Applied population biology: pacific Salmon

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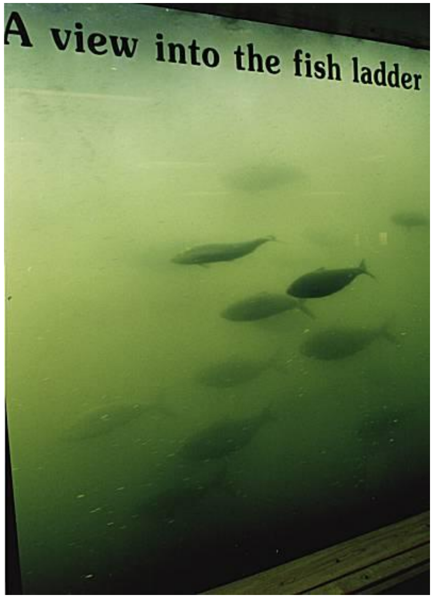
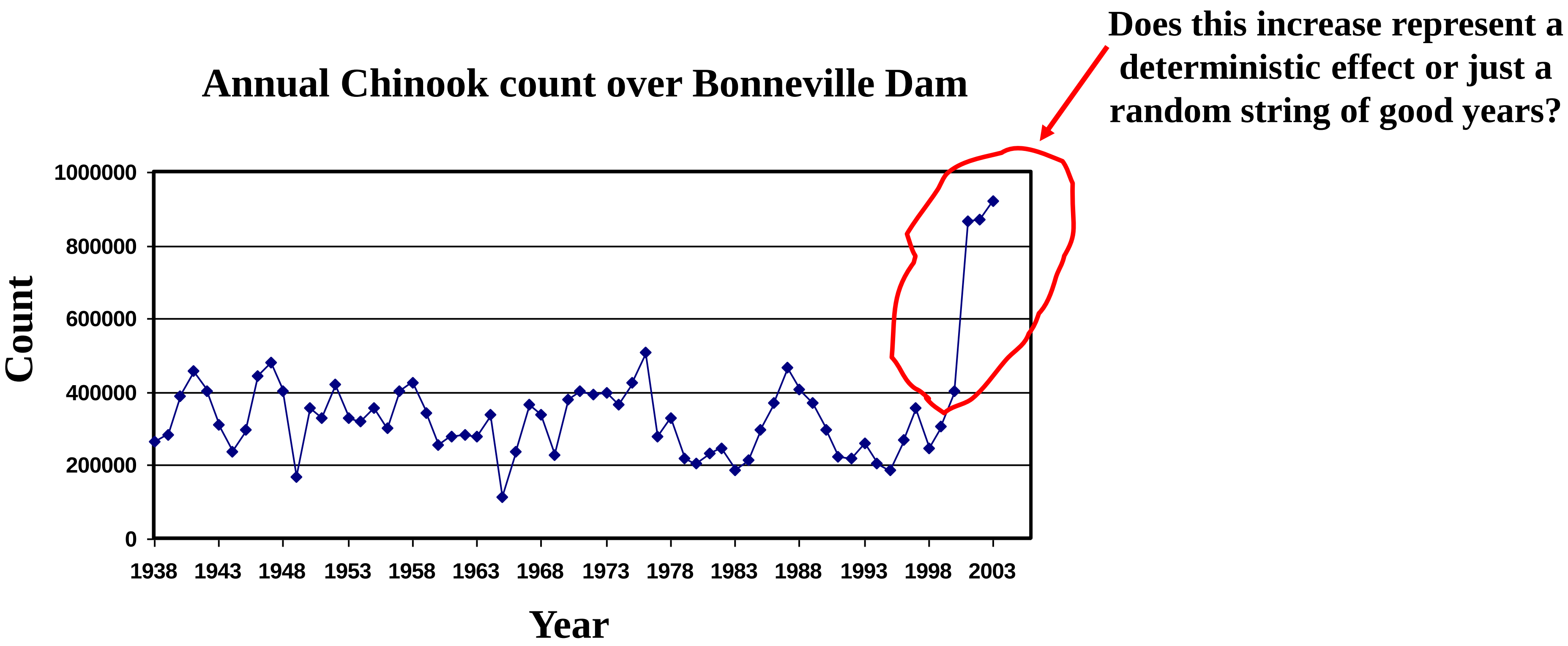


Topics relevant to salmon conservation

- Environmental stochasticity
- Selection vs. Drift
- Maladaptation
- Competition
- Gene flow and local maladaptation
- Hybridization

Environmental stochasticity

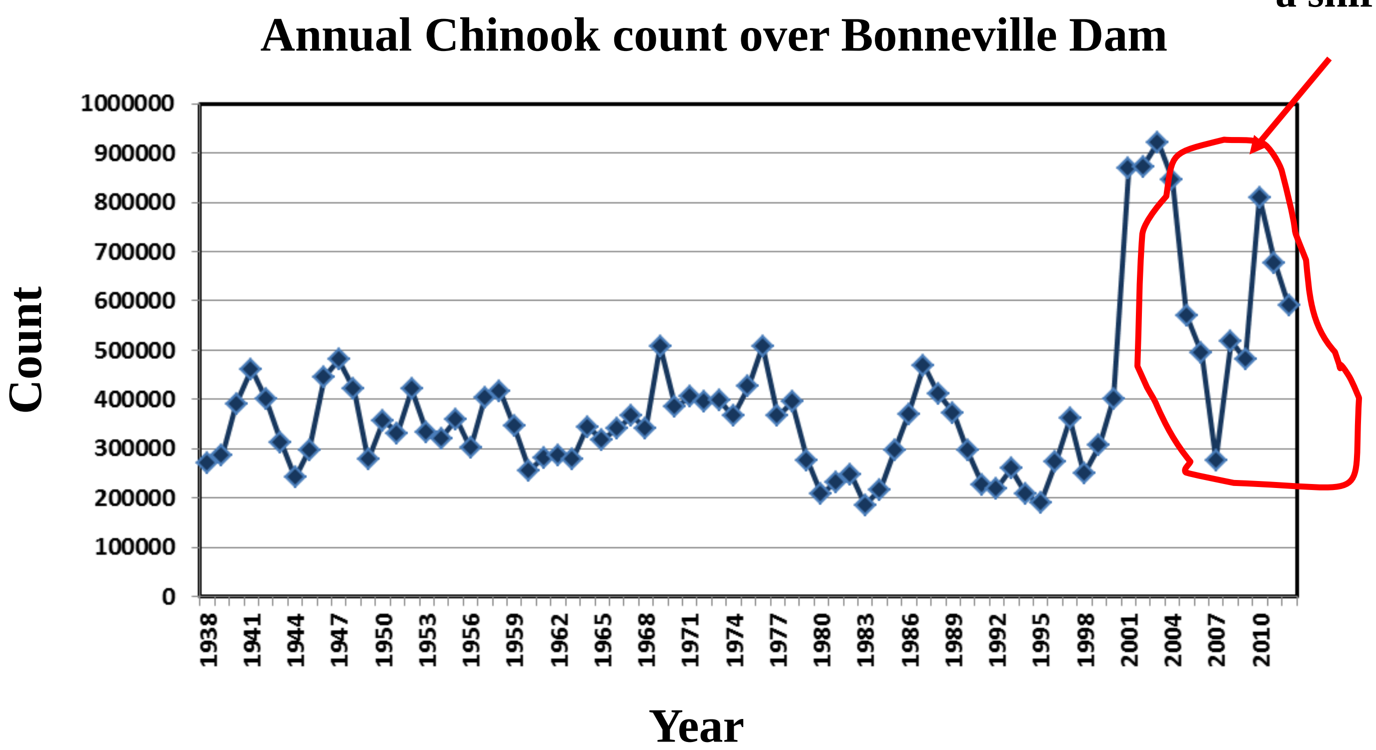


"We know that favorable ocean conditions have substantially boosted these adult returns… But, we also believe that the money and effort the region has invested in salmon recovery have appreciably contributed to these numbers."

Witt Anderson, chief of the Army Corps of Engineers fish management office. October 14, 2003

Environmental stochasticity

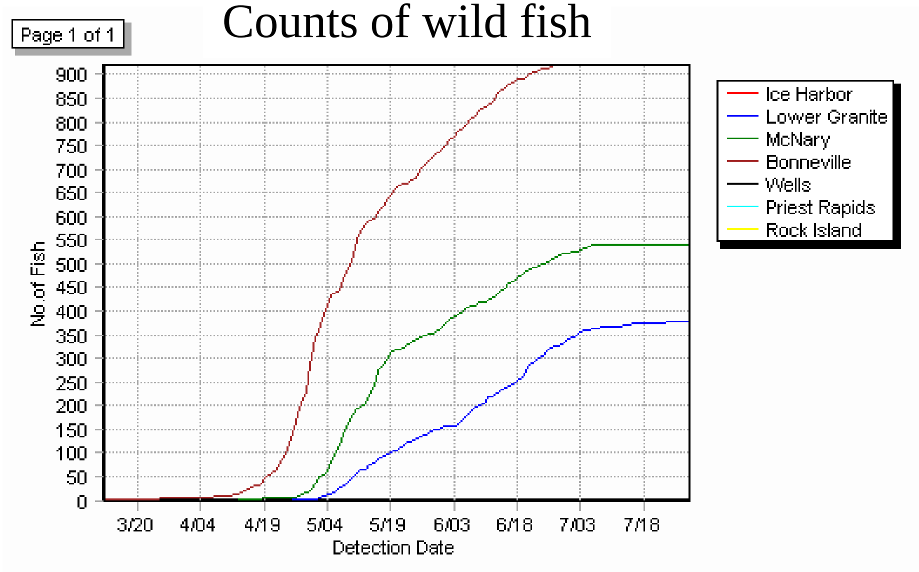
Recent data does not support a shift in $\bar{r}$, just stochasticity in r



Data supports the view that the population size of Pacific Salmon fluctuates substantially. Over the long run:

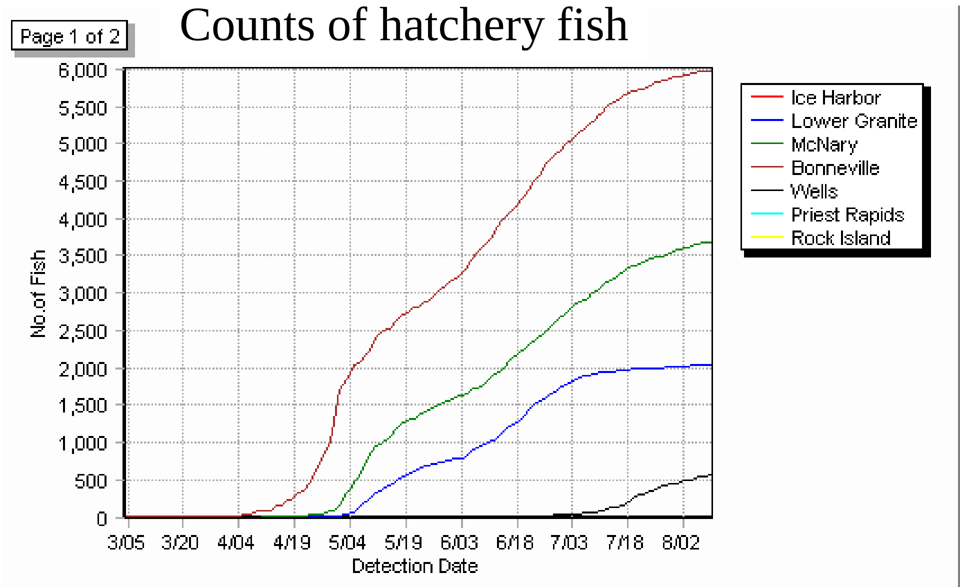
$$\bar{r} < 0$$

How many of these fish are wild?



Counts of wild fish

The vast majority of returning salmon are from hatcheries



Counts of hatchery fish

Hatchery vs. Wild fish and the ESA

1993: NMFS Hatchery Listing Policy recognizes that hatchery and wild fish can be one ESU but allows listing decisions based upon only wild counts. Results in Oregon coast Coho salmon being listed as endangered under the ESA.

2001: U.S. District Court Judge Michael Hogan revokes the endangered species designation of Oregon coast Coho salmon arguing that hatchery fish should be included in population size estimates

2005: In response to Hogan's ruling, NMFS issues a new hatchery listing policy eliminating the distinction between hatchery and wild fish when listing ESU's and re-evaluates all listing decisions. ***New policy continues to weight biological contributions of wild and hatchery fish differently when making listing decisions.*** 16 West Coast salmon stocks, and Upper Columbia steelhead are listed under the Endangered Species Act.

NMFS new listing policy is challenged by conservation and fishing groups (favor using only wild fish) and Building and Farm groups (favor using all fish).

2009: 9'th circuit court rules in favor of NMFS, finding that NMFS listing decisions were based on the best available science and were not "arbitrary and capricious".

POLICY FORUM

ECOLOGY

Hatcheries and Endangered Salmon

Ransom A. Myers,[1] Simon A. Levin,[2] Russell Lande,[3] Frances C. James,[4] William W. Murdoch,[5] Robert T. Paine[6]

The role of hatcheries in restoring threatened and endangered populations of salmon to sustainable levels is one of the most controversial issues in applied ecology (*1*). The central issue has been whether such hatcheries can work, or whether, instead, they may actually harm wild populations (*2*, *3*). A new and overriding issue, however, has arisen because of a recent judicial decision.

On 10 September 2001, U.S. District Court Judge Michael Hogan revoked the listing, by the National Marine Fisheries Service (NMFS), of all Oregon coast coho salmon under the Endangered Species Act (*4*). He ruled that, if hatchery fish were included in the same distinct population segment as the wild fish with which they are genetically associated, then they must be listed together. This approach could have devastating consequences: Wild salmon could decline or go extinct while only hatchery fish persist. Petitions are now pending to delist 15 other evolutionarily significant units (ESUs) (*5*).

An ESU is defined as a genetically distinct segment of a species, with an evolutionary history and future largely separate from other ESUs (*6*). For taxonomic purposes, one could use genetic similarity to classify hatchery fish as part of the ESU from which they were derived. However, for assessing ESU extinction risk and/or potential listing under the Endangered Species Act, including hatchery fish in an ESU confounds risk of extinction in the wild with ease of captive propagation and ignores important biological differences between wild and hatchery fish.

We define "hatchery fish" as fish fertilized and/or grown artificially in a production or conservation hatchery. Inevitably, hatchery brood stock show domestication effects, genetic adaptations to hatchery environments that are generally maladaptive in the wild. Hatchery fish usually have poor survival in the wild and altered morphology, migration, and feeding behavior (*7*). On release, hatchery fish, which are typically larger, compete with wild fish (*1*). Their high local abundance may mask habitat degradation, enhance predator populations, and allow fishery exploitation to increase, with concomitant mortality of wild fish (*1*, *8*). The absence of imprinting to the natal stream leads to greater straying rates, and that spreads genes not adapted locally (*1*). Also, hybrids have poor viability, which may take two generations to be detected (*9*).

Interagency draft criteria (*10*) describe hatchery fish most appropriate for inclusion in an ESU as those founded within two generations or those that had regular infusions of fish from the wild population. However, fish grown in hatcheries for even two generations may not assist population recovery; their rate of survival in the wild is much lower than that of wild fish (*11*). Regularly infusing hatchery stocks with natural fish may also be a drain on the natural system. Hence, even these hatchery fish should not be included in an ESU, even if they are indistinguishable at the quasi-neutral molecular genetic loci typically used to identify an ESU.

Much evidence exists that hatcheries cannot maintain wild salmon populations indefinitely (*7*). In the inner Bay of Fundy in Eastern Canada, hatchery supplementation of Atlantic salmon occurred for more than a century (*12*). Despite the longevity of this program, it failed to maintain viable natural populations. Hatcheries effectively disguised long-term problems, which probably contributed to the near extirpation of native Atlantic salmon. Moreover, as recommended by the World Conservation Union (IUCN), long-term reliance on artificial propagation is imprudent, because of the impossibility of its maintenance in perpetuity (*13*).

Although their effectiveness has not been shown (*14*), conservation hatcheries may play a role in future salmon recovery. However, to avoid the dysgenic effects of domestication, even conservation hatcheries should be strictly temporary and should not prevent protection of wild populations under the Endangered Species Act.

To address one of the subsidiary lawsuits, NMFS has pledged to complete a review of eight ESUs by 31 March 2004. NMFS should continue to pursue its current recovery goal of establishing self-sustaining, naturally spawning populations. The danger of including hatchery fish as part of any ESU is that it opens the legal door to the possibility of maintaining a stock solely through hatcheries. However, hatcheries generally reduce current fitness and inhibit future adaptation of natural populations. Hence, the legal definition of an ESU must be unambiguous and must reinforce what is known biologically. Hatchery fish should not be included as part of an ESU.

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References and Notes

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13. IUCN, 2002, www.iucn.org/themes/ssc/pubs/policy/exsituen.htm.
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Should hatchery produced fish be counted?

What are the scientific issues?

- Defining ESU's
- Competition
- Local maladaptation
- Hybridization

A brief history of hatcheries

• **Hatcheries were built to compensate for fish lost to dam building activities in the Columbia River drainage**

How do hatcheries work?

• Salmon return to the hatchery each year

Adult salmon are caught in traps along rivers and streams, and are spawned at hatcheries around Idaho. The chinook shown here are moving up a fish ladder from the trap to a holding pond.

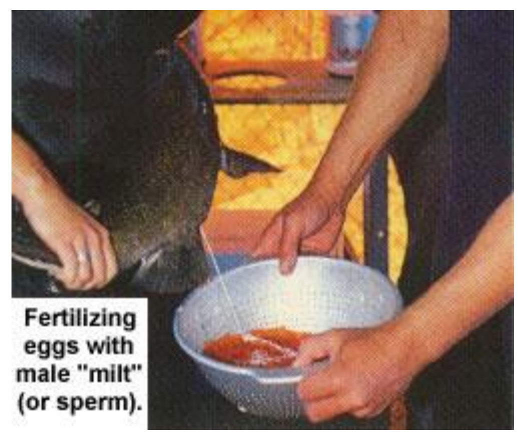
• All fish are captured in the hatcheries fish traps

Fish are sorted

• Most wild fish are allowed to continue up stream

• Hatchery fish are retained and used for sperm and eggs. In some systems genetic material from wild fish is also used to reduce inbreeding

Harvesting eggs from a mature female salmon.



Fertilizing eggs with male "milt" (or sperm).

Fertilized eggs are incubated

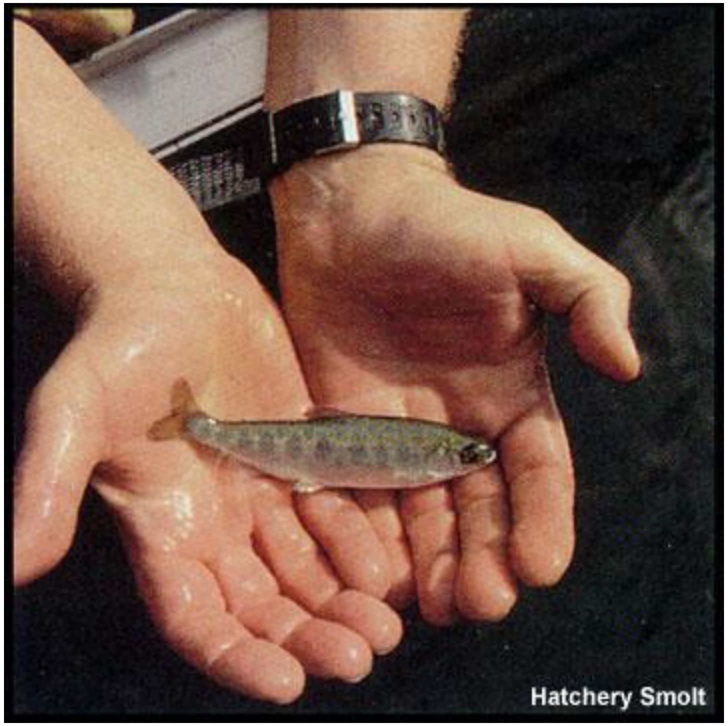
After milt is added to a batch of eggs, the mixture is held under water for a short time to help ensure even fertilization.

Juvenile fish are then placed in rearing ponds

Young chinook salmon
Photo courtesy of S. P. Cramer & Associates, Inc.

• During this time adipose fins are clipped to identify hatchery fish

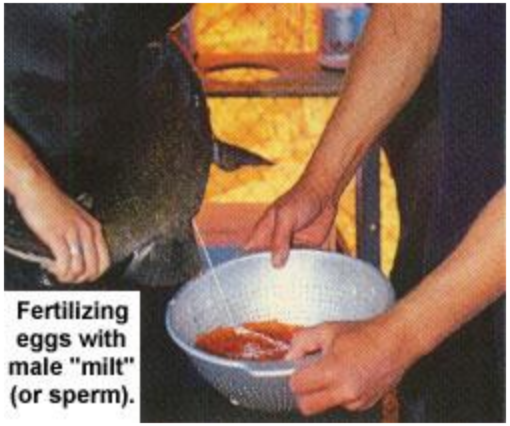
Fish are released upon smoltification



Smoltification – Suite of physiological, morphological, biochemical and behavioural changes, including development of the silvery color of adults and a tolerance for seawater, that take place in salmonid parr as they prepare to migrate downstream and enter the sea

Salient points regarding hatchery practice

• In theory, hatchery salmon are prevented from mating with wild salmon (In some systems one way gene flow from wild → hatchery is encouraged)



Fertilizing eggs with male "milt" (or sperm).

• Hatchery environment is extremely different from the natural environment

Policy Forum

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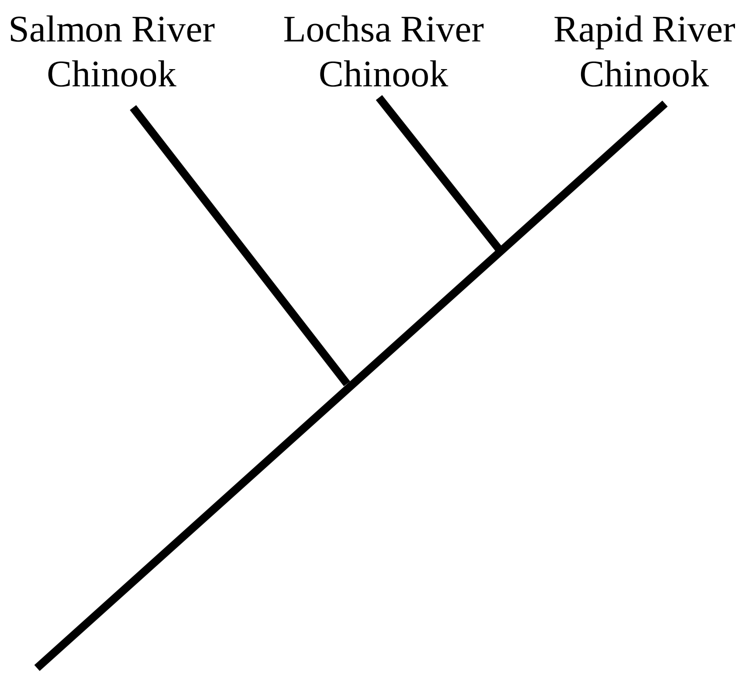
Important issues raised:

- Defining ESU's
- Competition
- Local maladaptation
- Hybridization

ESU's and the ESA

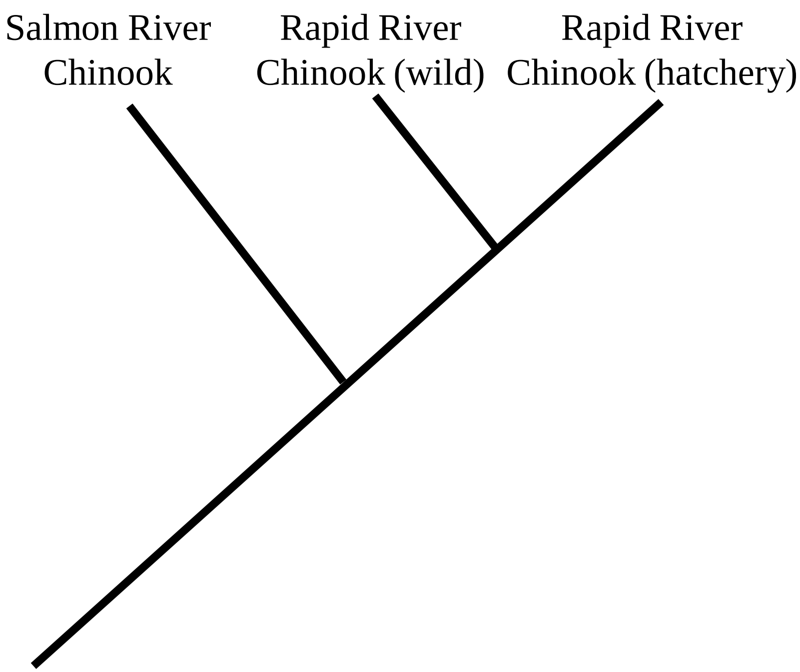
Evolutionary significant unit (ESU) – A genetically distinct segment of a species, with an evolutionary history and future largely separate from other ESU's



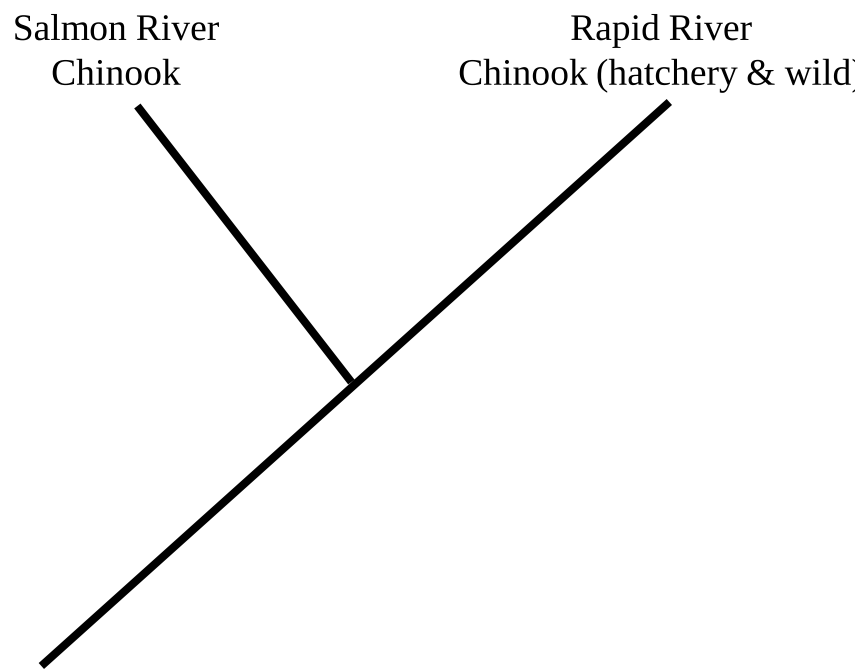
ESU's are protected under the endangered species act

Issue 1: Are wild salmon ESU's?

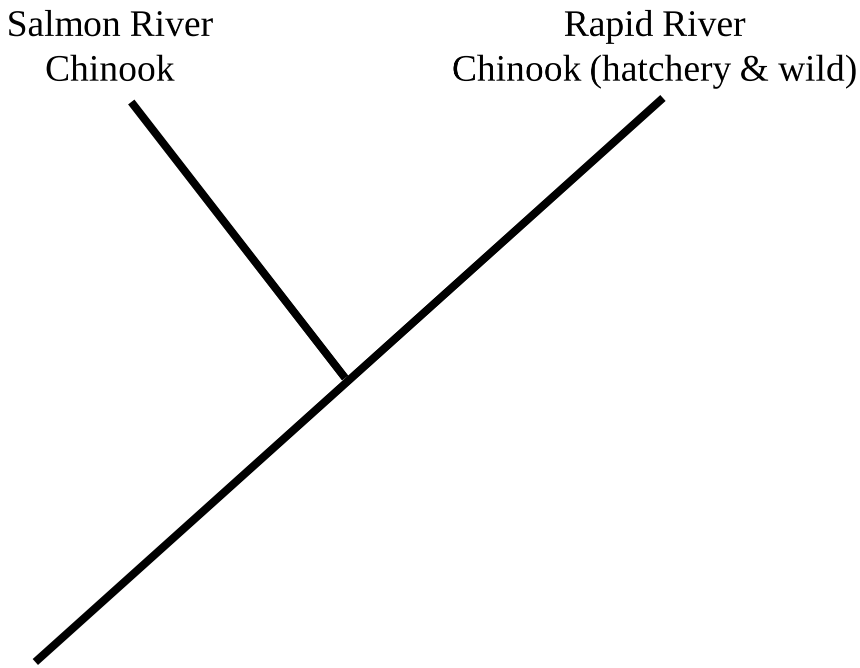
Yes



No



If neutral genetic markers are used to define ESU's?



It is generally not possible to differentiate hatchery from wild fish
→ might be claimed that wild fish are not ESU's

But what drives evolution at neutral loci?

- **How fast is this process?**

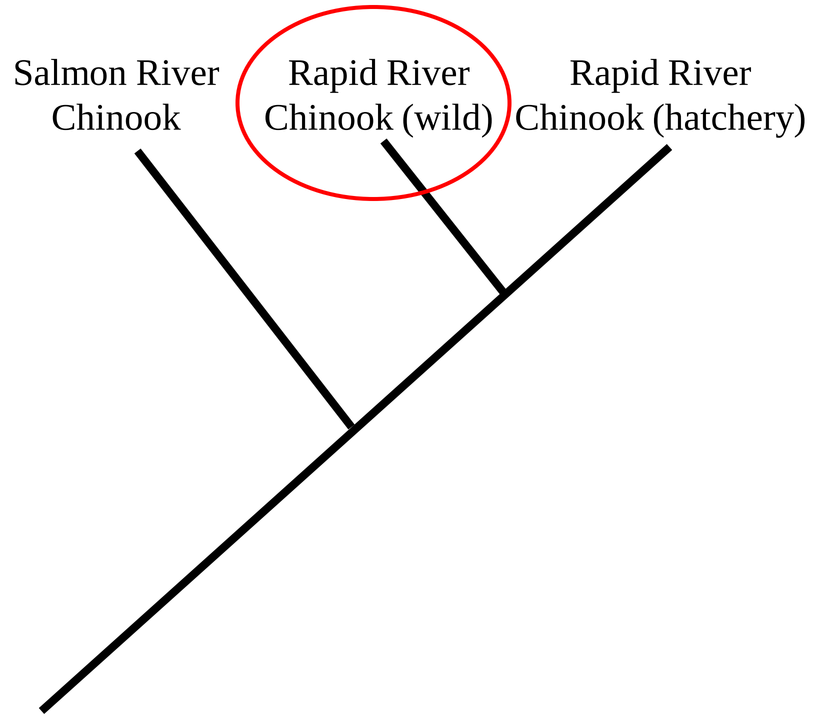
- **Is evolution at selected loci more or less rapid?**

If traits exposed to natural selection are used?

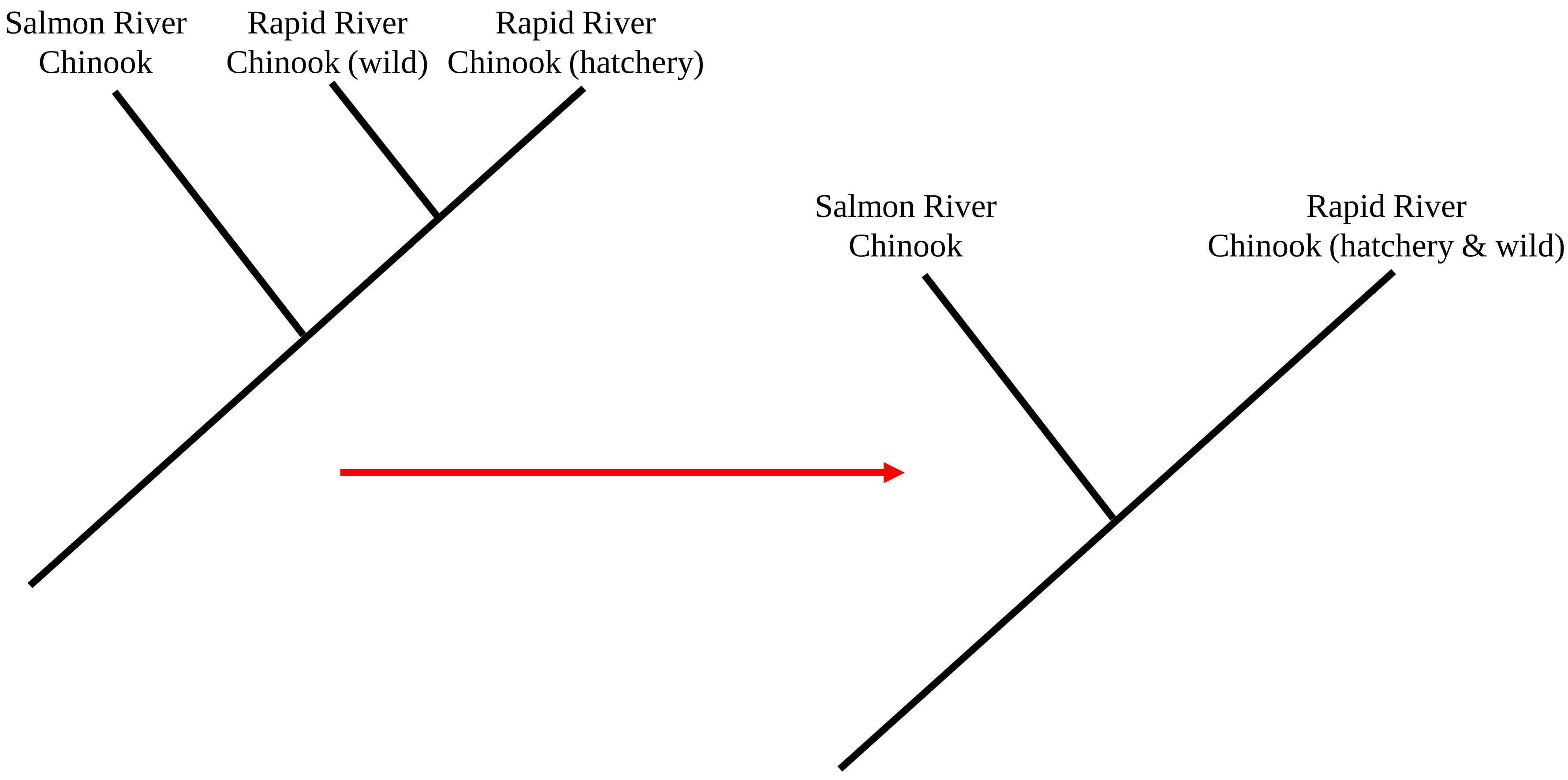
<u>Hatchery fish have genetically based differences in many traits:</u>

- Feeding behavior
- Migration patterns
- Morphology
- Agressiveness

Selected traits indicate that wild fish are certainly an ESU



What are the consequences of lumping wild and hatchery fish together as a single ESU?



Consequence 1: maladaptation

Hatchery fish have genetically based differences in many traits:

• Feeding behavior

• Migration patterns

• Morphology

• Agressiveness

These differences are generally maladaptive in the natural environment

An example: feeding behavior

- Hatchery fish are grown at high densities

- Feeding is very stereotypical

- Leads to the evolution of increased aggressiveness and fearlessness in hatchery fish

Feeding time at the hatchery!

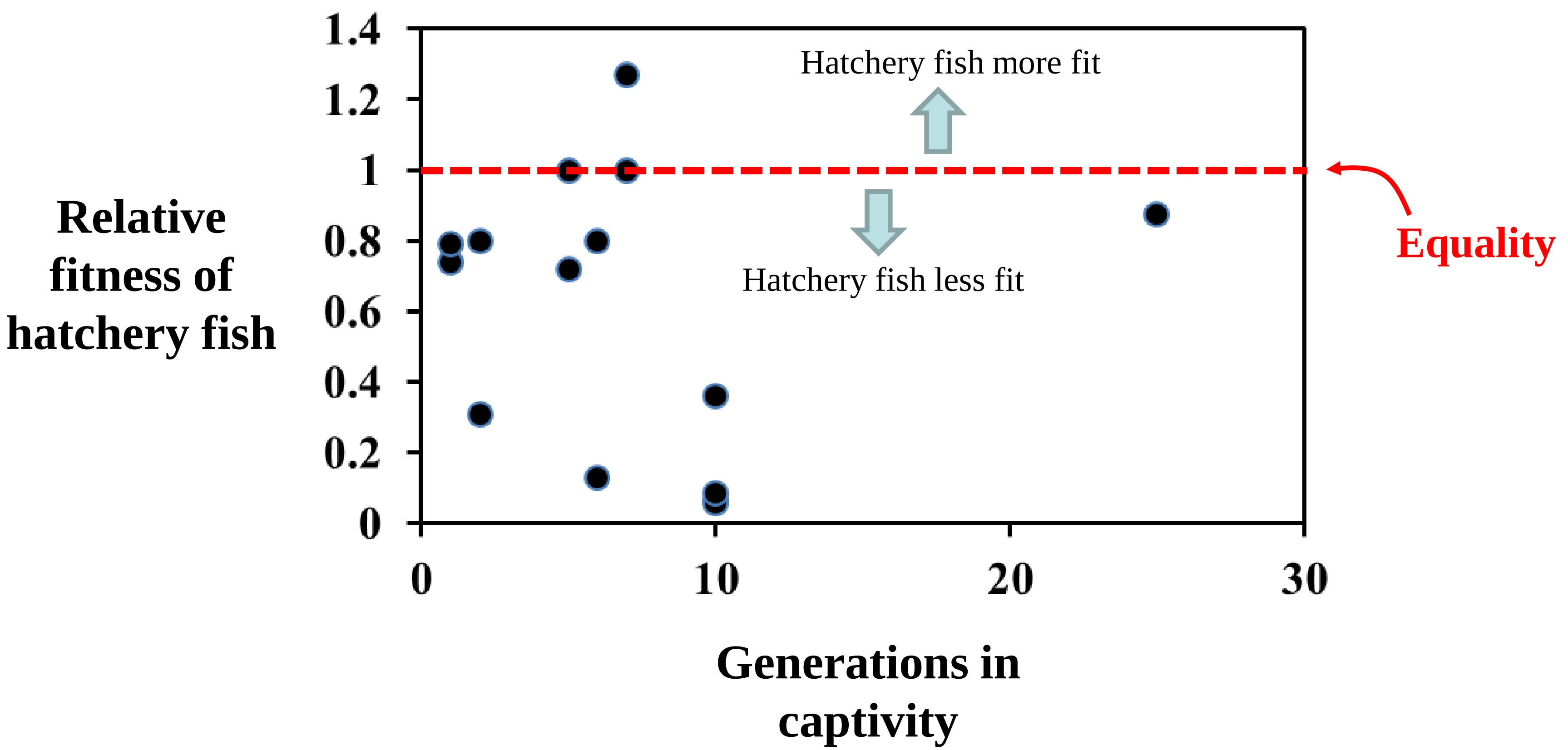
Outside the hatchery, these behaviors are often maladaptive

Tern with salmon

Just how maladpted are hatchery fish?

(Araki et al. 2008)

- **Compiled data from studies comparing fitness of wild and hatchery fish**



On average, hatchery fish are vastly less fit than are wild fish

Consequence 2: Competition

- The Rapid River fish hatchery releases ≈ 3 million Chinook smolts each year

What is the effect on wild fish?

• Intraspecific competition – If hatchery and wild fish are assumed to be the same species. (i.e., an individual hatchery fish has the same competitive effect on a wild fish as another wild fish. $\alpha = 1$)

→ Simply depresses the density of wild fish by using up a fraction of K

• Interspecific competition – If hatchery and wild fish are assumed to be different species (i.e., an individual hatchery fish does not have the same competitive effect on a wild fish as another wild fish. $\alpha \neq 1$)

→ Can drive wild fish to extinction

The answer depends on whether or not hatchery and wild fish are competitively equivalent

Are hatchery and wild fish equivalent?

- **Hatchery fish are generally more aggressive**
- **Hatchery fish generally grow more rapidly**
- **Hatchery fish are generally larger**
- **Hatchery fish are generally numerically superior**

Hatchery and wild fish are unlikely to have similar competitive abilities

The outcome of interspecific competition

Wild fish:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1} \right)$$

Hatchery fish:

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2} \right)$$

What are the possible outcomes of competition between wild and hatchery fish?

Possible outcomes of inter-specific competition

Ecological:

- Competitive exclusion
- Coexistence → seems unlikely given the differences in competitive ability

Evolutionary:

- Character displacement

Consequence 3: Gene flow and local maladaptation

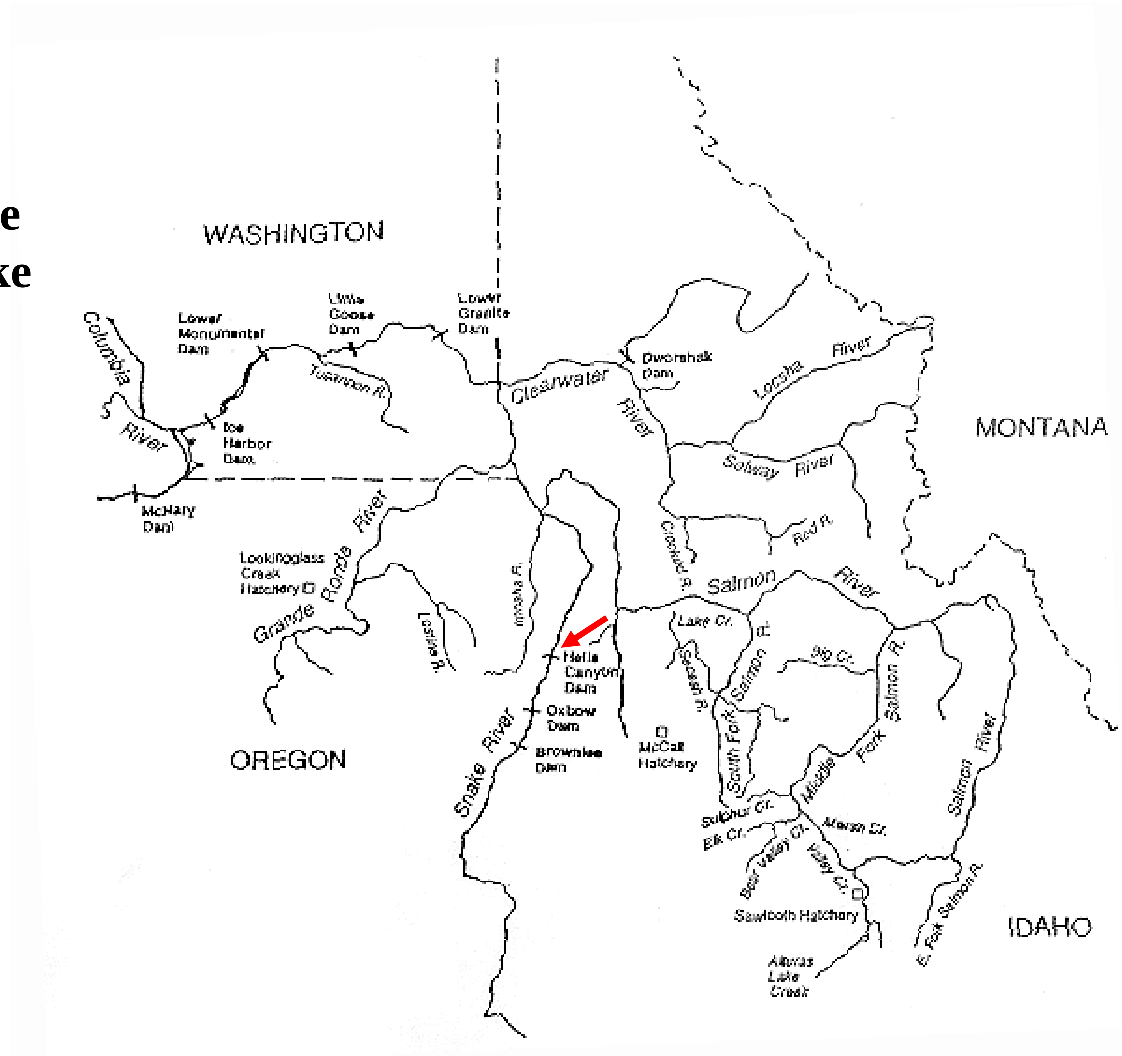
- Hatchery fish are often transplanted to distant streams

- Hatchery fish are more likely to wander than are wild fish

- Both create the potential for gene flow between river drainages

Gene flow

• **Each year up to 1,000,000 chinook smolts are taken from the Rapid River hatchery to the Snake River below Hell's Canyon Dam**



The Snake River Drainage

Gene flow

Rapid River

Snake River

Local maladaptation often results

- Genes adapted to one environment are introduced into another

- Decreases the populations ability to respond to local selection pressures

- The result is local maladaptation

- Demonstrated for traits such as:

  - Timing of smoltification
  - Timing of return to natal stream
  - Crypsis

Consequence 4: Hybridization

- **Hatcheries are designed to eliminate hybridization between wild and hatchery fish or to allow gene flow only from wild to hatchery fish**

- **Hatchery fish have decreased fidelity for their natal stream and an increased propensity for wandering**

- **As a result, hybridization between natural and wild strains may occur**

Hybridization between hatchery/farm and wild fish

(McGinnity et. al. 2003)

Table 2. Lifetime successes of the wild, farm and 'hybrid' groups.
(Results averaged over several cohorts where available (this study and McGinnity *et al.* (1997)). Survival of the wild group is taken as 1.0. Where another group is not significantly different from the wild group, at a particular stage, it is also given a value of 1.0. Where a group is significantly different from the wild group, then the actual survival relative to the wild group is used. Note that data for marine survival of the F_2 hybrid group are not available and a value of 1.0 is used, hence lifetime success values are maximum estimates.)

group	fertilization–eyed egg	eyed egg–smolt[a]	eyed egg–smolt[b]	smolt–adult	lifetime success[a]	lifetime success[b]
wild	1.0	1.0	1.0	1.0	1.0	1.0
BC_1W	1.0	0.89	1.0	1.0	0.89	1.0
F_1HyW	1.0	0.73	1.0	0.58	0.42	0.58
F_1HyF	0.87	0.50	0.63	0.61	0.27	0.33
F_2Hy	0.34	1.0	1.84	n.a.	(0.34)	(0.63)
BC_1F	1.0	0.79	1.59	0.39	0.31	0.62
farm	0.79	0.41	0.76	0.07	0.02	0.04

[a] This assumes that displaced parr have the same survival as parr of the same group remaining in the experiment river, i.e. that the river is not at its parr carrying capacity and spare habitat is available for displaced parr.
[b] This assumes that displaced parr emigrating from the experimental river do not survive, i.e. that the river is at its parr carrying capacity.

Hybrids have LOW fitness

Summary of issues raised

- **Defining ESU's (drift vs selection)**
- **Competition**
- **Gene flow and local maladaptation**
- **Hybridization**