



HATCHERY SMOLT QUALITY AND ACHIEVING THE WILD SALMON TEMPLATE

Smoltification

Anadromous salmonids undertake a metamorphosis, the parr-smolt transformation, as they prepare for migration to the sea. Photoperiod-induced changes in physiology, body shape, and behavior transform the cryptic, bottom-oriented resident form, or parr, to the migratory, schooling form. This metamorphosis is termed smoltification and the resulting migrant is termed a smolt. The process of smoltification is a major life history event, with fundamental changes in body form and function likened to the metamorphosis of a frog to a prince (Grimm's Fairy Tales).

Timing and duration of the metamorphosis and downstream migration to the sea is determined by a species-specific, genetically-determined life history pattern and environmental events governing growth rate and size. For example, chum and pink salmon smoltify almost immediately upon absorption of their yolk sacs and swim up in the late winter or early spring. Chinook, coho, sockeye, and steelhead normally smolt as yearlings or two year-olds during the period of increasing day length in late spring. Depending on life history type (stream or ocean form), or the size attained in their first year of life, some Chinook may smoltify as yearlings or sub-yearlings. In some instances, Chinook salmon may exhibit smolt-like characteristics during declining photoperiod in the fall of the year, and migrate seaward to the estuary.

Smolted salmonids exhibit rapid downstream migration, increased hypo-osmoregulatory capability (enhanced seawater tolerance), sustained growth in the ocean and high survival to adulthood. The linkage between smoltification, growth rate, and seawater tolerance and migration rate has been reported frequently in the literature (Wagner et al. 1969; Varnavsky et al. 1992). These processes are under hormonal control and mediated primarily by photoperiod. The same hormones controlling growth rate (growth hormone, insulin-like growth factor-I) also stimulate the development of seawater tolerance in salmonids (Sakamoto and Hirano 1993). It is also recognized that survival is not the only valuable quality measure of released hatchery fish, especially in integrated conservation programs,⁵⁷ where fish are released to intermingle with their wild counterparts.

Defining Quality Hatchery Smolts

During the course of its regional reviews of hatchery programs, the HSRG has noted that the *quality* of hatchery-origin fish was almost always described in terms of size, numbers, or condition index of fish produced, and whether they meet a pre-determined time window for release. Fish *size at release* almost invariably seems to be used as a surrogate for fish *quality*. In some cases, the health of released fish is discussed as a measure of quality at the time of release from the hatchery,

⁵⁷ See *Emerging Issues paper on Integrated vs. Segregated programs*.



but rarely is fish quality adequately described, or monitored, prior to or following release. Most hatchery personnel have difficulty defining smolt or fingerling quality beyond obvious behavioral and silver coloration changes, yet the scientific literature is rich in descriptions of physiological, morphological, and behavioral definitions of a quality smolt. This deficiency may stem from past hatchery practices and the focus and direction of past research.

It is interesting to note that following the advent of the coded wire tag, most hatchery improvement studies were aimed at manipulating the size and time of release of smolts to maximize survival. Additionally, some researchers concentrated on the role of nutrition (proximate composition, constituent quality, etc.) in optimizing adult survival. But in most cases, optimization has meant manipulating fish size and timing of release. In contrast to the 1970s and 1980s, the hatchery operator now has many additional tools with which to measure and manipulate the quality of smolts during the culture phase.

The *quality of a smolt* is embodied in the rate and completeness of the parr-smolt transformation. In the hatchery, the timing, magnitude, and duration of the metamorphosis are a surrogate for smolt quality and can be quantified using *physiological, morphological, and behavioral* measures. Therefore, it is strongly recommended that the definition of smolt quality be expanded to include additional physiological, morphological, and behavioral measurements taken throughout the culture cycle. Examples include some specific physiological measures of smoltification status linked to improved survival such as gill Na-K ATPase enzyme activity, blood concentrations of thyroid hormones, growth hormone, insulin, insulin-like growth factor, and body lipid levels, among others. A simple measure of physiological smolt development easily measured at the hatchery is the rate of change in growth rate, immediately preceding and during the parr-smolt transformation (Beckman et al., 1996). The definition of a quality hatchery smolt is therefore equal to the definition of a quality natural smolt. Smolt quality is defined as a metamorphosed, anadromous salmonid that exhibits rapid downstream migration, increased hypo-osmoregulatory capability (enhanced seawater tolerance), sustained growth in the ocean, and high survival to adulthood. Smolt quality is measured along a continuum of physiological, morphological, and behavioral changes that occur during the metamorphosis from fingerling to migrant.

Wild Salmon Template

In the years following ESA listings, researchers and managers have recognized the need to conserve and recover depleted natural stocks and have used hatcheries as one potential tool. Research emphasis is now concentrated on the physiological, morphological and behavioral traits of hatchery fish that may impart benefits when released. In these programs, the wild fish may provide the best template for duplicating a quality hatchery smolt. For example, mimicking the growth pattern, size, and out-migration timing of natural fish has been shown to produce higher quality hatchery smolts with greater smolt-to-adult survival. An added advantage would be an equivalent hatchery contribution to adult harvest with fewer smolts released. Producing, high quality smolts that migrate downstream rapidly reduces opportunity for hatchery-wild fish interactions and minimizes negative ecological impacts of hatchery fish on wild fish. Rapidly migrating smolts will be less likely to residualize and imprint on inappropriate stream sites, and therefore be less likely to stray during their homing migration.



If one were to use wild salmon as a template, for juvenile hatchery fish, what morphological, behavioral, physiological, and genetic fitness traits would characterize locally adapted stocks? The following dialogue gives examples of physiological, morphological and behavioral templates characteristic of wild fish:

Physiology

Conditions in the hatchery environment affect physiological fitness. Water quality affects the duration and rate of smolt development and other physiological processes in the hatchery environment. Primary amongst these are temperature and photoperiod. Physical and chemical characteristics such as suspended solids; dissolved gases, pH, and mineral content may also control physiological processes such as fish health (immune resistance) and osmoregulation.

Energy reserves and growth rate affect physiological fitness. Growth, survival and the physiological processes of smoltification and maturation in salmonids are controlled in part by the availability and quality of forage organisms. During periods of declining day length, circulating levels of the metabolic hormones IGF-1 and growth hormone are low and protein synthesis rates in the body are reduced. Fish convert both dietary protein and lipid into stored body fat during these periods. In contrast, when day lengths increase, as during the period of spring smolting, body metabolism patterns change, with increases in protein synthesis rates and lipolysis, resulting in lower percentage whole body fat levels. In late autumn and early winter wild fish reduce growth rate, feeding activity, and metabolism and lose substantial amounts of body fat over the winter (Beckman et al. 1998). In late winter and early spring, wild yearlings dramatically increase feeding, accumulate body fat, resume growth and exhibit a dynamic pattern of physiological development (Dickhoff et al. 1997). In contrast, hatchery salmonids are fed diets high in lipids at feeding levels that encourage sustained rapid growth, even during cold winter periods when growth of natural fish is zero. In natural salmonids there is a positive relation between growth rate during the two months immediately preceding out migration and survival to adulthood (Dickhoff et al. 1995). Furthermore, increased spring growth of spring Chinook salmon improves their downstream movement.

In general, wild smolts differ from hatchery smolts in four ways; wild fish are generally smaller than hatchery fish; show more rapid growth rate during the smolting period; have less body fat than hatchery smolts; and show a more dynamic change in physiological and metabolic status from over-wintering to the spring smolting period.

Morphology

Conditions in the hatchery environment should promote morphological fitness by emulating natural fish body size, body shape, and coloration. For example, body size affects foraging effectiveness, vulnerability to predators, fecundity and reproductive success.

The size of a juvenile salmonid affects its ability to compete with its peers, escape predators, adapt to seawater, migrate rapidly, mature early, and most importantly, survive and recruit into the fishery or spawning population (Bilton et al. 1982, Martin and Wertheimer 1989). Natural



populations generally contain fish within a size range governed by hatch time, available food resources, and environmental conditions.

Releasing young, high-quality smolts within a size range similar to the natural population from which they are derived, as opposed to releasing larger smolts, will reduce competition with wild smolts and minimize selection pressures that occur when there is clear disparity in size.

Cryptic coloration. In nature, salmonid eggs incubate, and alevins develop, in the darkened, matrix-rich environment of the gravel substrate of the redd. Following hatch, juveniles rear in a complex lighted environment of shade, sunlight filtering through riparian vegetation, and light-absorbing dark gravel substrate. This environment produces cryptic coloration and body camouflage patterns most likely to reduce vulnerability to predators. At smoltification, guanine is deposited in the epidermal tissues, and the fish becomes silvery in appearance as it undertakes its downstream migration. Hatcheries can simulate these conditions through the use of enriched environments.

The body shape of a wild salmonid changes with the season of the year and the availability of nutritional resources. During winter, a period of low feed availability or even starvation, body weight and condition (relationship between body length and weight) drops, resulting in a slimmer fish with lower body fat. In spring, prior to smoltification, resident non-migratory juveniles feed heavily and regain body fat and condition. During the parr-to-smolt transformation, and as the period of downstream migration nears, the condition index changes again and a slimmer, more streamlined, silvery smolt is produced.

Overall, fecundity is generally lower in hatchery fish, owing to juvenile rearing protocols and smaller age at maturity. In some species, the release of large hatchery fish results in a larger percentage of precocious males in the population, early return of females to the hatchery, and smaller age and lowered fecundity at return.

Behavior

Conditions at the hatchery should promote the competency of juvenile fish to migrate, establish territory, and displace other individuals, prey and forage.

Social behavior Juvenile salmonids have been shown to reduce their territory size as fish density increases. Territory size may limit the maximum density of juvenile salmonids in streams (McNicol and Noakes 1984). Density is an important factor in adult survival, with high-density culture causing a breakdown in social hierarchies in cultured salmonids.

Migration/homing/straying Before out-migration, juvenile salmon learn odors associated with their natal streams, which guide their homing migrations as adults. Imprinting in salmon may occur at multiple life history stages. To maximize imprinting opportunity, juvenile salmon must experience the odors of their natal system at various times and physiological states when the odors can be learned. It is well-known that olfactory imprinting occurs during sensitive periods associated with surges in plasma thyroxin levels during parr-smolt transformation (Dittman et al 1995). This may indicate the occurrence of multiple pre-smolt imprinting periods.



Predation avoidance behavior Natural salmon juveniles experience and observe predation of their cohorts by birds, fish and a variety of mammals. Observed predation, or attempted predation on themselves and other salmonids, results in expression of an innate predator-avoidance response that protects natural salmon juveniles. Because they are protected in the hatchery environment, hatchery salmon are lacking this naturally learned predator-avoidance response.

Foraging ability From the time of first feeding to returning as adults, natural salmon learn to feed on a variety of swimming, moving, prey organisms. The recognition of a specific type of prey movement is probably recognizable to naturally rearing salmon juveniles. By comparison, hatchery salmon are fed a regimen of prepared feeds that are generally uniform in size, color and movement. Hatchery fish have been shown to be less successful in stalking and capturing natural prey organisms.

Genetics

Genetic changes from artificial propagation can affect both the productivity and viability of wild populations (Reisenbichler and Rubin 1999). To produce a quality smolt for use in conservation and recovery of wild populations, hatchery practices should minimize both random and directional selective changes that contribute to domestication and loss of local adaptation. Domestication is the process of a population changing over time in response to an artificial or human-controlled environment and is manifested in directly-measurable genetic characteristics (e.g. allele frequencies) as well as in physiological, morphological, and behavioral traits discussed above. Principal factors that lead to domestication include relaxation of natural selection that would naturally occur in the wild, natural selection to the hatchery environment, and direct human-controlled selective breeding.

Maintenance and Selection of Broodstock

The goal of developing a wild-template smolt is to minimize the changes that contribute to domestication. The level of domestication selection is affected by both hatchery practices and the amount of exchange between hatchery and wild populations. Hatchery practices that minimize changes in physiological, morphological and behavioral traits, as well as such traits as time, age and size of return will decrease the risk of domestication, as many of these traits have inheritable components.

Broodstocks should be selected from locally-adapted populations. Introduction of spawners from exogenous populations should be avoided, to minimize risks of outbreeding depression. The periodic infusion of adults of natural-origin spawners retards the rate and level of domestication, but may not completely eliminate its effects (Ford, in press).

Effective population size

Hatchery practices should be designed to maximize effective population size to maintain genetic diversity and reduce potential detrimental effects of inbreeding. Small effective population sizes can increase the likelihood of deleterious effects by random drift, even in the absence of an altered selective environment. Effective population size is defined in terms of numbers of reproducing adults (breeders) per year and the generation time of the population. Techniques that ensure every



adult has an equal probability of producing progeny maximize effective population size. These techniques include equal sex ratio, equal family size, and mating protocols that equalize contributions among individuals.

The effective population size of the hatchery program can also directly affect the health and viability of the wild population. A reduction in diversity and in the effective size of the wild population can result from “genetic swamping,” where a large number of hatchery fish from relatively few parents interbreed with wild fish. This is particularly likely if the effective population size of the hatchery population is substantially less than that of the wild population, (Ryman and Laikre 1991).

Achieving the Wild Fish Template in the Hatchery

How would a hatchery manager rear fish to approximate the wild fish template? The following section describes hatchery methods that can be employed to mimic the wild fish template in hatchery fish:

Physiology

Swimming efficiency (stamina, stride efficiency)

Solution: exercise, growth modulation.

Smolt development (silvering-guanine deposition, hormonal and enzyme cycles, hyp-osmoregulatory ability)

Solution: growth modulation, dietary salt, photoperiod control, rearing density.

Energy stores (whole body proximates, liver glycogen, hepatosomatic index)

Solution: feed amount, growth modulation. Simulate proximate composition by controlling diet composition.

Morphology

Growth pattern (seasonal change in length, weight, and condition factor).

Solution: growth modulation. Simulate growth rate and body size by controlling water temperature and feeding rates. Slow growth during winter followed by rapid growth during spring ensures better quality smolts.

Length frequency distribution (mean length/weight, variance, skewness)



Solution: feed amounts and frequency of feeding, staggered egg take, thermal control of incubation, rearing density, feed schedule. Fish are grown using methods of feed ration and/or water temperature manipulations to match growth cycles of hatchery fish to growth patterns of wild fish. Growth of hatchery fish will be reduced in the winter and accelerated in the spring.

Smolt development (condition factor, coloration, body shape, fin quality, dentition, cloacal folds)

Solution: dietary salt, growth modulation, rearing density, environmental enrichment.

Out-migration timing

Solution: volitional, forced, staggered release.

Behavior

Competition for feed.

Solution: environmental enrichment, forage training on live foods, rearing density.

Competition for space (territoriality)

Solution: environmental enrichment, reduced rearing density.

Migratory behavior (schooling, downstream orientation, restlessness, migration)

Solution: growth modulation, exercise?

Predator avoidance

Solution: exercise, predator conditioning, avoid human feeder imprinting.

Genetics

Minimize Domestication Selection (selection in the hatchery environment)

Solution: select locally adapted broodstock, periodically infuse wild spawners.

Run timing

Solution: monitor run timing, adjust egg take to emulate wild timing, modulate developmental rates to emulate wild timing, cull as needed.

Age at maturity (age structure, precocity)



Solution: utilize cohorts in proportion to wild run.

Size at maturity (average size at age)

Solution: monitor size at age changes within hatchery relative to wild populations; minimize directional changes in hatchery by equalizing contributions of individuals irrespective of size within age cohort within the bounds of the wild template.

Maximize effective population size (inbreeding and variance effective population size)

Solution: equalize sex ratio, follow fertilization protocols that equalize contributions among individuals (e.g. factorial matings, pairwise matings), equalize family size, cull as needed.

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