of characteristics that enable the fish to survive in natural streams, then stocking programs meant to increase fish abundance may cause 'collateral damage' by replacing well adapted 'wild' fish with maladapted 'hatchery fish. This may lead to an overall decrease in abundance. The basic premise of this line of thought is that culturing salmon in hatcheries for part of their lives makes them less capable of surviving in natural conditions, even during other parts of their lives. The concern is that this incapacity not only exists, but is wired into the salmon's genes and makes the hatchery fish unsuitable for mating with wild fish.

The proposed premise is illustrated in Figure 1 as a cascade of behaviours that leads to consequences in survival that are different for hatchery fish than for wild fish. Competition for food and status in a hatchery rearing pond leads to selection for more aggressive and dominance behaviour, which leads both to greater feeding and growth (leading to higher survival) and to greater risk of predation (lower survival). The degree of aggressiveness, dominance, feeding and predator response behaviours have been tested in the lab and in simulated natural conditions, with equivocal results, as discussed below.

Figure 1. Possible cascade of behaviours that might be expected if hatchery fish were inherently more aggressive than wild fish.



### Aggression

In 1969, Peter Moyle (Moyle 1969) noticed that wild-origin brown trout behaved differently in raceway ponds than fish that had been cultured for several generations. He suggested that these "domesticated" fry were more active than their "wild" cousins but no experiments were performed to test the difference. Subsequent workers also noted indications of increased aggression in hatchery salmon in comparisons with wild ones but could not separate out potential environmental influences from "innate" (genetically-driven) responses (Fenderson et al. 1968, Mesa 1991, Rhodes and Quinn 1998).

The first study of Pacific salmon that specifically tried to identify genetic effects used mirror image simulation (MIS) studies to measure aggressive tendencies (Swain and Riddell 1990). A fish is placed in an aquarium and exposed

periodically to its own image in a mirror, to which it reacts with behavioural displays. Many factors that might affect aggression -- individual differences in size, activity level, territoriality, density, competition, physical locations, value of the resource being competed for, perception of risk from predators -- are reduced in MIS tests. The results indicated that emergent fry from the two hatchery stocks tested were slightly more aggressive than those of the matched wild stocks. This paper caused some controversy as to the utility and relevance of using MIS studies to speculate on behaviour in natural conditions (Ruzzante 1991), but the original authors rebutted that their work had been taken out of context and that it was "only initial small steps in the empirical investigation of effects of domestication on agonistic behaviour of salmonid fishes," and that it was "not possible to rule out the possibility that our results are explained by interpopulational differences unrelated to domestication."

However, some later studies indicated the opposite of Swain and Riddell's findings, that newly emerged fry of wild stocks are more aggressive than "domesticated" ones (Berejikian et al. 1996), or that there was no difference in aggressiveness (Einum and Fleming 1997, Reinhardt 2001). The theory that a hatchery environment has a higher intensity of competition leading to selection for aggression can be countered by the theory that the abundance of food in the hatchery environment would decrease the payoff of aggressiveness leading to lowered aggression (Doyle and Talbot 1986). Also, selection for ever-escalating aggression in any environment would be maladaptive and not be an evolutionary stable strategy (ESS, (Krebs and Davies 2001)). These conflicting results do not lend much credence to the "domestication" concept.

Even so, for the ensuing 11 years, the paper by Swain and Riddell has been repeatedly quoted as proof positive of the increased aggressiveness of hatchery fish relative to their wild counterparts (Berejikian 1995, Busak and Currens 1995, Einum and Fleming 1997, Einum and Fleming 2001, Flagg and Nash 1999., Fleming et al. 1994, Johnsson et al. 1996, Johnsson et al. 2001, Mesa 1991, Petersson et al. 1996, Quinn and al. 1994, Reisenbichler 1997, Rhodes and Quinn 1998, Unwin and Glova 1997). There are many other reviews that have taken Swain and Riddell at their precautionary word, but the multiplier effect of the above list of papers is enormous. This citation of marginal results as solid proof is common to all of the studies discussed in this essay.

The next step in the model cascade is for the more aggressive hatchery fish to become dominant over wild conspecifics. This kind of experiment is very hard to control for extraneous influences like fish size, colour, shape, meristics (fin

length, body depth, eye size) that might just be stock characteristics but could have a strong influence on both initiating and responding behaviours (Fresh 1997, Pusey and Packer 1997). Evaluation of dominance can be quite subjective, involving assumptions about body posture and position, again in an extremely unnatural setting if carried out in an aquarium. The basic behavioural ecology principle that bigger fish become dominant has not been unseated by tests of hatchery versus wild salmon (Berejikian et al. 1996, Einum and Fleming 1997).

### **Feeding and Predation**

If increased aggression by hatchery fish has not been proven, one might think that the whole house of cards (Figure 1) would come crashing down, but there may be other reasons why wild and hatchery fish would have different success at feeding or susceptibility to predation. That is, the cascade of behaviours leading to differential survival might start further downstream than the diagram suggests.

Do several generations of eating pelleted feeds make fish incapable of knowing a good mayfly larva when they see one? Apparently not, since fish tend to sample and taste bite-sized things frequently and learn to determine what is edible and how to eat it (handling) very quickly (Mesa 1991, Reiriz et al. 1998). However, since feeding does not occur in isolation of other influences, the more interesting studies of feeding combine it with predation risk (see below).

Do generations of protection during freshwater rearing inure fish to disturbance and make them more susceptible to predation? The question here is twofold,

- 1) whether hatchery rearing can dull the wariness of fish to predators and
- 2) whether there is an innate difference in hatchery versus wild fish after identical early experience.

Fish learn from experience and certainly learn to surface-orient if that is where the food is and to ignore above-water disturbance if there is no apparent harm from it (Moyle 1969). These traits might be carried to the wild once hatchery fish are released, but hatchery fish are still capable of learning to change their behaviour in response to a new set of circumstances (Berejikian et al. 1996, Johnsson et al. 2001). Fish learn to recognize predators (but not necessarily a mock predator) and take appropriate action to avoid predation very quickly, whether they are from a hatchery or wild stock. Hatchery fish may not be able to swim away as quickly but this has not been studied, nor have post-release behaviours such as differences in schooling or migration patterns.

A gradient of measures of risky behaviour, going from the most indirect to the most direct would include:

- a) recording the behaviour of fish in the absence of a predator (tank position) and assuming that some positions are superior for predator avoidance;
- b) presenting a fake predator to the fish and assuming that certain kinds of subsequent behaviour would be better to avoid predation;
- c) noting the orientation of victims to a real predator and making assumptions as to suitability for predator avoidance;
- d) counting the number of approaches or attacks by a predator towards potential victims, and the responses to avoid getting caught;
- e) counting the number missing (successful attacks) after exposure to a real, effective predator.

Any of the above protocols can be combined with feeding of live or artificial feeds to up the ante in terms of payoff for bold behaviour. Tests can also be conducted in a variety of environments ranging from bland-featured aquaria to richly varied natural streams to see if the laboratory results are matched by field results.

The first artificial protocols require some faith in assumptions that may not have been tested. Even if the predator is real, judgements made about what locations or strategies are most suitable to avoid predation may not be correct. In a study where young salmon were kept from a big trout predator by a mesh net that only they could pass through, the 'hatchery fish' were more frequently observed on the 'risky' side of the barrier, although 3/4 of the fish actually killed by the predator were 'wild' (Johnsson and Abrahams 1991). The conclusion was that the hatchery fish were "more willing to risk exposure to a predator than a wild strain of trout" which is true, and that this "is likely to reduce the survival of the "hatchery" fish in natural habitats", which is pure, unfounded conjecture.

In the best study of an actual predator (as opposed to a cardboard cut-out) preying on hatchery-versus-wild salmon, the predation rate was low, averaging less than one fish caught in 18 hours in a confined space by a sculpin presented with six 3-week-old victims, and less than 10 fish caught in 3 days by 5 sculpins presented with a smorgasbord of 26 4-week-old salmon (Berejikian 1995). The differences between hatchery and wild fish predation rates was not significant. In other tests, prior experience with the predator made the salmon very cautious in its presence.

### **All Together Now**

When all of the factors are put together -- aggression, feeding and predator avoidance -- in a natural stream setting and tested for outcomes, survival studies should be able to prove or disprove the validity of the separate studies on each factor. In the final analysis, it is actual survival in a field situation that counts, not speculation as to which behavioural traits might lead to higher or lower survival. The few studies that have tested for differential survival have failed to detect a difference between hatchery and wild fish (Einum and Fleming 1997, Johnsson and Bjornsson 2001), even when the hatchery fish were domesticated farmed Atlantic salmon that had been bred in captivity for seven generations. If these fish have not become incapable of surviving on an equal footing with wild fish, then it cannot be expected that the ranched salmon of the Pacific would have lost their natural rearing ability.

### **Conclusions**

The small number of actual published studies of salmon juvenile behaviour (as opposed to reviews that cite them) does not really provide enough evidence to make a judgement one way or another as to the effect of hatchery rearing on the behaviour of subsequent generations. Contrary to the claim by some reviewers, there is not enough evidence to say that hatcheries cause a long term behavioural change in salmon stocks.

What would be required to prove conclusively whether there is genetic change from hatchery rearing? The papers discussed in this essay have made a valiant effort to detect differences, but several factors may make the task near impossible.

One consideration is that the simple act of culturing an organism under controlled conditions does not necessarily lead to domestication. Witness that only a handful of large mammals have been domesticated by humans despite thousands of years of concerted efforts to domesticate other species (Diamond 1997). If we consider domestication to be the dependence of an animal on man-made conditions for survival, rather than the flexibility of the animal to tolerate man-made conditions, then domestication is an extremely rare, and perhaps non-existent, phenomenon.

Another consideration is that observed behavioural differences do not necessarily represent different genotypes:

"A special caution is necessary when behavioral studies are undertaken.... Behavior can change as a result of experience, ontogeny, or the particular circumstances in which the animal finds itself. Some of these changes may be permanent; others may be reversible."(Noakes and Baylis 1990)

A built-in plasticity of behavioural responses is required in all species to meet changing environmental conditions. In addition to great plasticity in individual response, there can be changes in innate behaviour patterns (evolution) without requiring irreversible genetic change. It has been suggested that genetic change leading to a difference of one standard deviation in a characteristic takes at least 25 generations (Kingsolver and al. 2001), which is longer than any salmon species has been cultured to date.

Conflicting results as to whether 'hatchery' fish are more aggressive or less aggressive, plus the large intra-group variation and small inter-group differences indicate that there is no basic phenomenon at work leading to irreversible change in the behaviour of hatchery-origin fish compared to their wild counterparts.

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