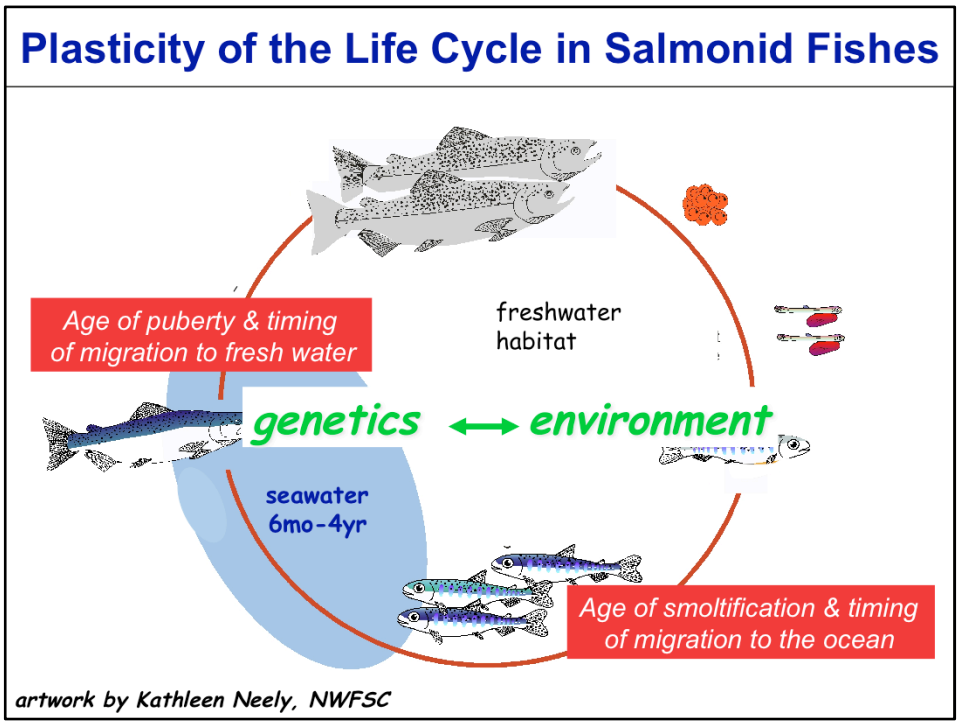
Timing of Puberty Onset in Male Salmon

Penny Swanson, Brian Beckman, & Don Larsen
Environmental Physiology Program
Northwest Fisheries Science Center
NOAA-Fisheries
Seattle, WA

Funded by Bonneville Power Administration & NOAA Fisheries



The figure depicts a basic life cycle of a salmonid fish, that begins as adults spawn in freshwater streams, rivers or lakes. Embryos, fry, and juveniles develop in fresh water for a variable amount of time depending on the species (or stock) and environmental conditions. Fish that are destined to migrate to sea undergo a metamorphic like process called smoltification that involves physiological, morphological and behavioral changes which allow them to adapt to the ocean environment. The age and seasonal timing of smoltification depend on both genetic and environmental factors. Once smolts enter the sea, they can spend anywhere from a few months to several years before returning to their natal streams for spawning. The return to fresh water is occurs after the initiation of puberty (ie. immature or sterile fish do not migrate back to natal streams). The age at which the fish mature varies within and between species. So the resultant life cycle depends on an interaction between the genetic makeup of the fish and environmental conditions. This talk focuses on the environmental factors that age of puberty and some aspects of the endocrine mediation of the environmental cues,

What is Puberty?

"process whereby an animal first develops reproductive competence"

- ✓ ***Morphological*- secondary sex characteristics**
- ✓ ***Physiological*- production of mature gametes, *activation of reproductive endocrine axis***
- ✓ ***Behavioral*- mating behavior**

Puberty in all animals is the process whereby an animal first develops reproductive competence- produces fertile gametes and exhibits appropriate mating behavior.

Puberty in semelparous salmon = completion of their first & only reproductive event in their life time*

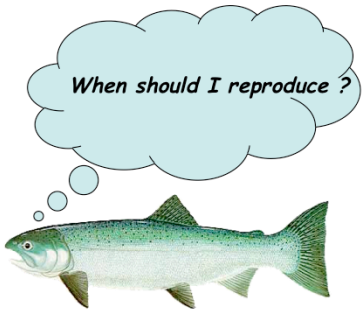
Puberty in iteroparous trout & steelhead = completion of the first reproductive cycle

Puberty onset-> also commonly referred to as "initiation of maturation"

* exception: male parr that may remature though this is not common

In semelparous Pacific salmon that only spawn once in their life and die, puberty is the process of completion of their first and only reproductive event. The exception is precocious male parr that can, but infrequently, remature. In rainbow trout and steelhead, that spawn repeatedly, puberty is the process of completion of their first reproductive cycle. Some fish will undergo what is called a "dummy run", which refers to a cycle of hormonal changes that are similar to a reproductive cycle, but the animals do not complete maturation and produce viable gametes. Puberty onset and "initiation of maturation" are often used interchangeably in the literature, but since initiation of maturation could also mean initiation of any cycle in iteroparous fish, puberty onset is the correct terminology for initiation of maturation for the first time.

Development of Reproductive Competence

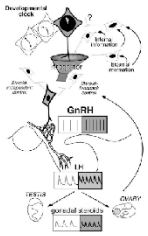


Relies on the integration of internal and external cues

- ✓ **metabolic**
  - sufficient size and energy stores
- ✓ **environmental**
  - optimal conditions for reproductive success (offspring survival)
- ✓ **social**
  - presence of a mate

Development of reproductive competence (i.e. completion of puberty) relies on the integration of a wide variety of internal and external cues. These signals provide critical information for timing of reproduction: whether it is of sufficient size or energy status to reproduce (metabolic cues), whether conditions are optimal for reproductive success (environmental cues), and whether an appropriate mate is present (social cues).

Stages of Puberty



Stage I: Development of neural connections

Stage II: Integration of internal information

metabolic cues

(e.g. fatty acids, amino acids, hormones)

Stage III: Integration of external information

photoperiod

-melatonin or other signals

social cues

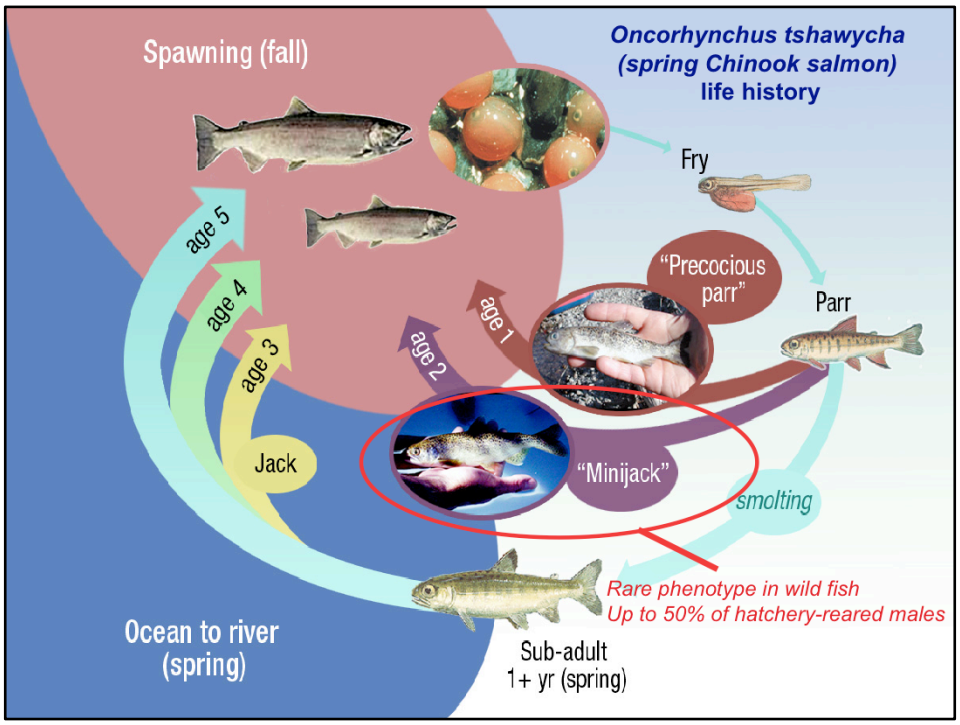
-pheromones, visual, etc.

Foster, D.L. et al. Biol Reprod 1999;60:205-215

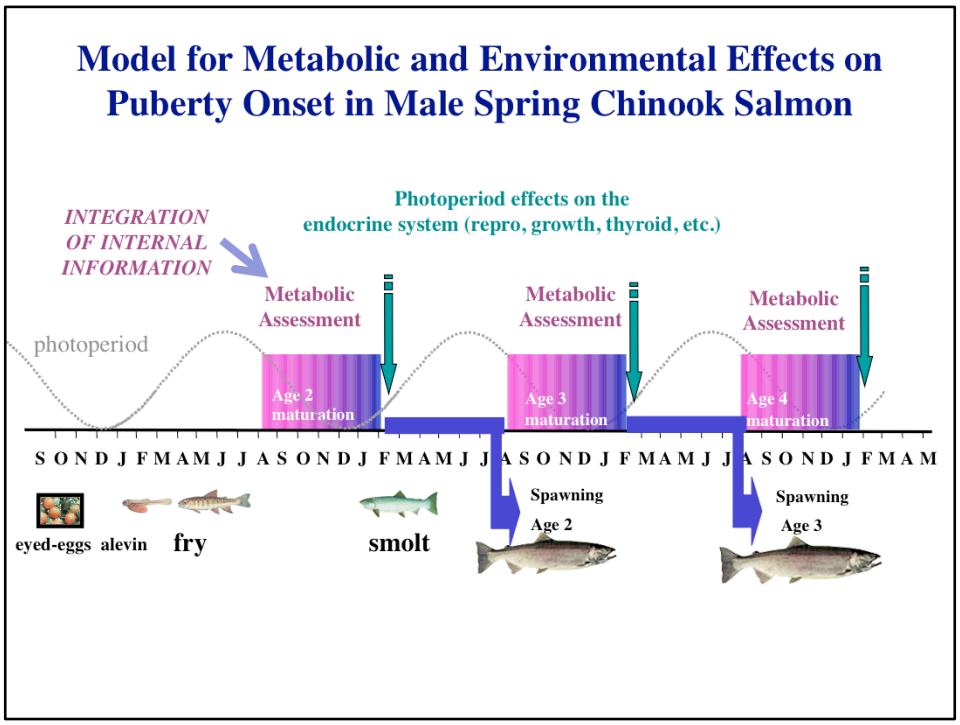
Puberty is a complex physiological process that has been most well studied in mammals and involves three stages (Foster et al. 1999). The initial stage involves the development of neural connections. Stage II is the integration of internal information such as those that reflect the metabolic status of the animal. Finally, Stage III is the integration of external information such as photoperiod, temperature, social cues (chemical or visual).

Timing of puberty onset

- ✓ ***Part of species specific life history- genetic***
- ✓ ***Occurs well in advance of spawning in fish with long spawning migrations (e.g. salmon, eels)***
- ✓ ***In seasonal breeders, the reproductive endocrine system must be functional to respond to environmental cues for appropriate seasonal timing of reproduction***
- ✓ ***Metabolic cues (fat levels, growth rates) generally act as permissive cues, not triggers***

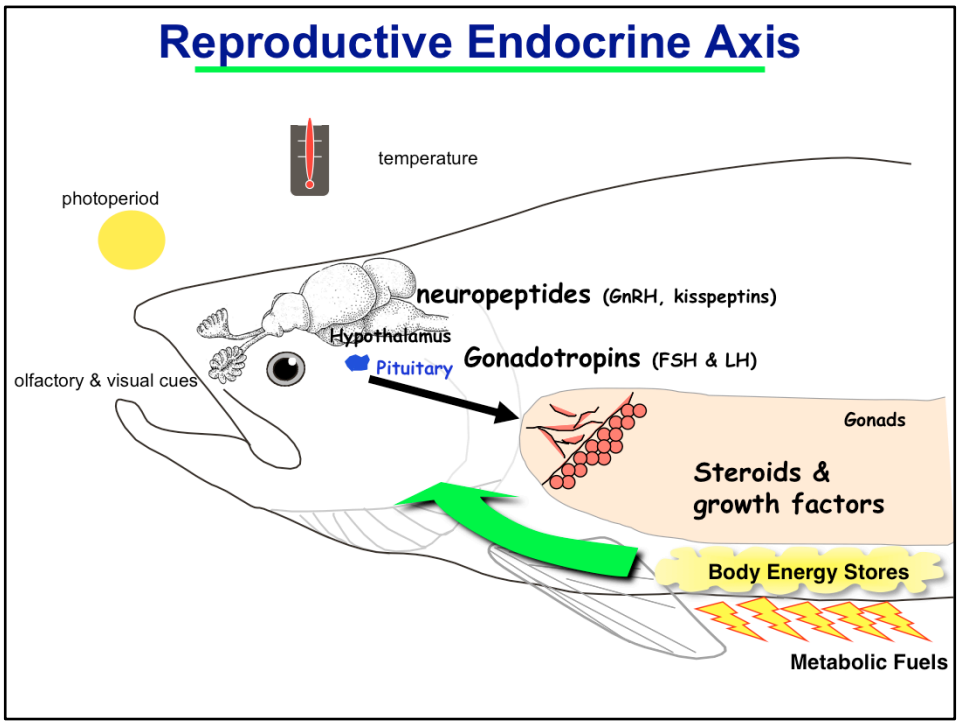


This diagram depicts the complex life cycle of spring Chinook salmon. Age of maturity in males is highly plastic and can occur from ages 1-5. Most spring Chinook salmon smolt in the spring as 1+ age fish. Males that mature at age 2 (mini-jacks) are not common in nature, however recent work has shown that some hatcheries produce a high proportion of minijacks.

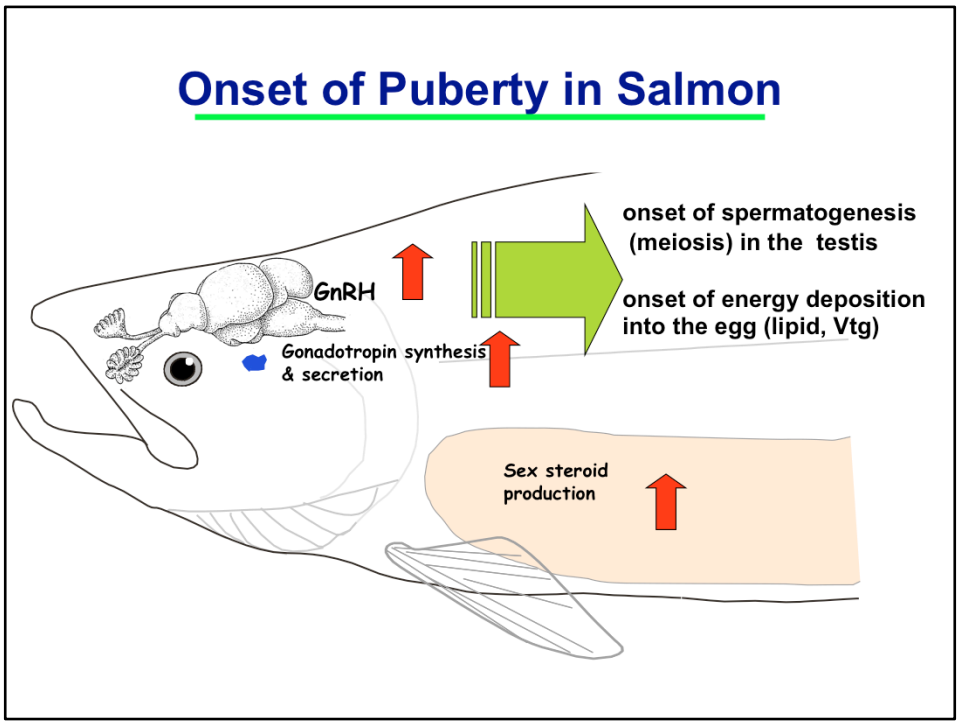


This figure depicts a PROPOSED model for how and when metabolic and environmental factors influence age of puberty onset in male spring Chinook salmon. The boxes represent critical seasonal periods wherein growth/body fat levels influence onset of puberty.

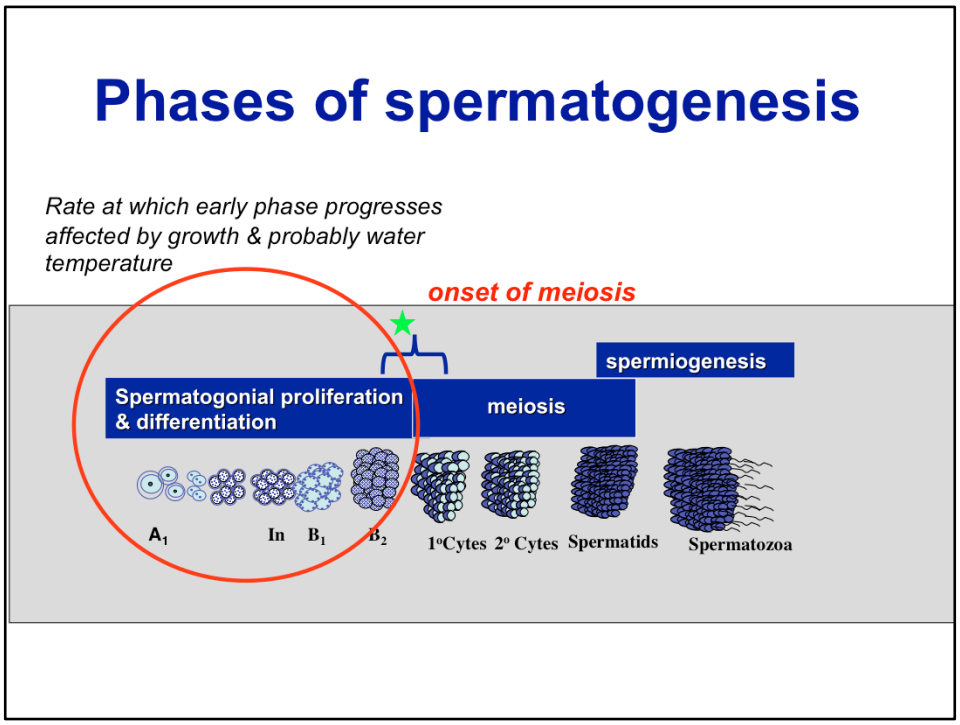
What are the physiological changes associated puberty onset or activation of the reproductive system?



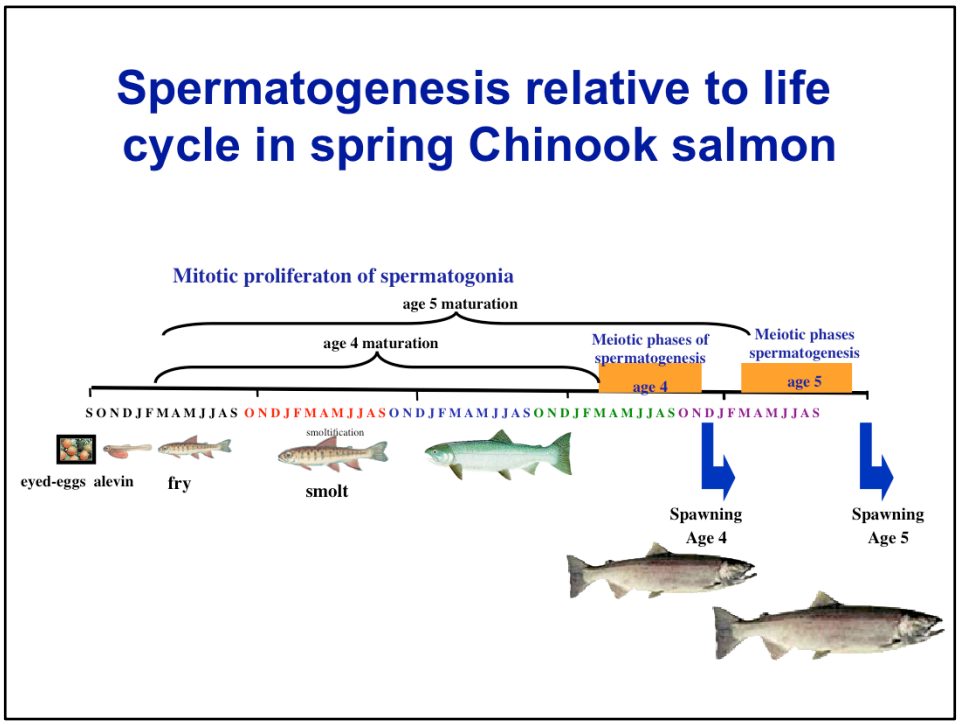
Reproduction is regulated internally by the endocrine system, which includes the brain, pituitary gland and gonads. Environmental information in perceived and processed by the brain, which in turn regulates the production and secretion of pituitary gonadotropins, follicle stimulating hormone (FSH) and luteinizing hormone (LH). FSH and LH regulate the growth and maturation of gonads via their effects on the production of gonadal steroids and growth factors.



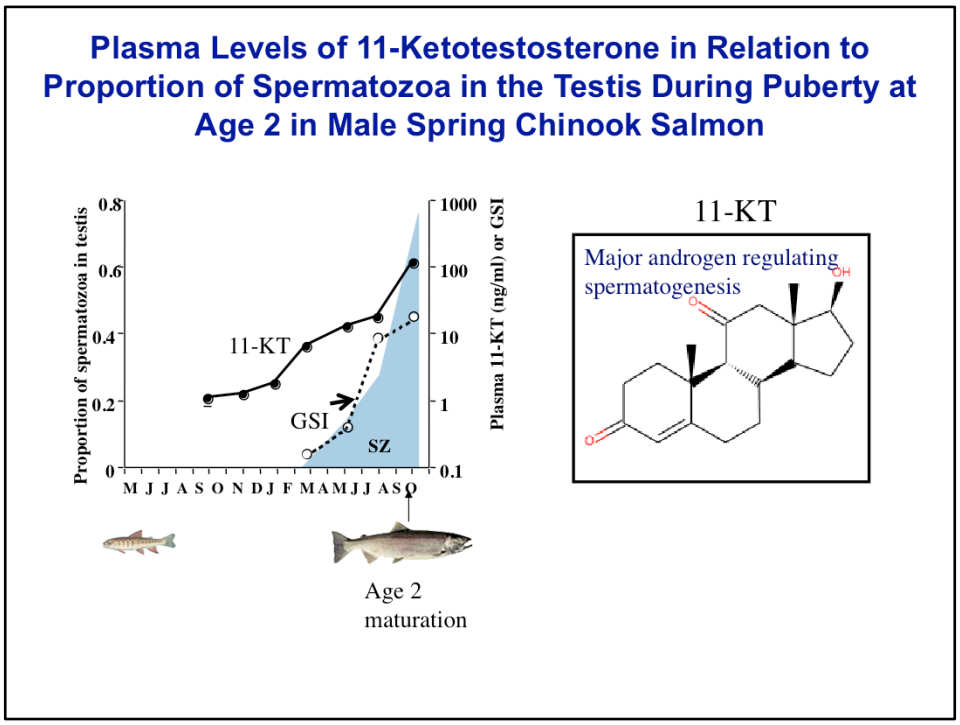
During onset of puberty in salmon, the reproductive endocrine system is activated. Increases in hormone production precede morphological signs of maturation.



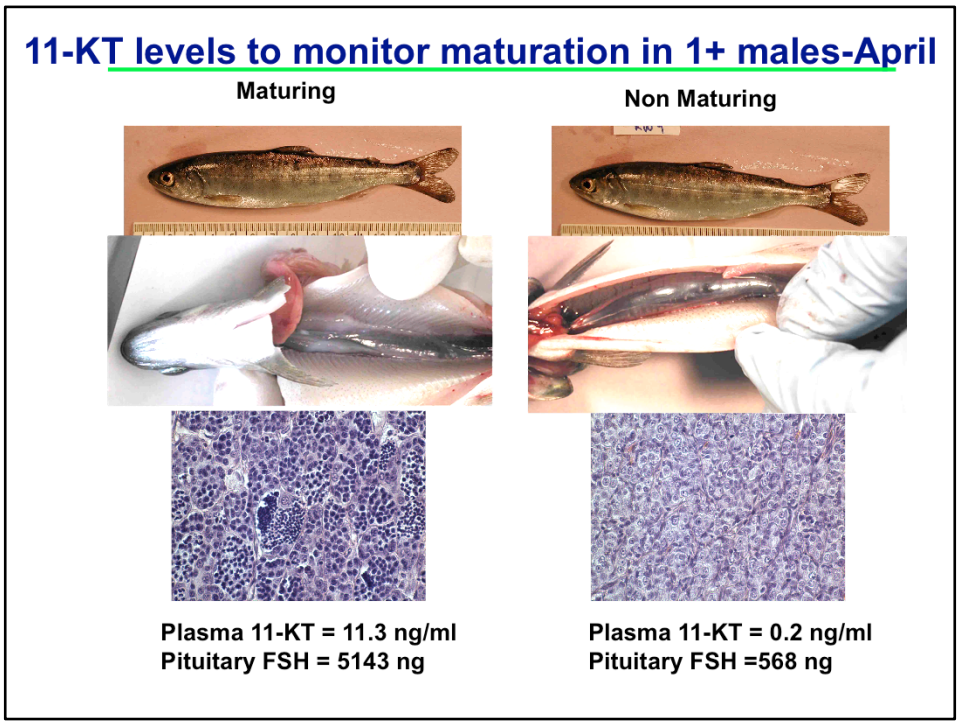
This figure illustrates the process of spermatogenesis. It includes a mitotic phase (spermatogonial proliferation) and meiotic phase (process of production of haploid cells). Spermiogenesis is the developmental process of formation of spermatozoa from spermatids.



This figure illustrates the timing of spermatogenesis relative to the life cycle of spring chinook salmon.

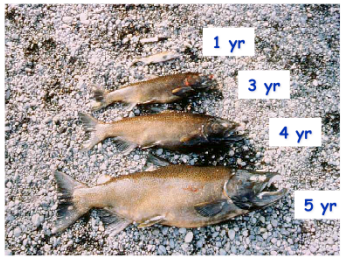


Plasma levels of an androgen, 11-ketotestosterone (11-KT), increase during spermatogenesis in salmon. 11-KT regulates spermatogenesis.



Levels of 11-KT can be used to identify males that have initiated spermatogenesis.

Factors Affecting Age of Maturity

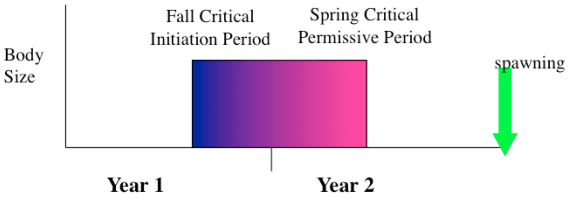


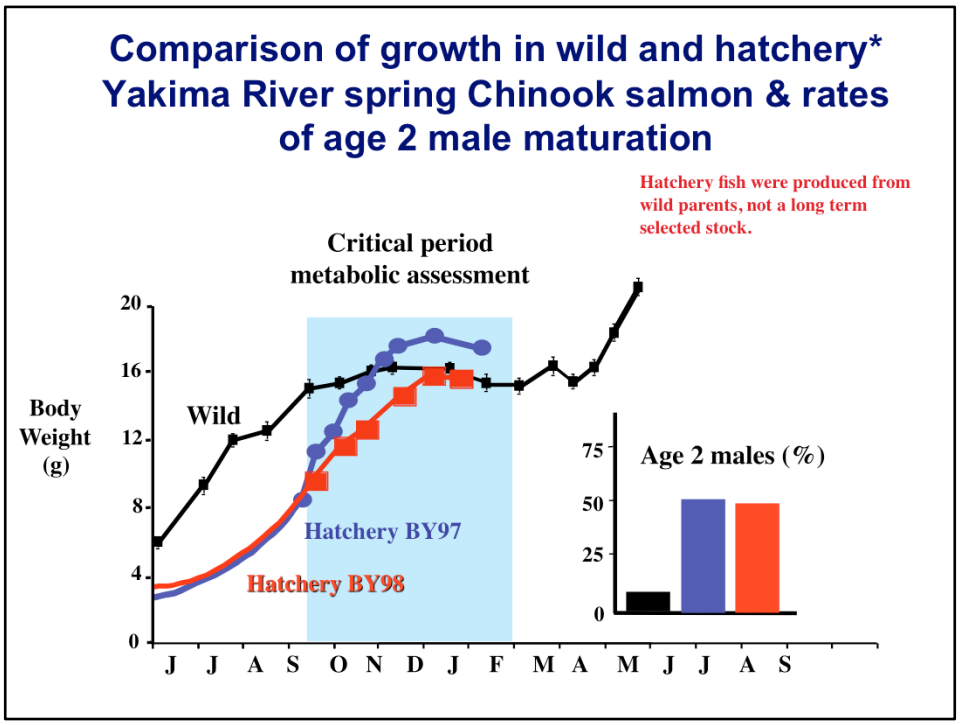
Mature male salmon

- ✓ Genetics
- ✓ Environment
  - temperature
  - food availability
  - food quality

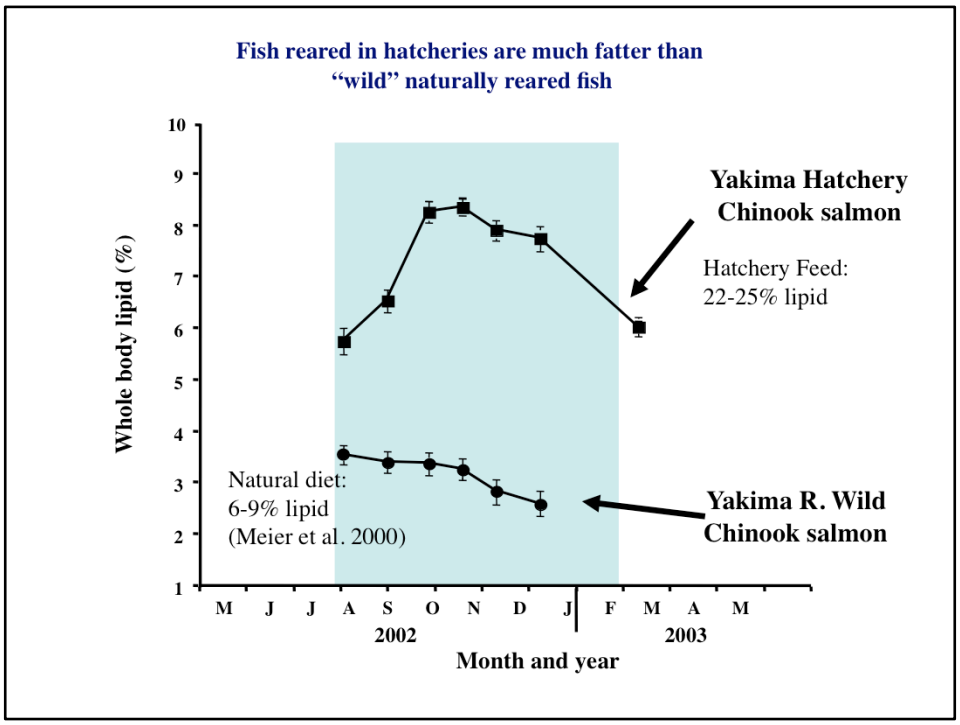
Growth & body energy stores

Critical Period Model
(Thorpe 1994 Aquatic Fish. Manag 25:77-87)





Patterns of growth in spring chinook salmon reared in the hatchery differ from that of fish in the natural environment. Rates of age 2 maturation are higher in hatchery reared spring Chinook salmon than wild fish of the same stock.



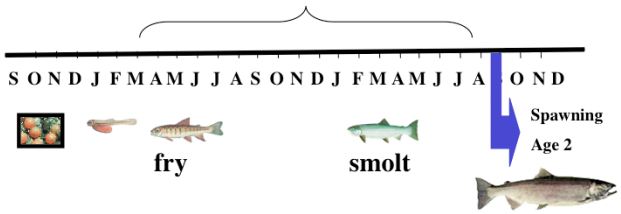
Hatchery spring Chinook salmon have higher body lipid levels than the same stock living in nature.

Experimental Approach

Nutritional manipulations

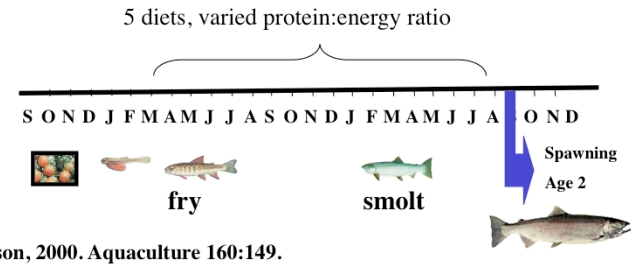
- Evaluate independent and interactive effects of somatic growth versus body energy stores on puberty in male salmon
- Determine critical period when growth affects onset of puberty
- All experiments done with water temps ranging from 10-12 ^{0}C

Evaluate endocrine & histological changes during critical periods



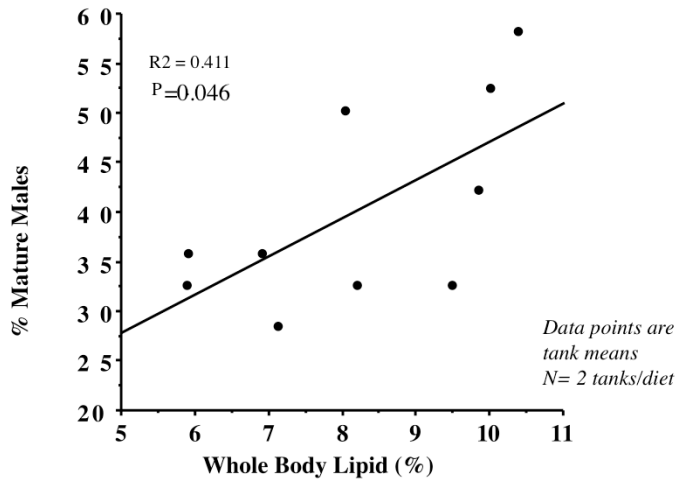
Body Fat

- ✓ Juvenile Chinook salmon on 5 diets containing 5 levels of protein energy ratios. Controlled ration so fish were same body size, but varied in body fat
- ✓ Monitored % males that matured at age-2
- ✓ Sampled fish monthly to perform gonad histology and measure reproductive hormones



Shearer & Swanson, 2000. Aquaculture 160:149.

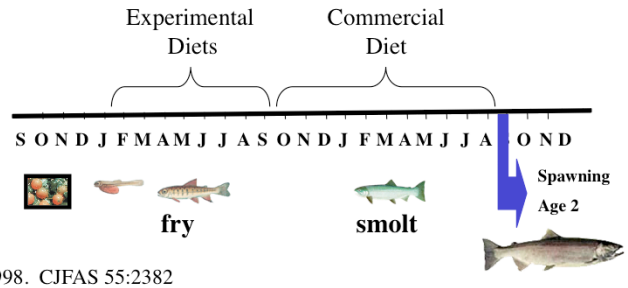
Relationship between whole body lipid in after the first year and male maturation in the following year



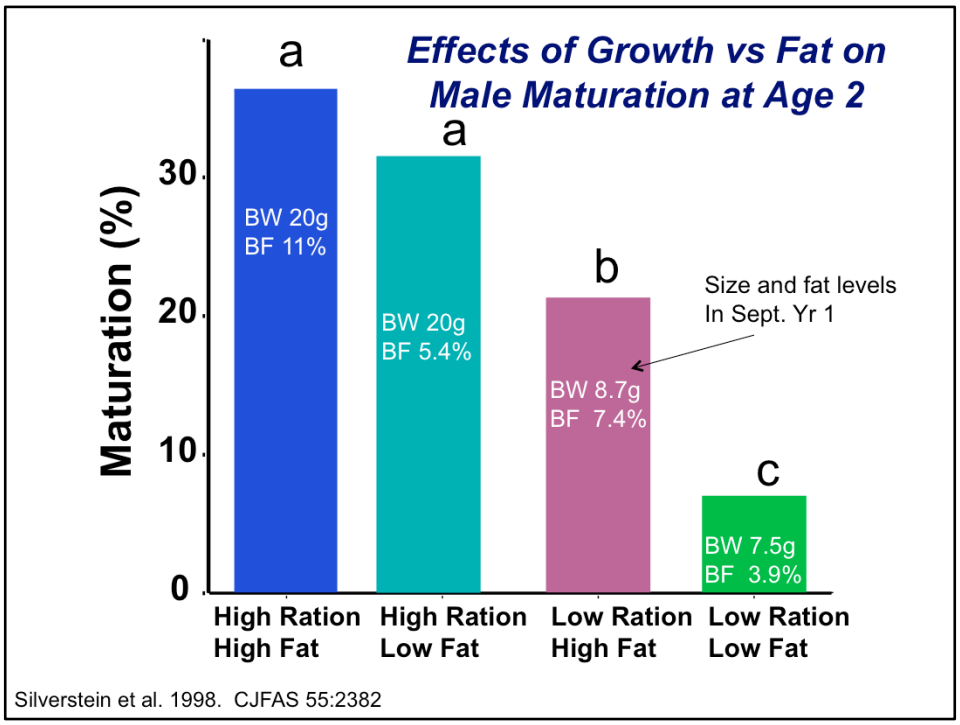
Shearer & Swanson, 2000. Aquaculture 160:149.

Fat & Size/Growth Rate

- ✓ Juvenile spring Chinook salmon were fed either a high fat or low fat diet, and either high or low ration for the first year. During the second year fish were reared on a commercially available diet.
- ✓ Produced "big fat fish, small fat fish, big lean fish, small lean fish"
- ✓ Monitored % males that matured at age-2

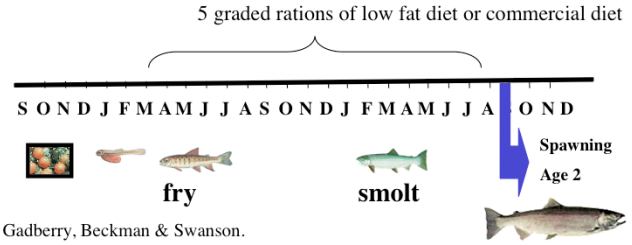


Silverstein et al. 1998. CJFAS 55:2382


Effects of Growth vs Fat on Male Maturation at Age 2
Maturation (%)
30
20
10
0
a
a
b
c
BW 20g
BF 11%
BW 20g
BF 5.4%
BW 8.7g
BF 7.4%
BW 7.5g
BF 3.9%
Size and fat levels
In Sept. Yr 1
High Ration High Fat
High Ration Low Fat
Low Ration High Fat
Low Ration Low Fat
Silverstein et al. 1998. CJFAS 55:2382

Size/Growth Rate

- ✓ **Exp. 1: Juvenile Chinook salmon on 5 different rations of a high protein/low fat diet. Body fat levels in these fish were 3-4% and weight ranged from 50-120g at end of first year.**
- ✓ **Exp 2. Juvenile Chinook salmon on 5 different rations of a commercial diet. Body fat levels in these fish were 2-5%. Size ranged from 12-55 g at end of first year.**
- ✓ **Monitored % males that matured at age-2**

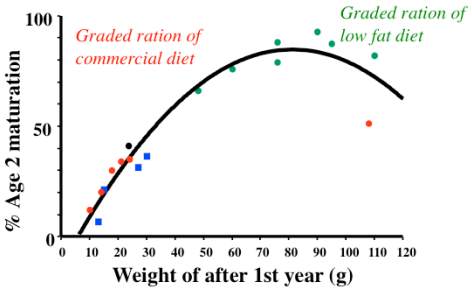


Shearer, Parkins, Gadberry, Beckman & Swanson. 2006. *Aquaculture* 252:545-5567.

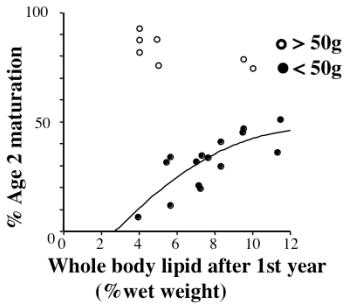
Body size & fat level at age 1 influence maturation of males at age 2

male spring Chinook salmon

Effect of size



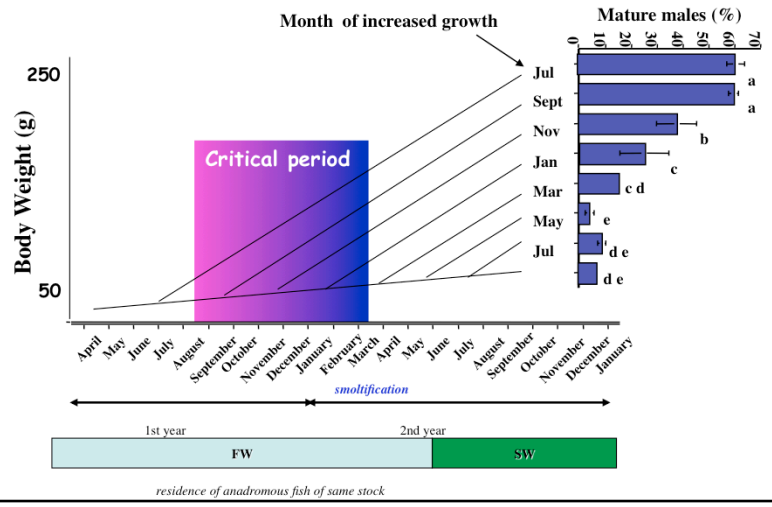
Effect of fat level



Shearer and Swanson 2000, *Aquaculture 190:343-367*

Shearer, Parkins, Gadberry, Beckman & Swanson. 2006. *Aquaculture* 252:545-5567.

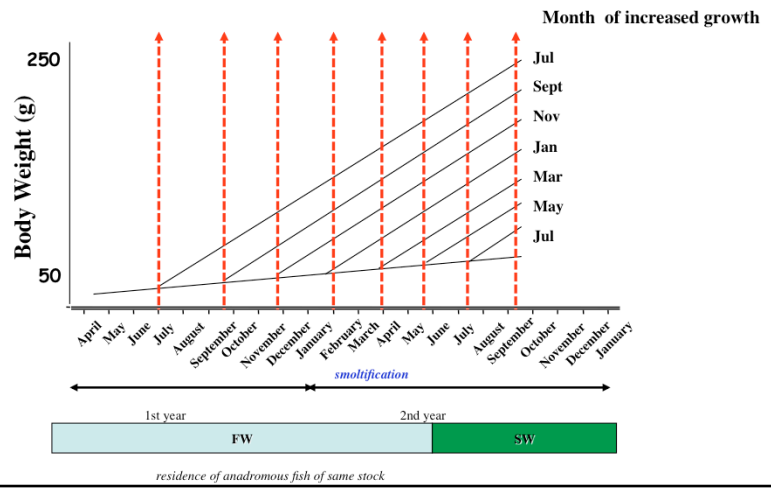
Effects of varying time of increased growth on rates of maturation at Age 2

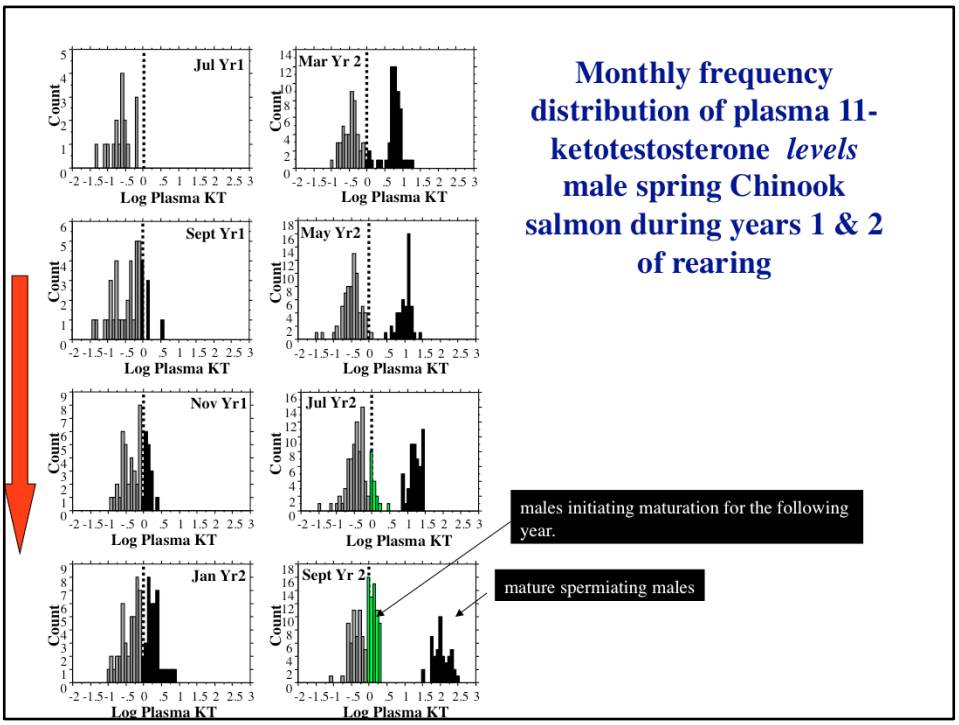


✓What about the males that did not mature at age 2?

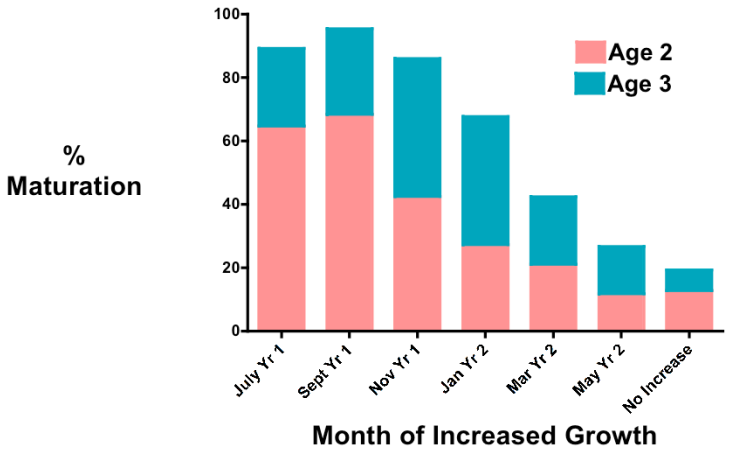
✓Were all the immature age 2 males uniform in reproductive status?

Sampling Dates for 11-KT Determinations

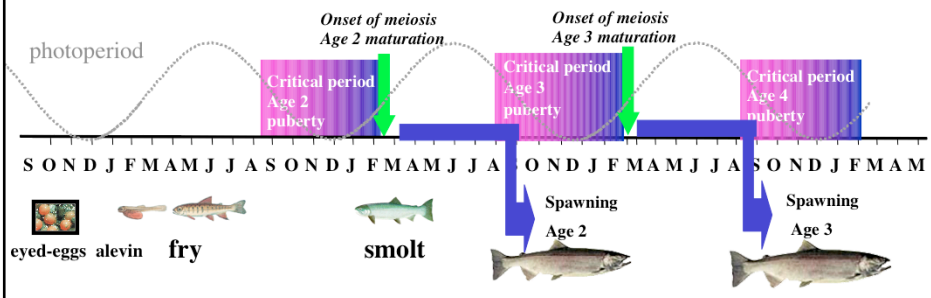



Monthly frequency distribution of plasma 11-ketotestosterone *levels* male spring Chinook salmon during years 1 & 2 of rearing
Jul Yr1
Mar Yr 2
Sept Yr1
May Yr2
Nov Yr1
Jul Yr2
Jan Yr2
Sept Yr 2
Count
Log Plasma KT
males initiating maturation for the following year.
mature spermiating males

Estimates of age -3 maturation based on plasma 11-KT in September of year 2

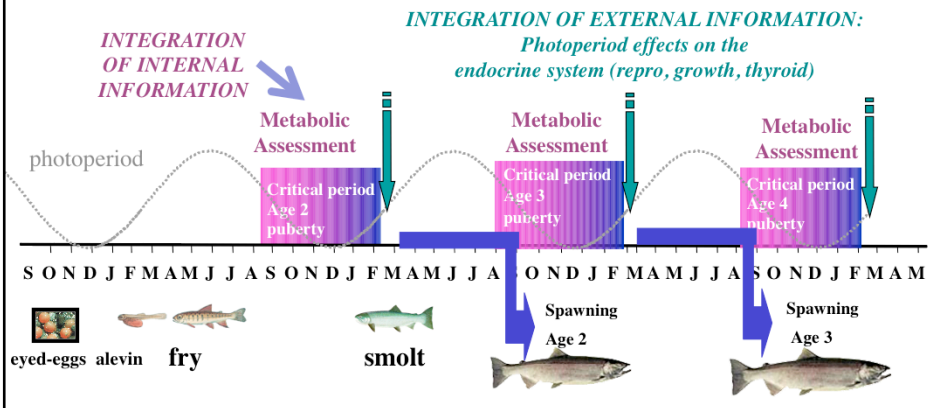


Model for Annual Critical Periods when Growth Affects Onset of Puberty in Spring Chinook Salmon



Silverstein et al. 1998, *Can. J. Fish Aquat. Sci. 55:2376-2382*
Shearer and Swanson 2000, *Aquaculture 190:343-367*
Campbell et al. 2003, *Biol. Repro. 69:2109-2117*.
Larsen et al. 2004 *Trans. Amer. Fish Soc.* 133:98-120
Shearer et al. 2006 *Aquaculture* 252:545-5567.
Swanson et al. unpublished.

Model for Annual Critical Periods when Metabolic Status Affects Onset of Puberty in Spring Chinook Salmon



Silverstein et al. 1998, *Can. J. Fish Aquat. Sci. 55:2376-2382*
Shearer and Swanson 2000, *Aquaculture 190:343-367*
Campbell et al. 2003, *Biol. Repro. 69:2109-2117*.
Larsen et al. 2004 *Trans. Amer. Fish Soc.* 133:98-120
Shearer et al. 2006 *Aquaculture* 252:545-5567.
Swanson et al. unpublished.

SUMMARY

1) Both growth rate/size and fat levels can alter rates during first year can alter rates of age 2 male maturation
2) Fat levels appear to be more influential in smaller fish (< 50 g in first year)
3) Growth regimes during early rearing can also affect puberty onset for age 3 fish
4) Growth rates in early rearing can also alter rates of ovarian development in females (data not shown)

Caveat - Experiments have been done on relatively constant temperatures. Effects of temperature on maturation rates of fish post release from the hatchery should be examined.