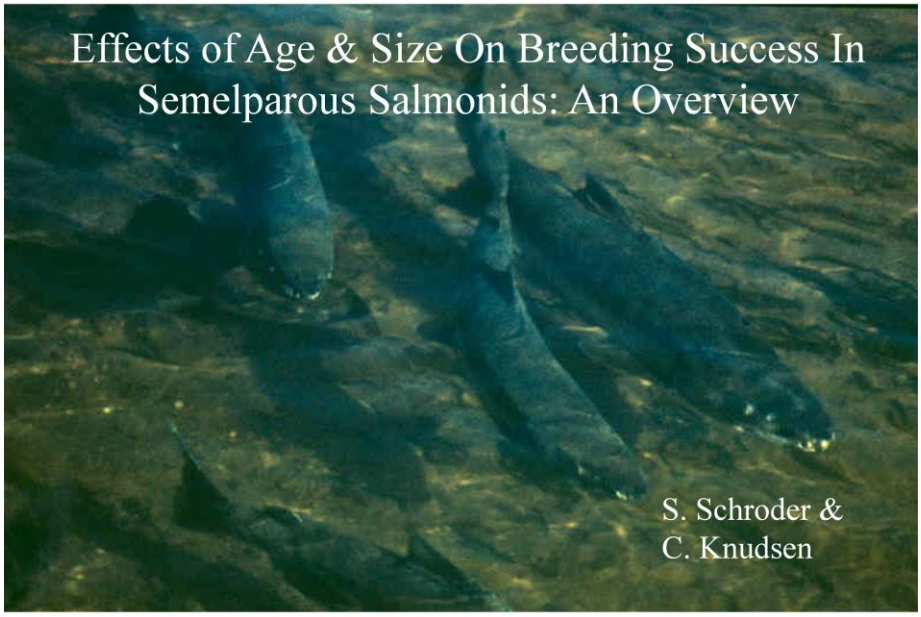
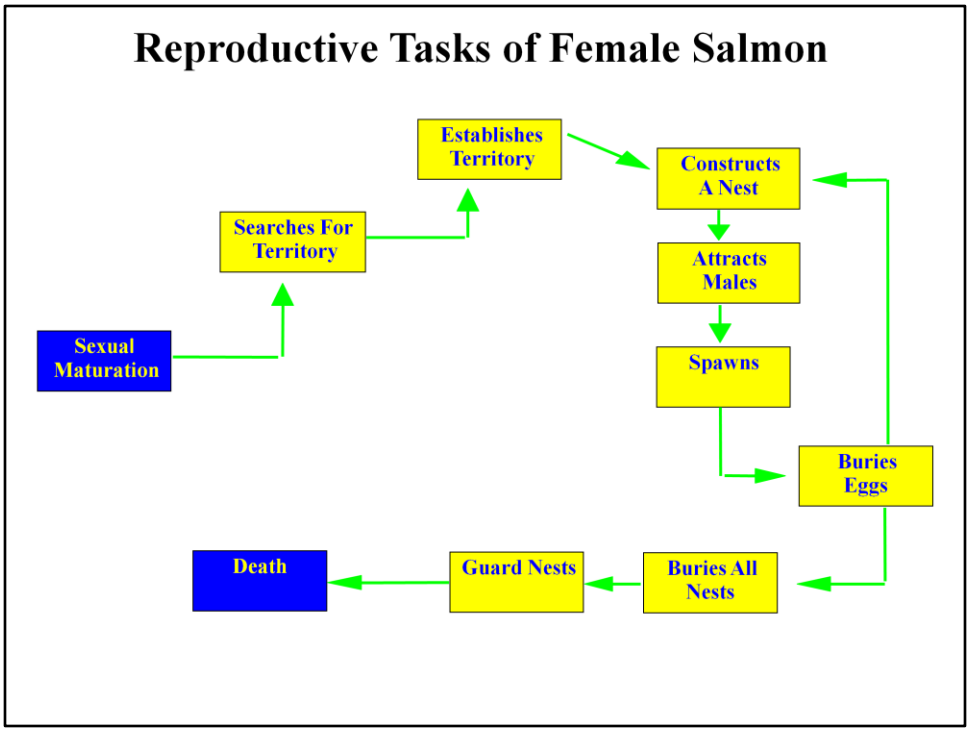


Simply reaching maturity or even making it to a spawning area does not guarantee that an individual will produce any offspring. A variety factors can influence breeding success in salmonids. Certainly two of them are the age and relative size of the fish when they reach maturity.

Factors Affecting Breeding Success

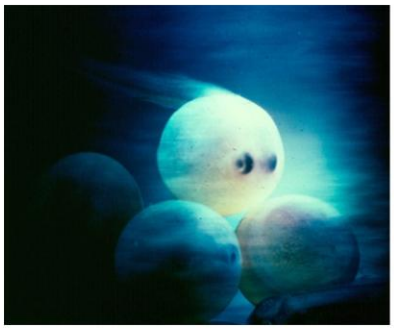
- **Intra-sexual Competition**
  - **Mates For Males**
  - **Space For Females**
- **Epigamic Selection**
  - **Mate Choice**

Once a fish arrives on a spawning ground it will be subjected to the two components of sexual selection. Males will compete among themselves for mates and females may compete for space to bury their eggs. Both may experience some degree of epigamic selection.



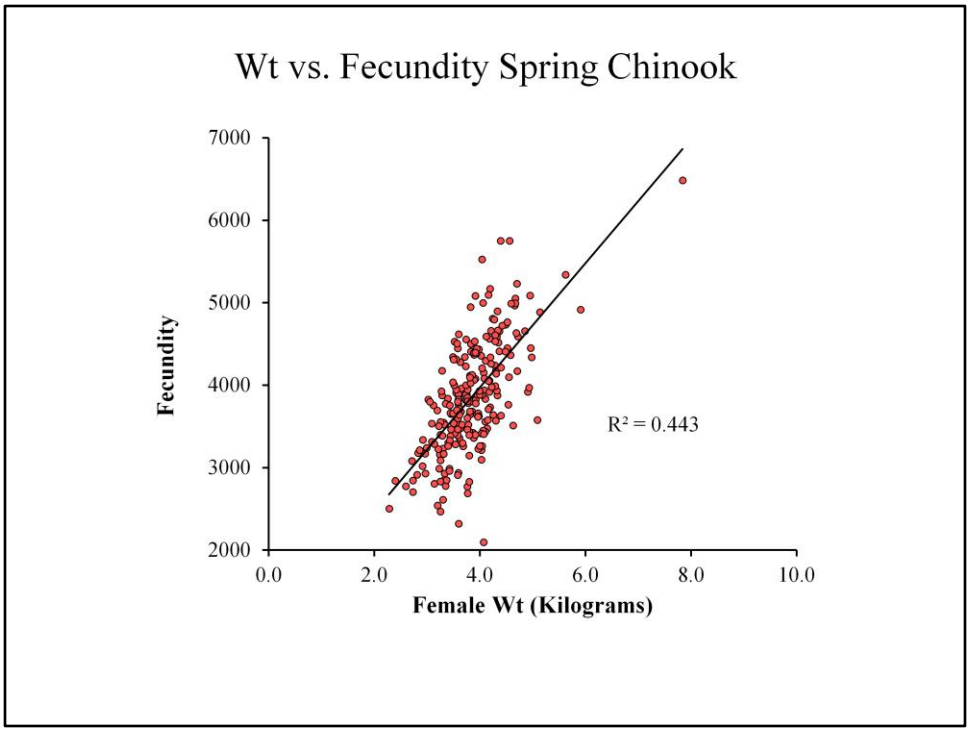
The breeding success of females depends, in part, upon their ability to complete a series of tasks. They must find suitable places to spawn, defend those sites from adjacent potential female competitors, dig a series of separate nests and guard their deposited eggs until senescence.

Effects of Female Size & Age On:

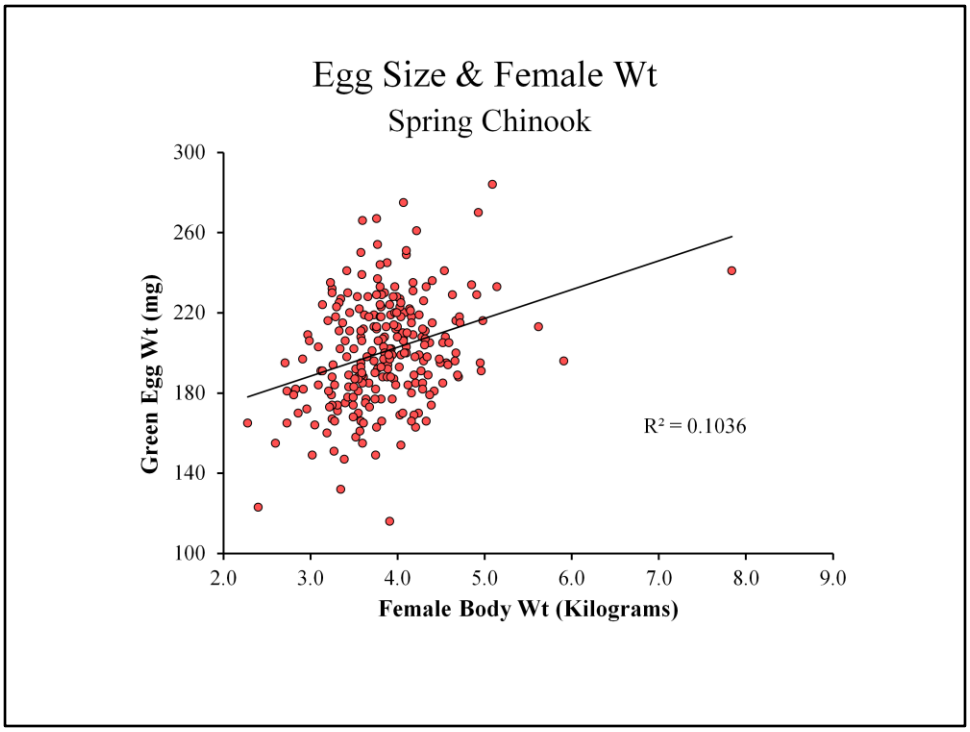


- Fecundity & Egg Size
- Intra-sexual Competition For Space
- Spawning Ground Longevity
- Nest Depths
- Epigamic Selection (Mate Choice By Males)
- Progeny Traits Affected By Egg Size

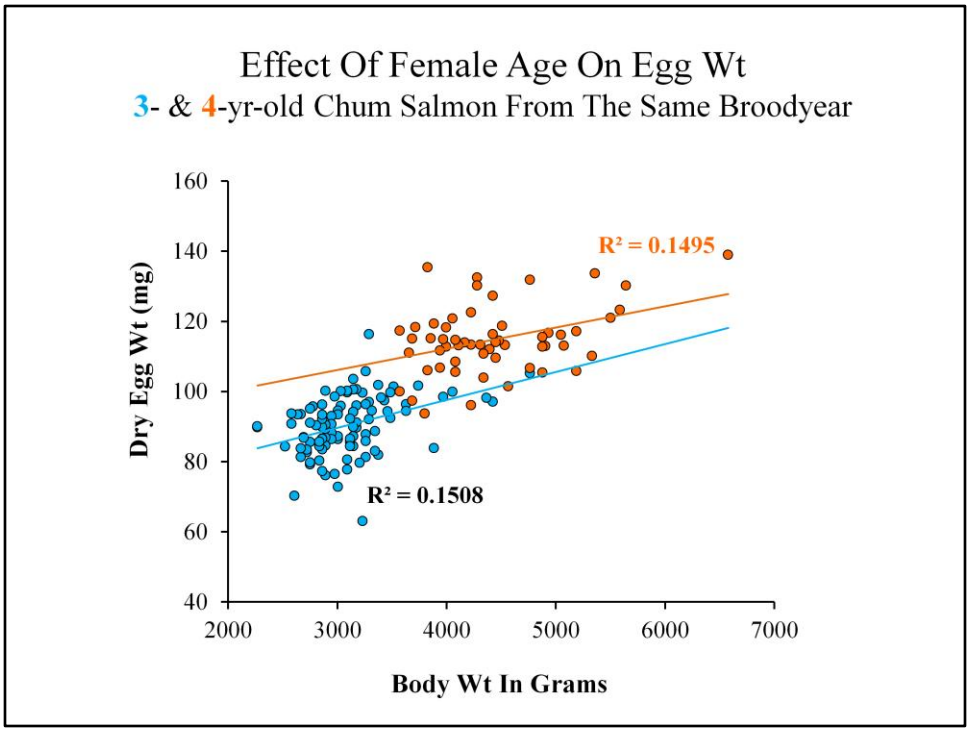
Here is a quick survey of what we know about the effects of female age and size on a variety of factors related to their potential fitness.



In general fecundity increases with female body weight. Here you can see that about 45% of the variation in fecundity is explained by body weight for upper Yakima River spring Chinook salmon. Typically, 40 to 60% of the variation in fecundity can be explained by female weight.



There is also a positive relationship between female weight and egg weight. In many instances this is a relatively loose relationship, with regression coefficients that are often in the 10 to 30% range



Age can also influence egg size. In this case, four-year old females produced larger eggs than three-olds even though both had comparable body weights.

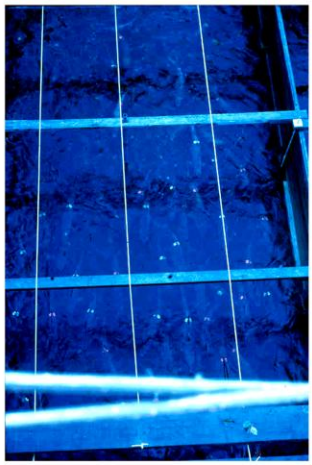
Effects Of Age On Female Traits

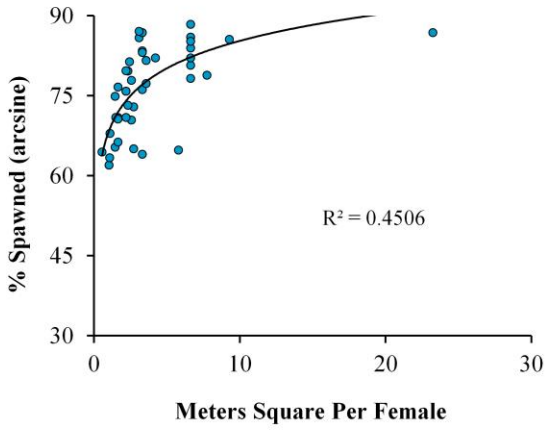
(Grays River Chum Salmon Brood-Yrs 1995 – 2004)

Female Age	Body Wt (g)	Fecundity	Egg Wt (mg)
3-yr-olds	3,723	2,794	266
4-yr-olds	4,578	2,994	311
% Increase	19%	7%	14%

For every additional year spent in the ocean female chum salmon from Grays River experienced increases in weight, fecundity, and egg weight.

Egg Retention & Competition For Space:
Chum Salmon

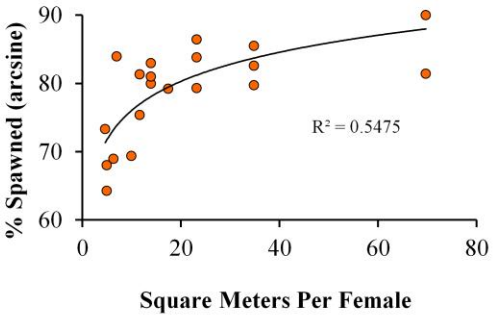




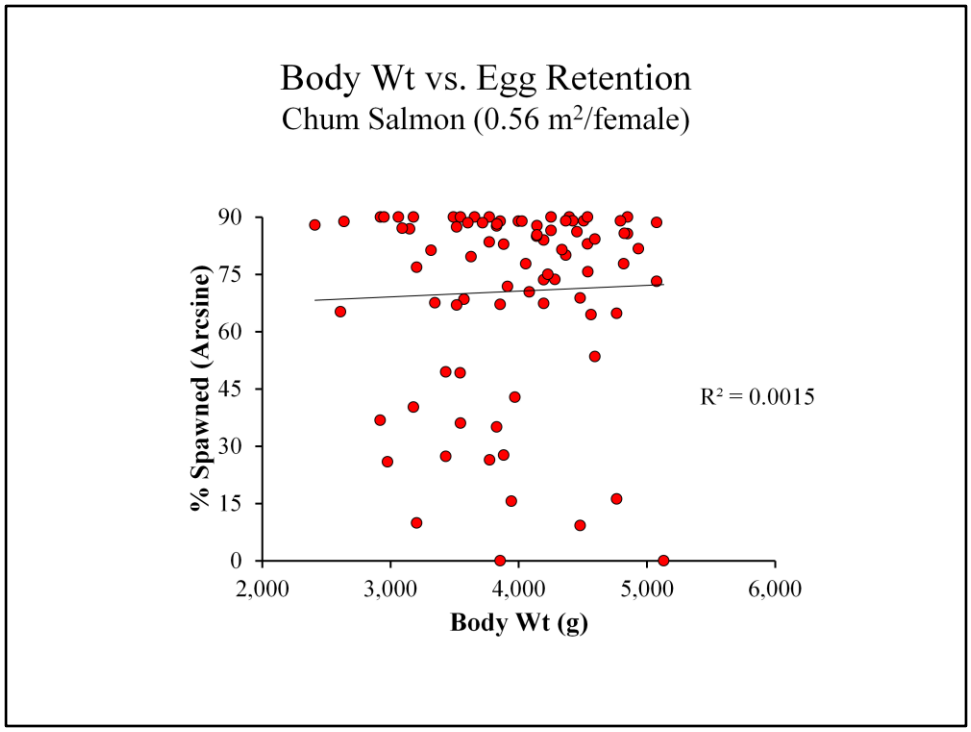
When competition for space is intense some females will not be able to deposit all of their eggs. For example, egg retention in chum salmon females goes up when the amount of space per female declines.

Effect Of Female Density On Egg Deposition

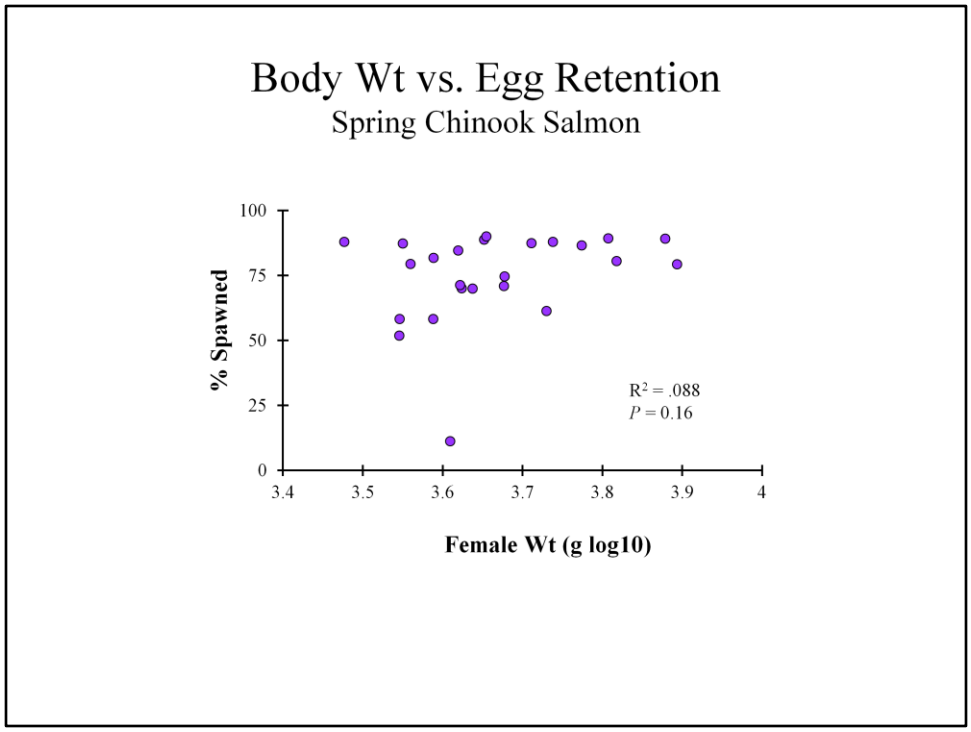
Spring Chinook Salmon



The same is true in Chinook salmon. Perhaps surprisingly, body size . . .

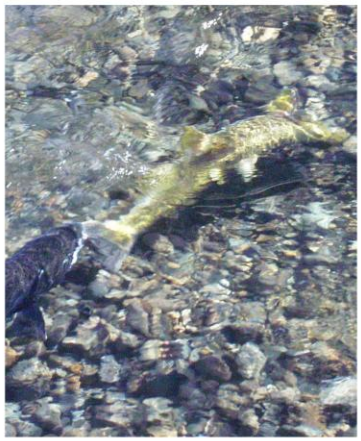


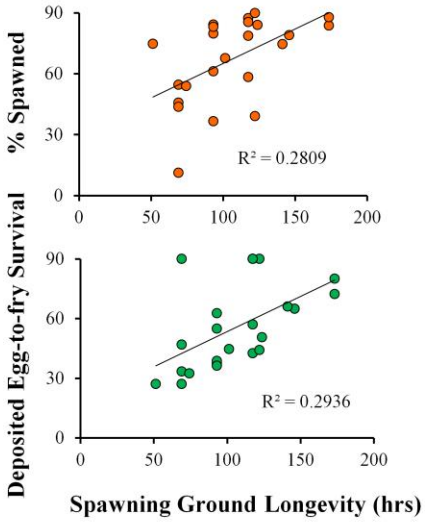
…has no effect on egg deposition in chum salmon or in. . .



Chinook salmon.

Spawning Ground Longevity
Spring Chinook

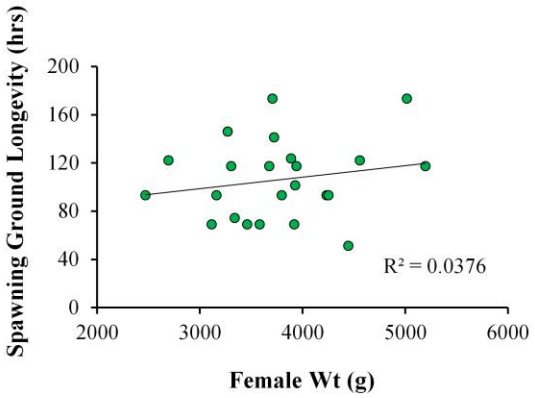




Longevity or spawning ground residency in spring Chinook was positively correlated to egg deposition and to the survival of deposited eggs

Body Wt vs. Spawning Ground Longevity

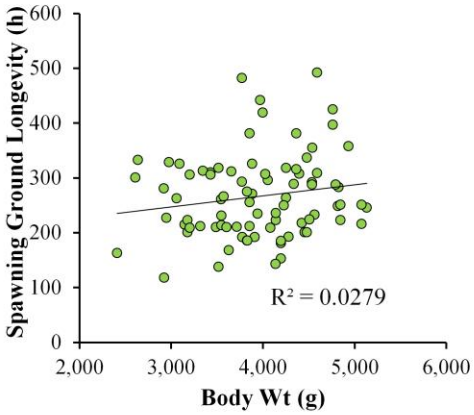
Spring Chinook Salmon



However, no relationship existed between female body weight and longevity in this species

Body Wt vs. Spawning Ground Longevity

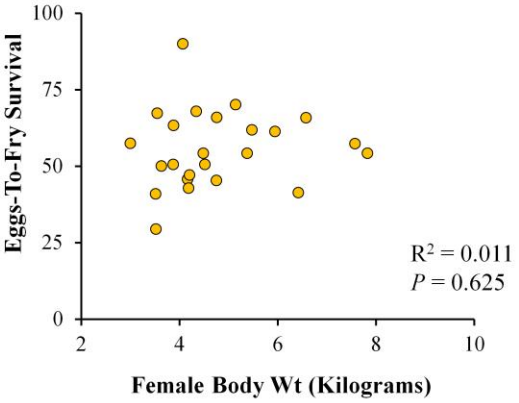
Female Chum Salmon



As with spring Chinook there was no relationship between spawning ground longevity and body wt in chum salmon females.

Effects of Female Size On Survival of Deposited Eggs

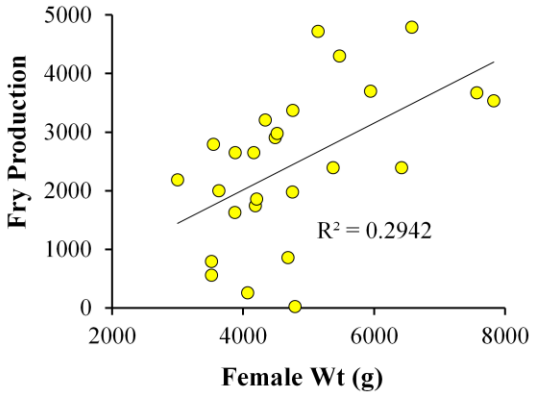
Spring Chinook Salmon



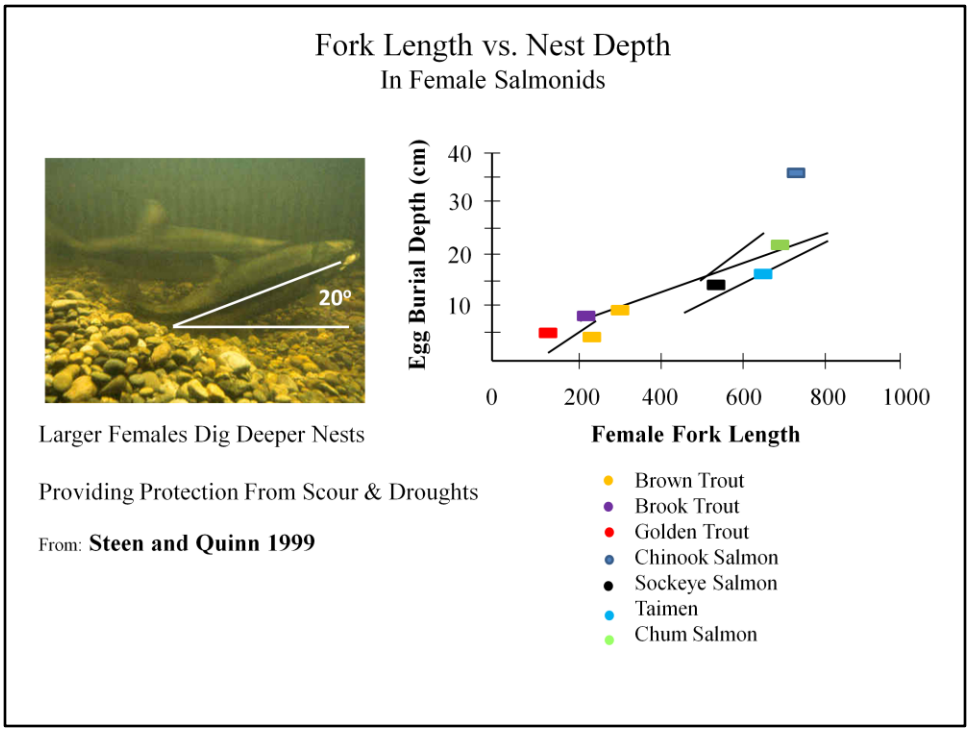
No relationship existed between female size and the survival of deposited eggs in spring Chinook. (for seven populations spawning in the observation stream at Cle Elum)

Female Wt vs. Fry Production In Naturally Spawning
Upper Yakima River Spring Chinook

No. Of Groups	7
R^2 Values	0.03 to 0.34
Mean Slope	720 fry per kilo



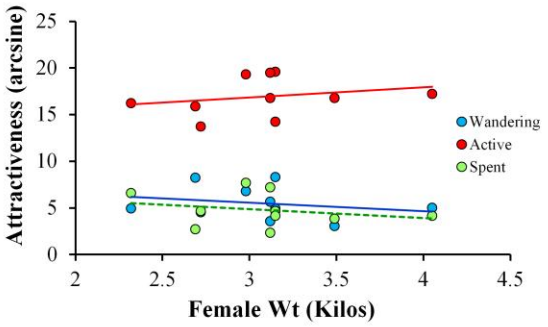
A significant but relatively weak positive relationship was found between female wt and fry production. Mainly because as we have seen, fecundity does go up with female size. In upper Yakima spring Chinook a 1 kg gain in body weight produced, on average, another 720 fry



There is a positive relationship between female length and the depth of the nests that are built. This appears to be the case across a broad spectrum of species. Females test the depth of their nests by performing probing activities. In one population of chum salmon, a 20° degree probe angle had to be reached before ovi-deposition would occur. Deep nests provide protection from scour and droughts

Effects Of Female Size & Behavior On "Attractiveness*"

Chum Salmon



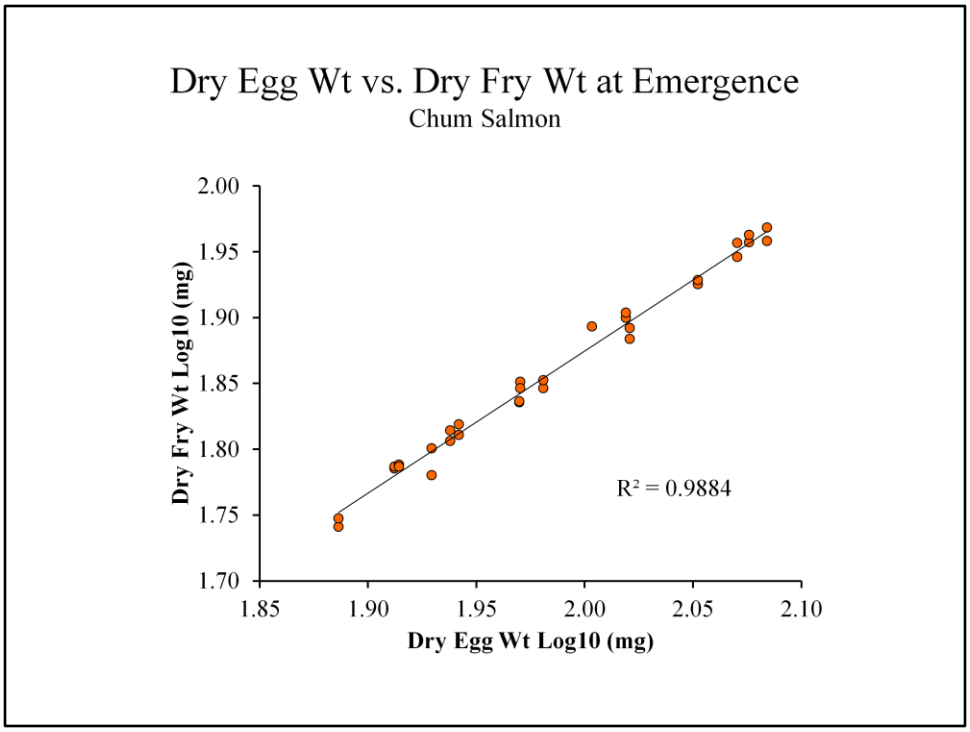
*% Of Males In A Population Courting Or In Close Proximity To A Female

The absolute size of a female had little effect on how attractive she was to a male, instead the reproductive status of a female (how she behaved) strongly effected how many males would attempt to court her or remain in close proximity

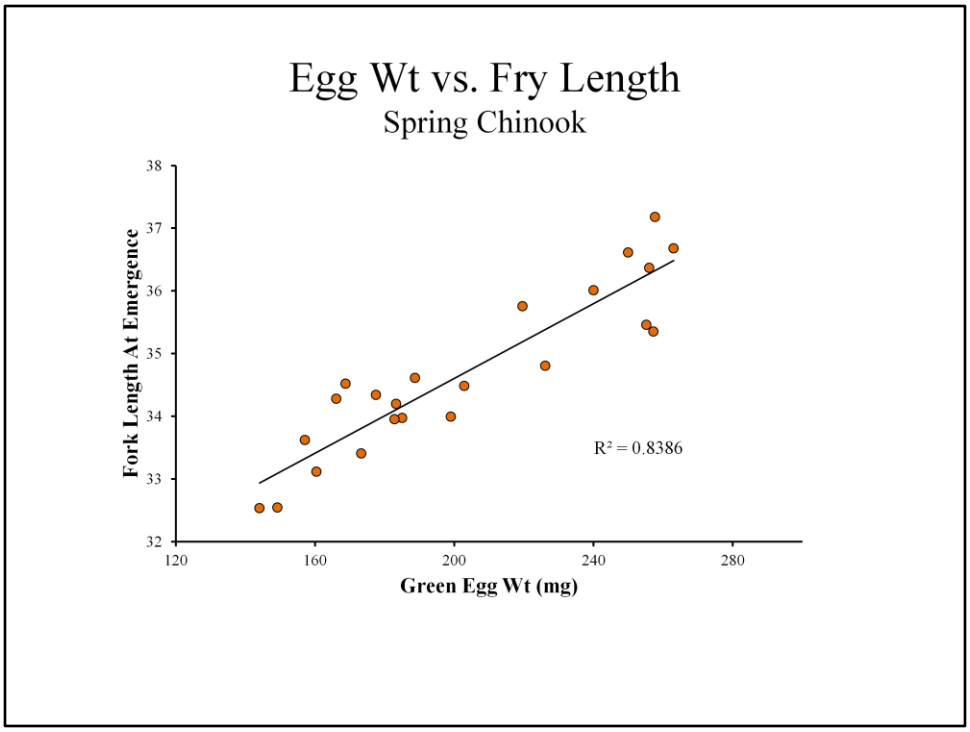
The Legacy Of Egg Size On Progeny Traits

- Size at Emergence
- Size After 100 Days Of Rearing
- Yolk Reserves at Emergence
- Rate of Development
- Duration of Emergence Period

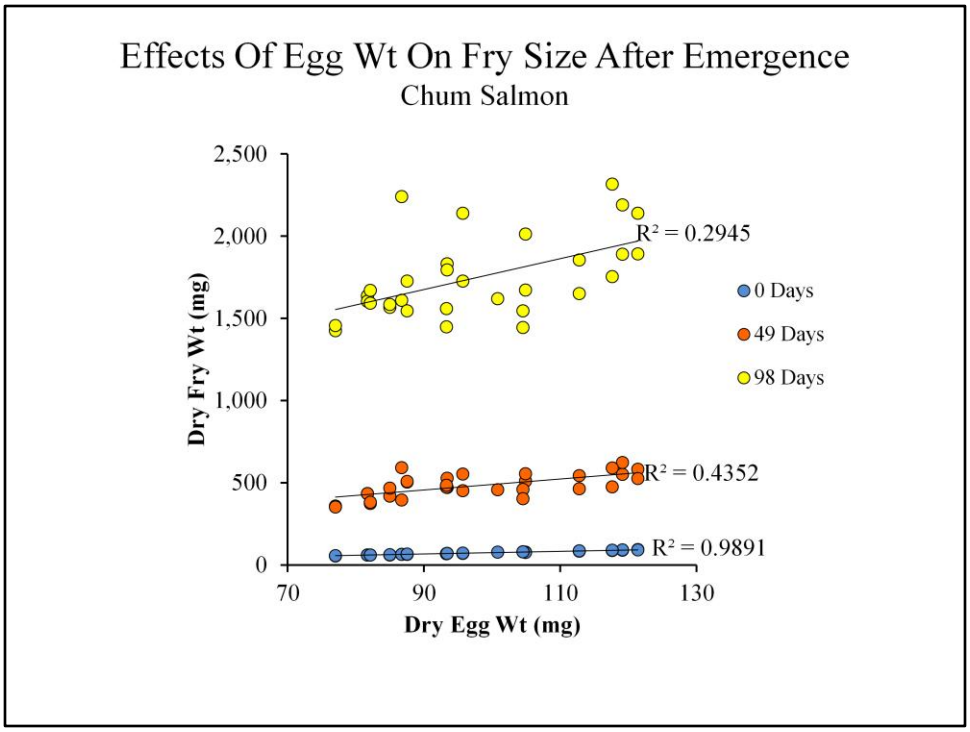
Not only do females make parental investments in territory acquisition, nest construction, redd development and defense they also provide significant nutrients to their offspring via the size of their eggs. The effects of egg size on a suite of juvenile traits is shown below



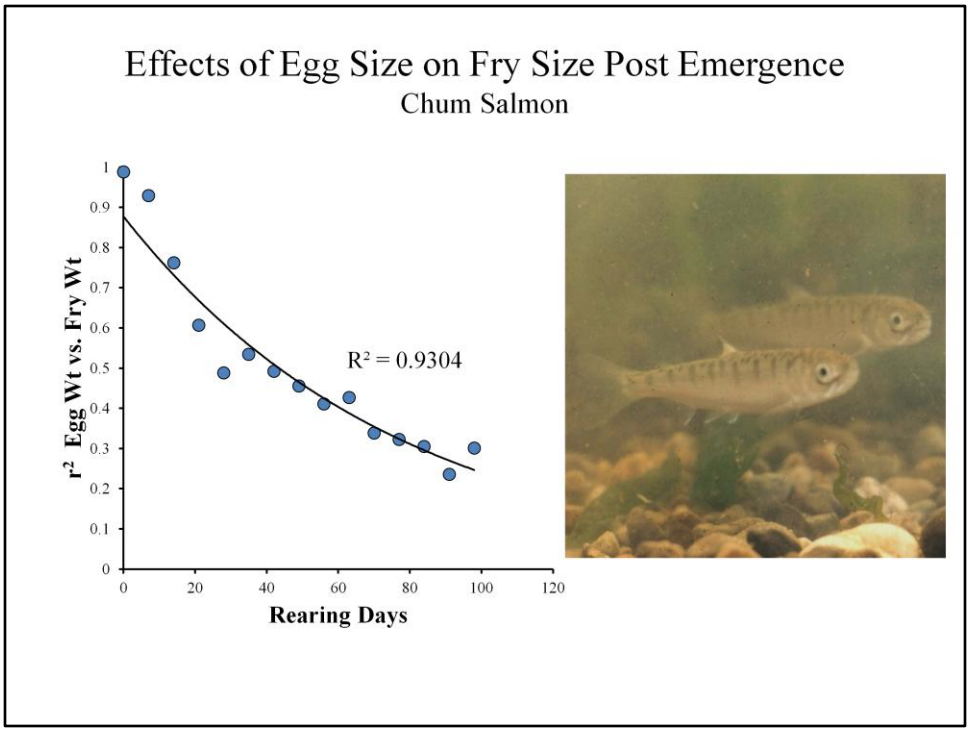
Egg weight has a significant effect on fry size at emergence. For this group of chum salmon almost all of the variation in fry weight could be explained by egg weight.



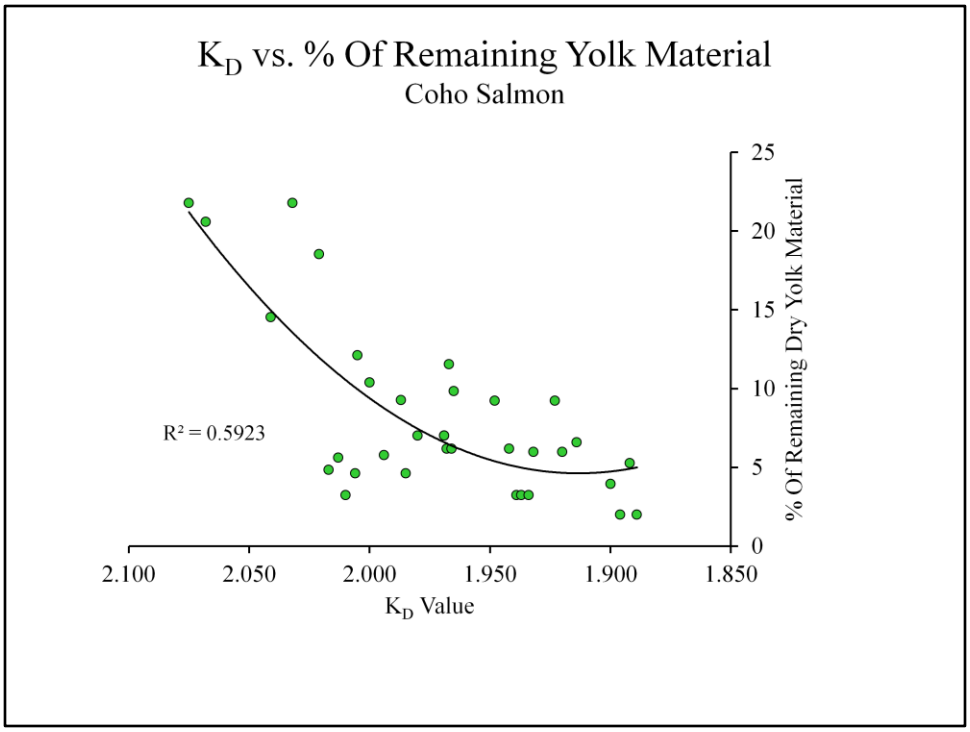
The relationship between egg wt and fry size appears to be universal in Salmonids, in this case, egg wt explains about 84% of the variation in fry length at emergence in spring Chinook salmon



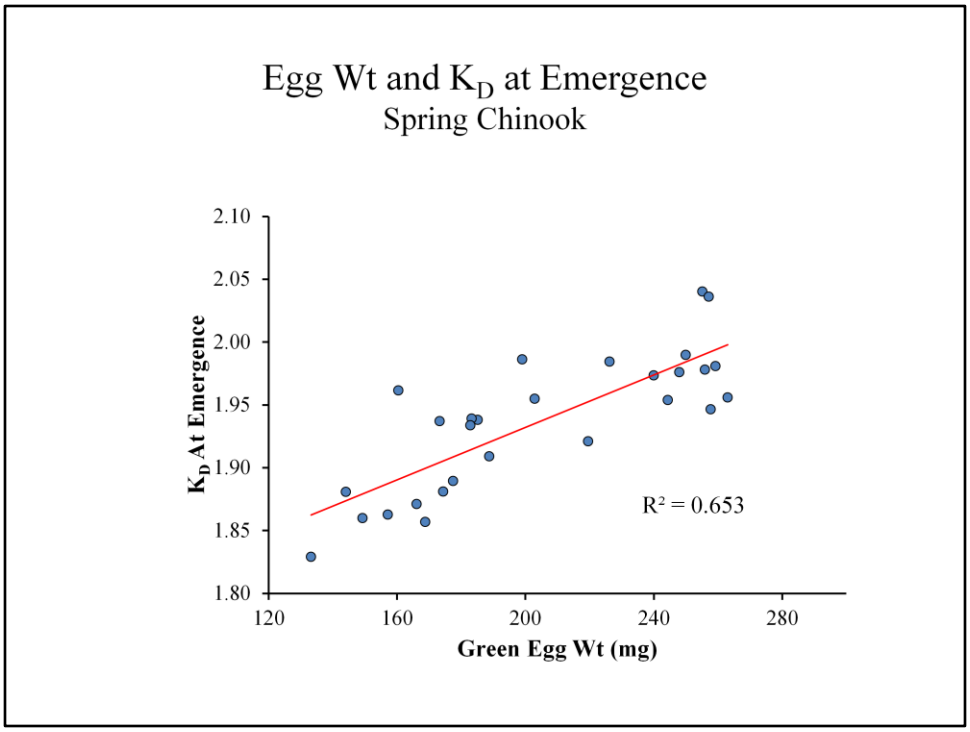
Not only does egg size influence fry size at emergence but it may have an effect on size during the juvenile period. In this instance you can see that egg size still explained almost 30% of the variation in chum salmon weight even 98 days after emergence.



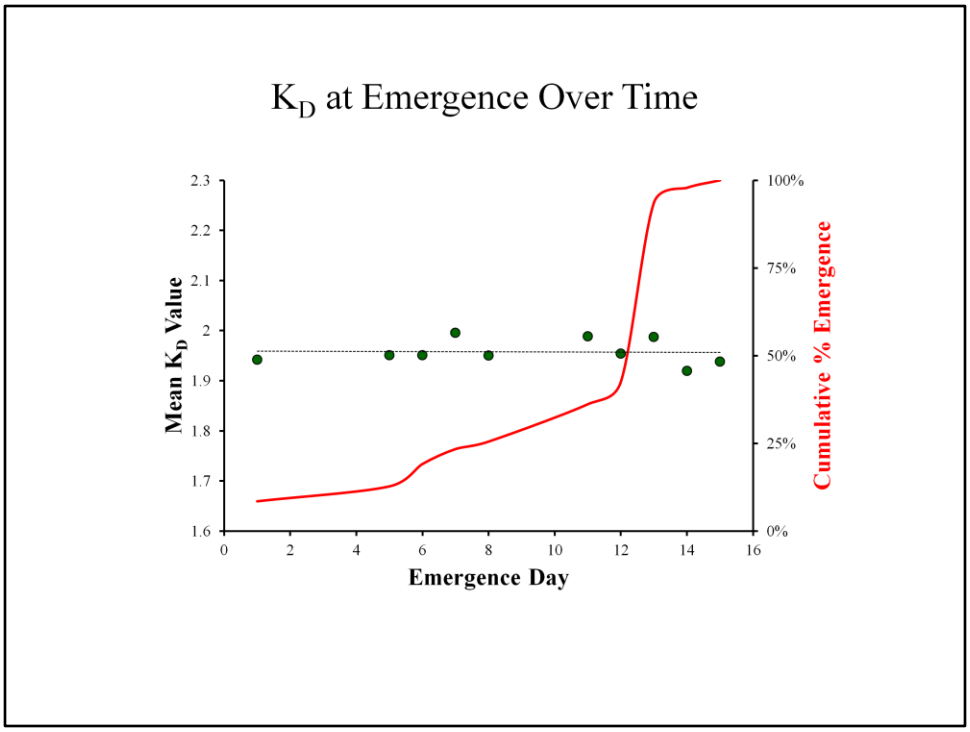
The influence of egg size on juvenile size decays exponentially over time – nonetheless, investments in egg size appear to have profound effects on fry size during one of the most vulnerable periods of juvenile life—the first 17 to 40 days post emergence where a significant portion of juvenile mortality due to starvation and predation takes place.



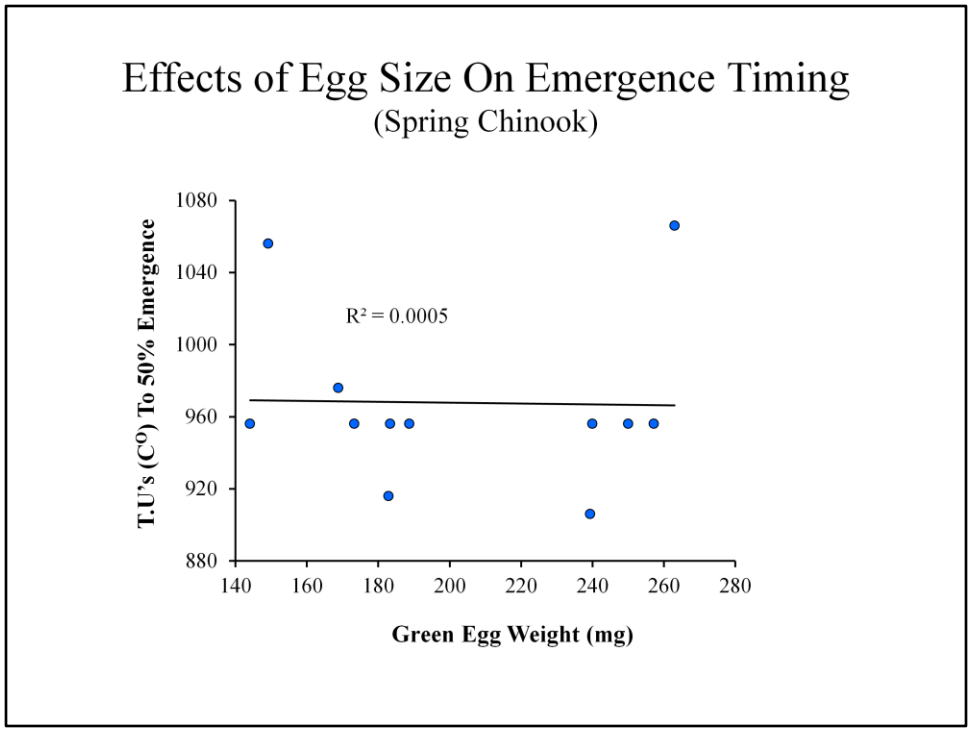
Robi Bams (1970) was one of the first researchers to develop a condition index for newly emerged fry which he called K_D. Here you can see the relationship between remaining yolk material in an alevin and its K_D value. Fry with high K_D values have greater amounts of yolk material than those with lower values.



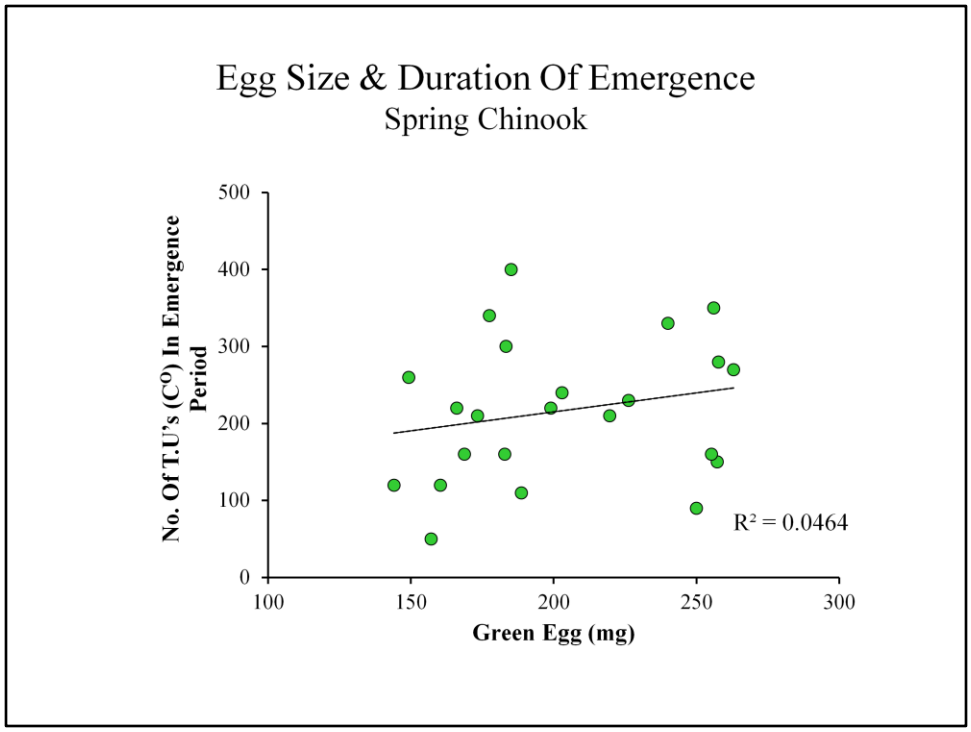
Not only are juveniles produced from large eggs bigger but they also possess more yolk reserves at emergence than those produced from smaller eggs. This means that they have a greater capacity to resist starvation during early post-emergence life.



The K_D values of fry produced from the same family but emerging at different times remain relatively stable across an entire emergence period. This is likely an adaptation to potentially dynamic rearing conditions—allowing a female to release her juveniles over an extended period of time. Moreover, this relationship changes by race and population suggesting that yolk reserves at emergence is an important survival trait.



Egg size does not influence emergence timing



Nor does it influence how long fry from a single male x female mating take to develop and emerge

Large Egg Legacies

Decreased Risk Of:
Starvation & Predation

Due To Increases In:

Social Dominance & Territory Acquisition

Potential Prey Items

Swimming Speed

Stamina

In general, juveniles produced from large eggs have a decreased risk of starvation and predation because of differences in social dominance, availability of a greater range of potential prey, greater swimming speed and stamina.

Are There Optimal Female Sizes/Ages?

"A wide range of female sizes is normally present in any spawning population "

"We could find no evidence that the eggs of large females consistently survived better than small females"

"We were unable to demonstrate that the reproductive success of large females was consistently higher than that of small females"

Holtby & Healey (1986)

Given that large females are more fecund, produce in general larger eggs, and dig deeper nests is there an optimal female age and size for each population. The simple answer is no.

Are There Optimal Female Sizes/Ages?

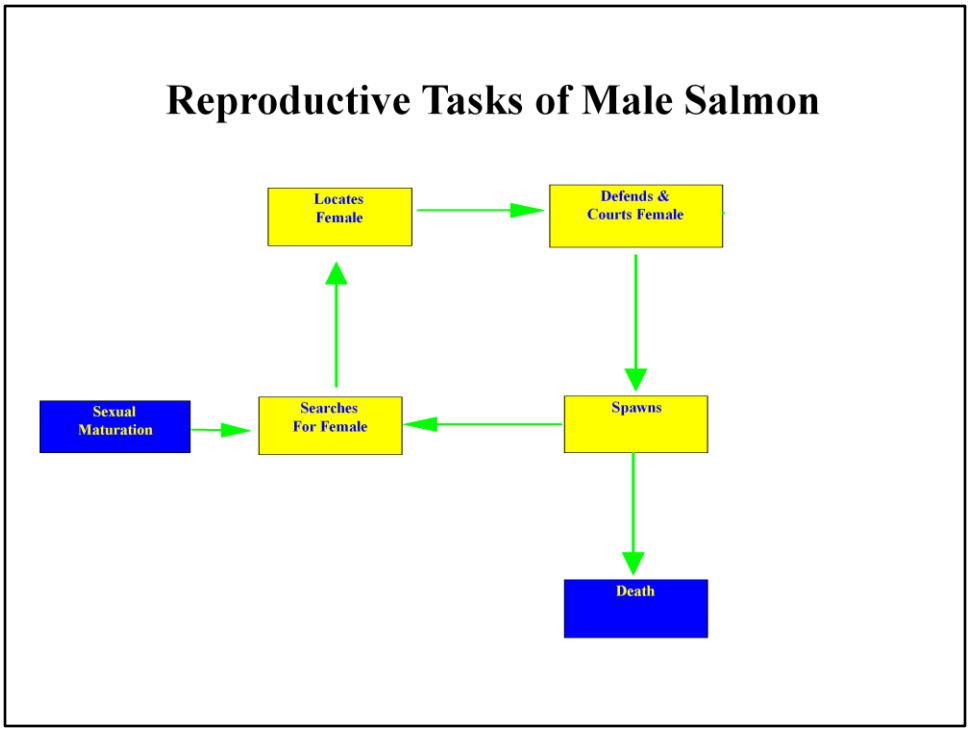
"The relative frequency of large and small females in a population [is] driven by spatial variation in gravel quality and by temporal variation in discharge"

"**Some combination of sizes and ages confers greater fitness than a single age or size**" (Healey 1987)

"…little of the variation in offspring number was explained by female size…although smaller females tended to have fewer YOY offspring"

"…fitness may be equal among females of various sizes or may be explained by variation in nest site characteristics" (Seamons et al. 2003)

This occurs because of the interactions that transpire between a female and her offspring with the dynamic environmental conditions they experience during spawning, incubation, and juvenile freshwater residency. Environmental conditions will favor some fish (genotypes/phenotypes) over others and since the environment is constantly changing in a relatively unpredictable fashion there is no ideal strategy. Instead, Mike Healey probably expressed it best when he wrote that "some combination of female sizes and ages [will] confer greater fitness than a single age or size" The key then for us, as managers, is to provide a diversity of female sizes and ages on a spawning ground.

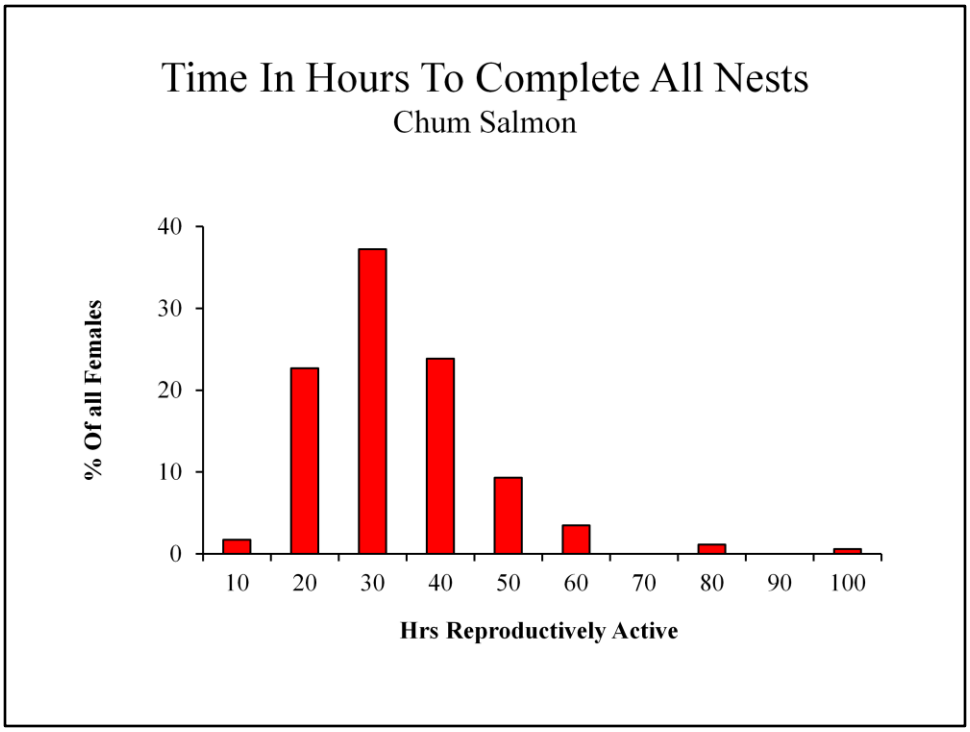


The reproductive tasks for males are much simpler than those for females. Once they reach maturity their goal is to find receptive females, court and defend them, spawn, and begin the cycle again until they are energetically depleted.

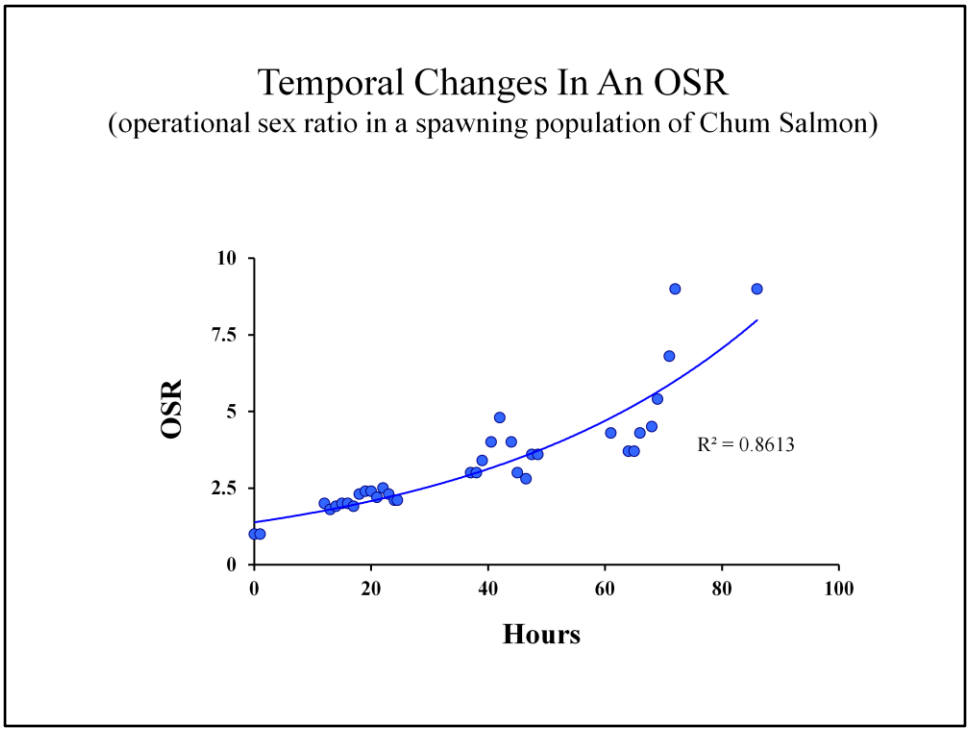
Reproductive Activity Level For Males

Males Are Reproductively Active For About 90% Of Their Spawning Ground Residency.

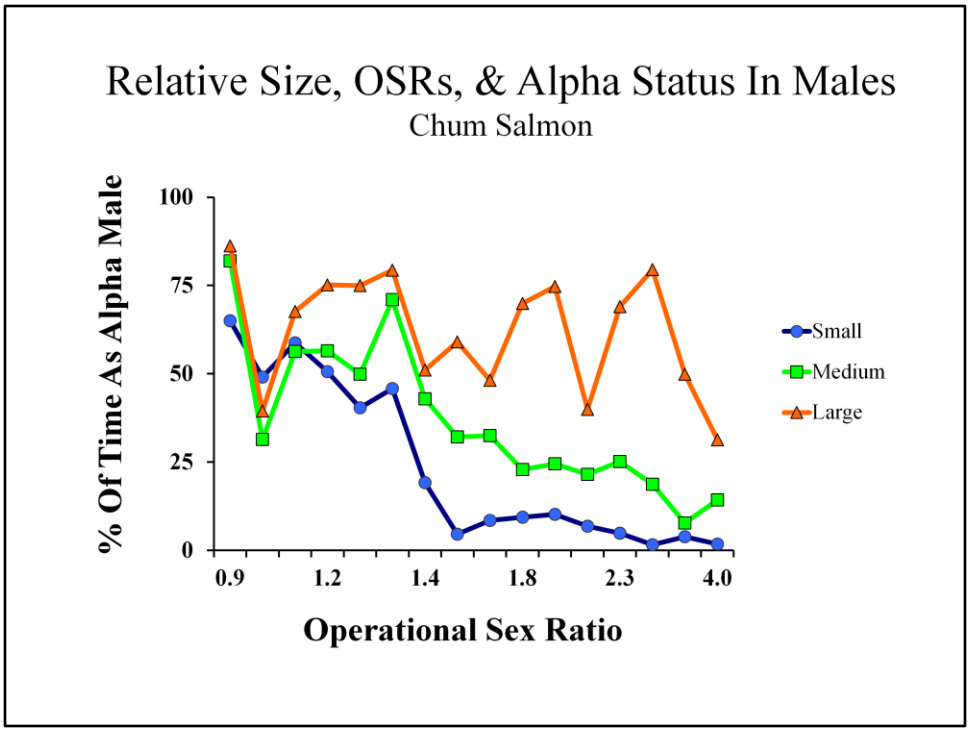
Males remain reproductively active for about 90% of their spawning ground residency



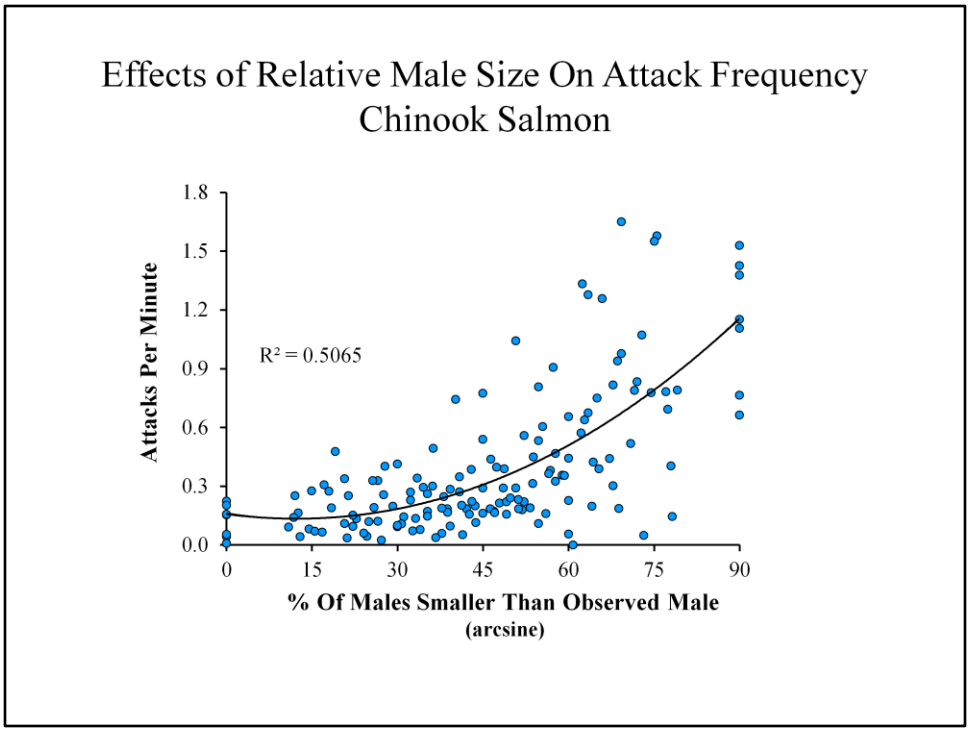
Contrary to males, females are reproductively active for a relatively short period of time, because once they establish a territory total egg deposition may occur over a 1 to 2 day period.



This difference in reproductive life times in males and females means that male competition for females will escalate over time. One measure of male competition for females is the operational sex ratio which equals the number of sexually active males per female in a population. In this population the OSR rose exponentially over time.



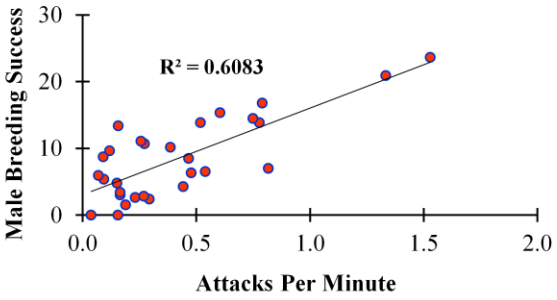
When competition among males is low then every male may have access to an active female. As OSR's rise then male size becomes increasingly important in determining who is able to be a primary courting male. At high OSRs competition will occur among the largest males for alpha status.



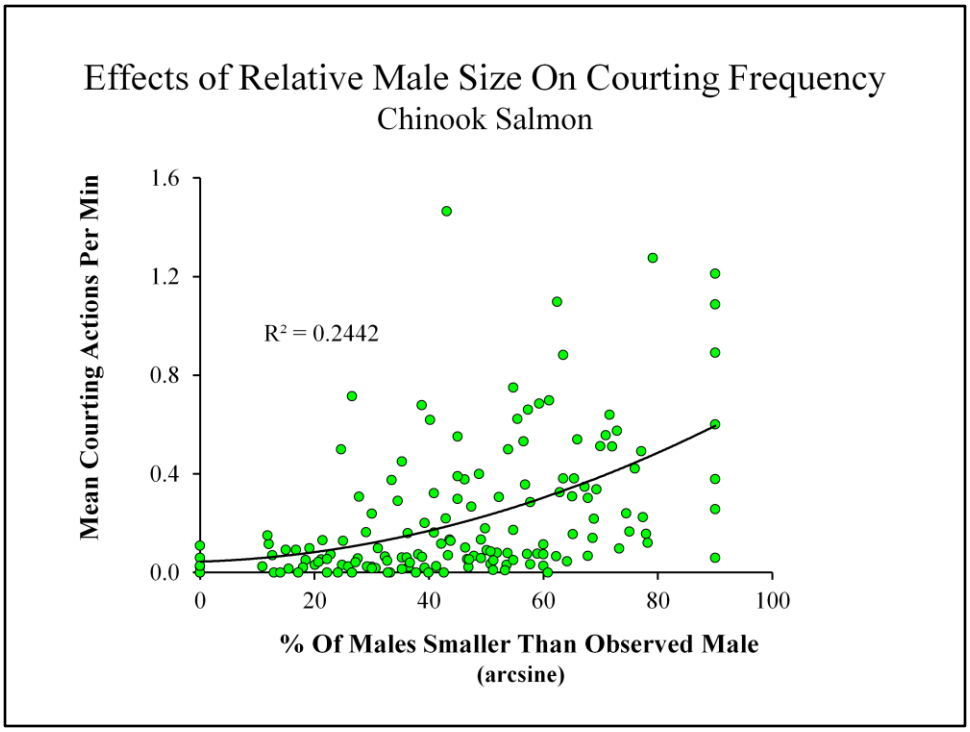
Males will attack rivals in an attempt to drive them away from the females they are courting. Size plays a significant role in how often males attack potential rivals

Attack Frequency vs. Breeding Success

Male Spring Chinook Salmon

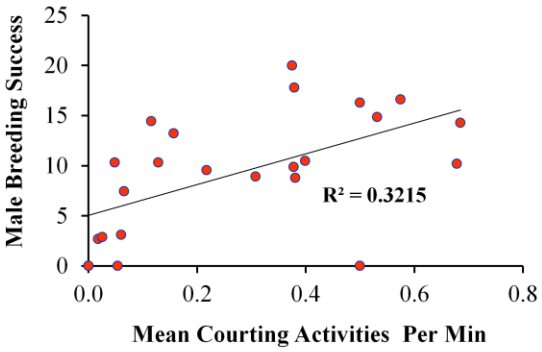


And attack frequency is also closely linked to breeding success in spring Chinook males

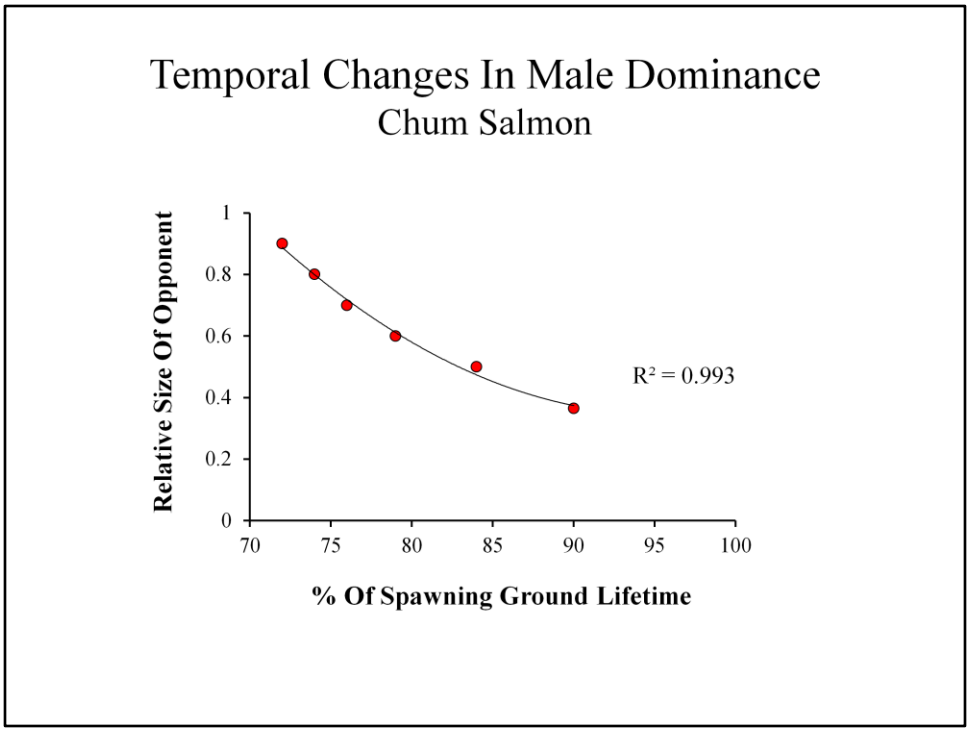


Like attack frequency, the ability to court females was positively correlated to the relative size of a male.

Courting Frequency vs. Breeding Success
Spring Chinook



And as might be expected there is a positive relationship between courting frequency and male breeding success



As males remain on spawning grounds they become progressively weaker due to their energy expenditures. Size does however seem to convey a long lasting effect as males can defeat opponents 9/10^{ths} of their size for 70% of their spawning ground residency, as they continue to age their ability to defeat newly arriving opponents decreases.

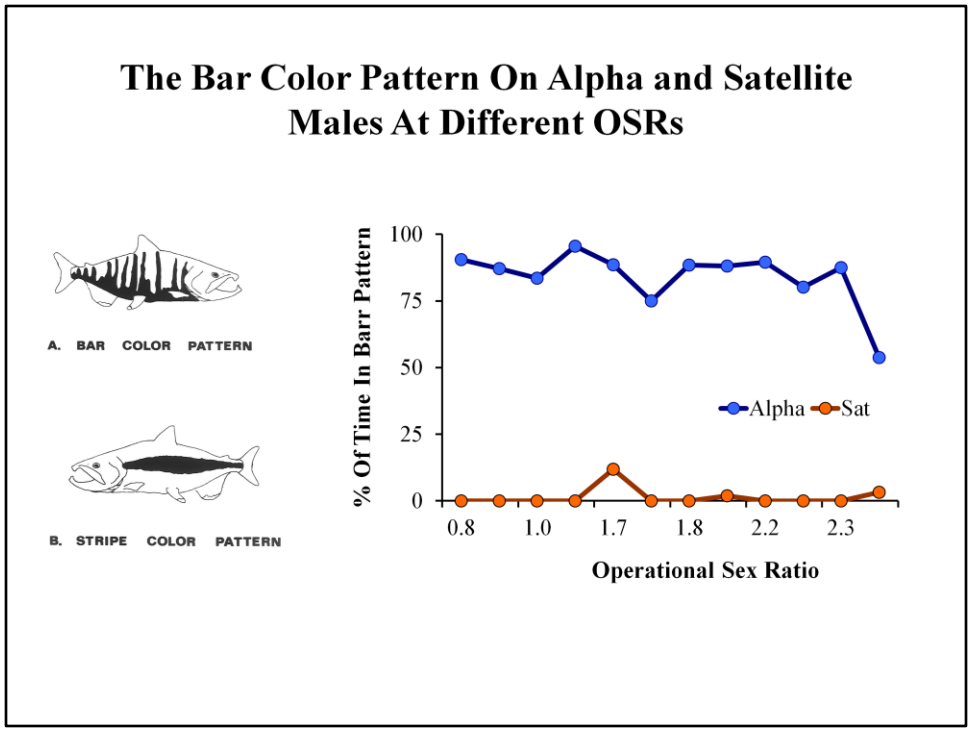
Color Patterns, Social Status & Epigamic Selection

" Black" & "Stripe" Patterns: Chinook

"Stripe" & "Bar" Patterns: Chum Salmon

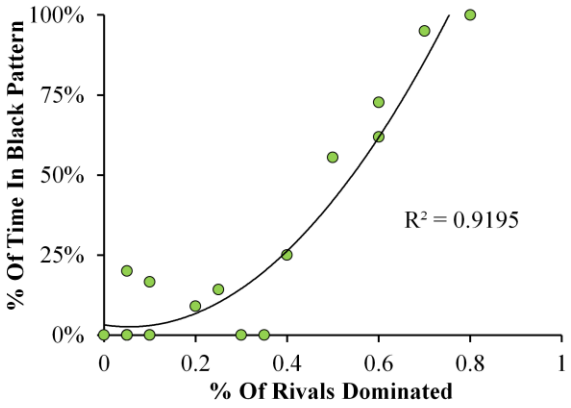
"Stripe" Pattern : Jack Chinook

Males may also be subjected to epigamic selection or mate choice by females. Spawning salmon are known for their color patterns some of which can be linked to the behavioral status of an observed fish. For example, socially dominant chum salmon males have the bar pattern while dominant Chinook salmon males turn a uniform dark brown to black. Territorial females and subdominant males in both species develop a single dark longitudinal stripe.



Dominant courting chum salmon males are typically in the bar pattern while satellites use the stripe pattern

Relationship Between the Black Color Pattern & Social Dominance: Male Spring Chinook Salmon



The black color pattern in male Chinook salmon is also linked to social status, as males that are socially dominant are often observed using the black pattern

Epigamic Selection

Chum Salmon

Female Responses To Different Male Phenotypes (Time Needed To Complete A Nest In Min)		
Type Of Pair	**First Nest**	**Second Nest**
Male < Female	240	170
Male = Female	129	123
Male > Female	107	140

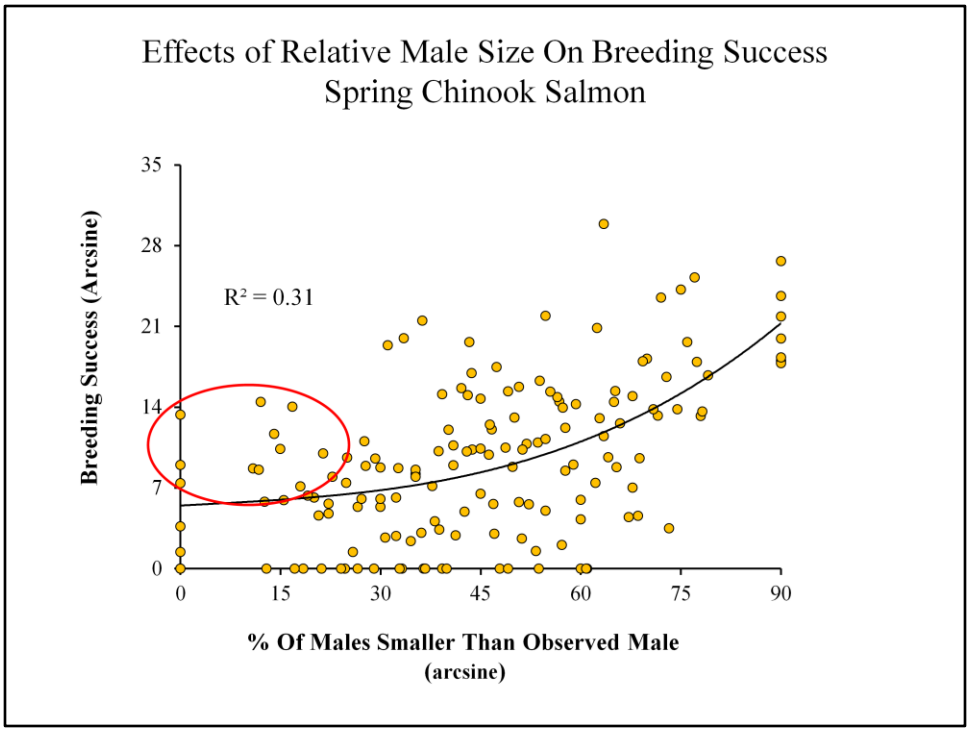
Female chum salmon delay nest construction and spawning when courted by males smaller than themselves and similar delays in spawning have been observed in Chinook (Berejikian et al. 2000) and sockeye (Foote 1989). They may also regulate the number of eggs they deposit during a spawning.

Epigamic Selection

Chum Salmon

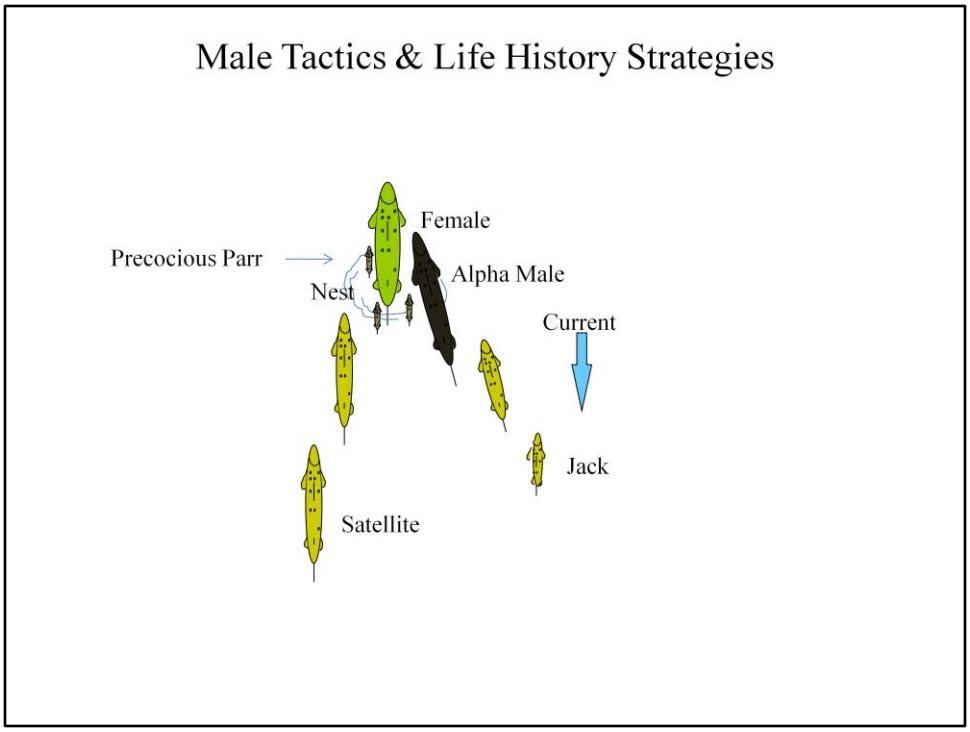
Female Responses To Different Male Phenotypes (Time Needed To Complete A Nest In Min)		
Color Pattern Of Male	**First Nest**	**Second Nest**
Bar	138	120
Stripe	163	203

Female chum salmon also delay nest construction when courted by males with stripes

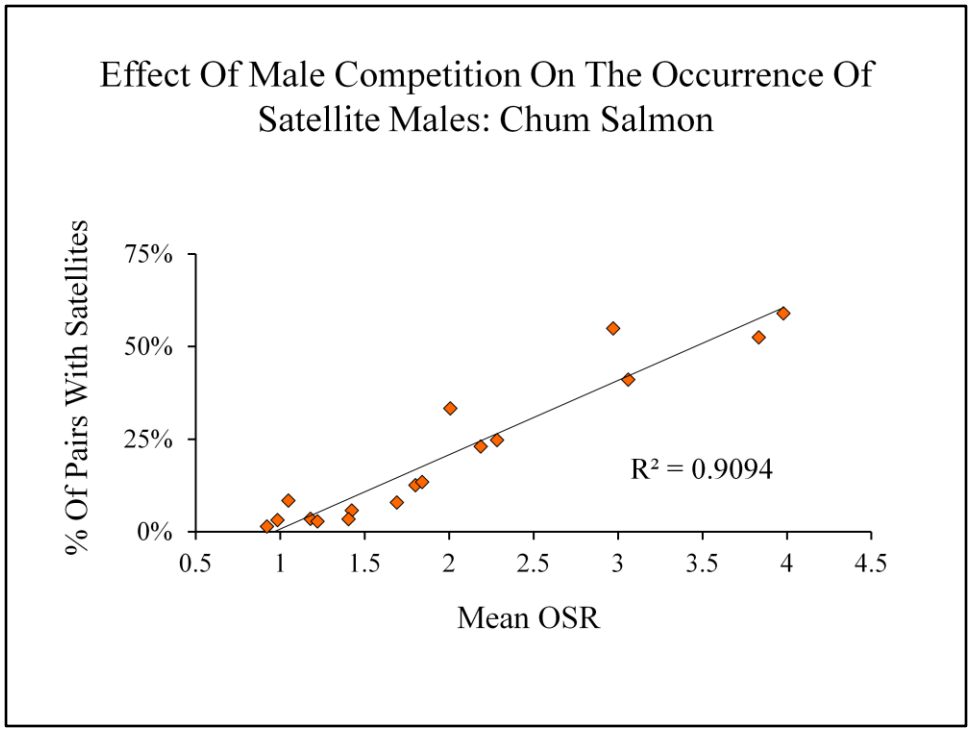


About 30% of the variation in male breeding success can be explained by size. This might seem a little lower than we would expect due to the advantages that relatively large males apparently have when competing against smaller rivals and on the preferences that females exhibit toward large and socially dominant males

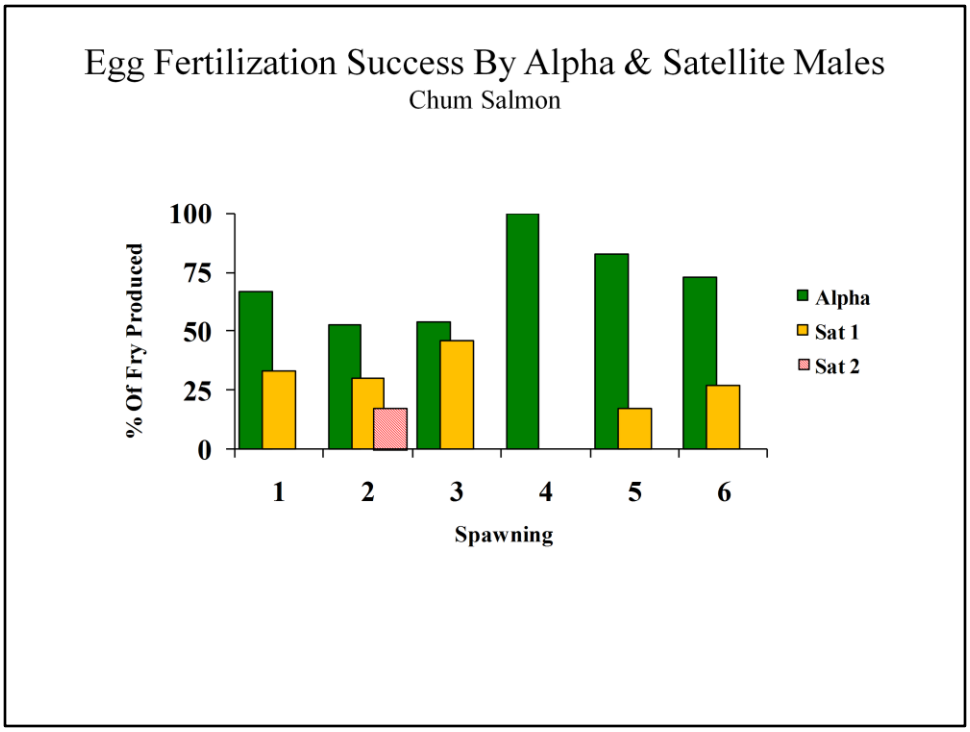
However, as you can see, some males, despite their relatively small size are remarkably successful. How do they do it?



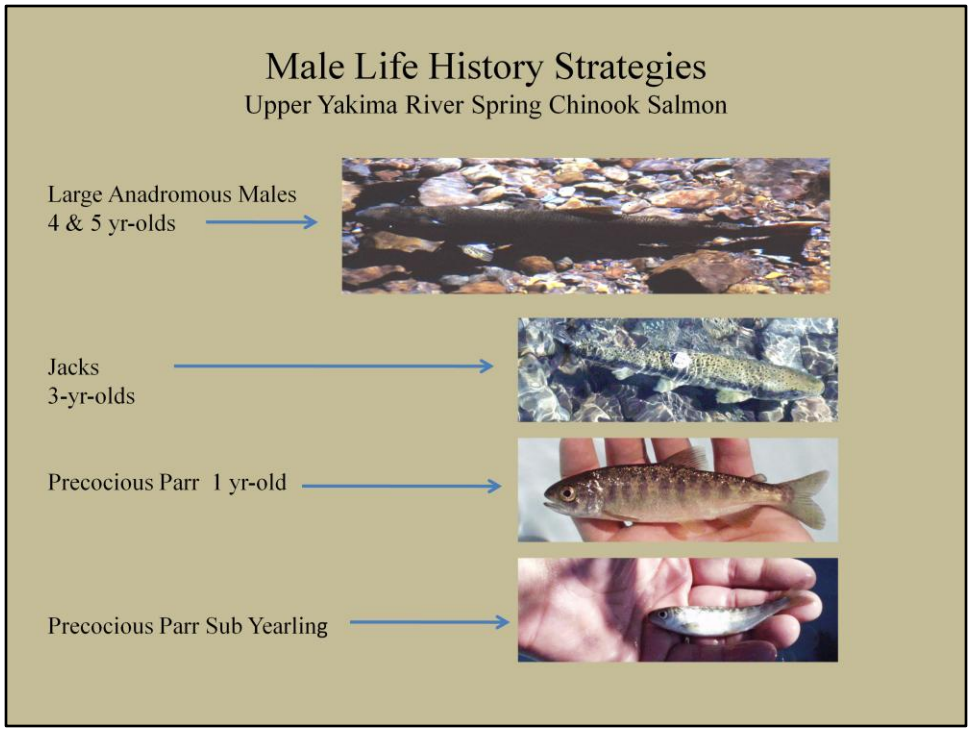
Both behavioral tactics and life history strategies are used by males to circumvent the effects of intra-sexual competition and mate choice. For example the satellite strategy is used by subdominant males in order to fertilize eggs and produce offspring. In some salmon species, precocious parr and jacks are life history strategies that are employed for the same purpose



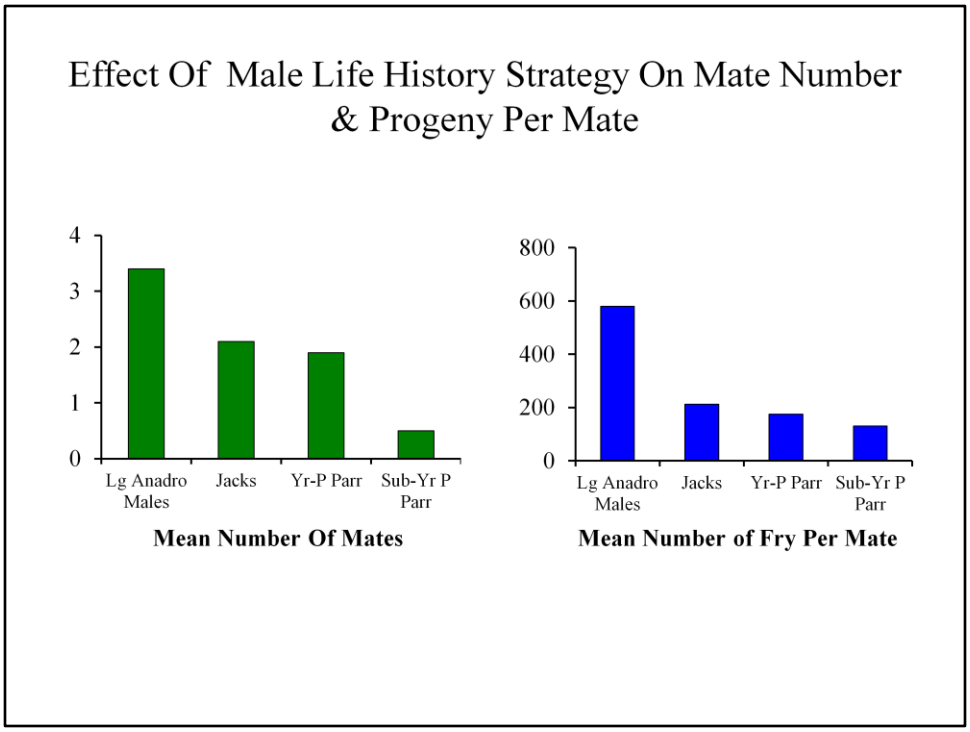
Satellite behavior is probably a BBS tactic, here you can see that the number of spawning pairs with satellite males increases as the OSR in a population rises.



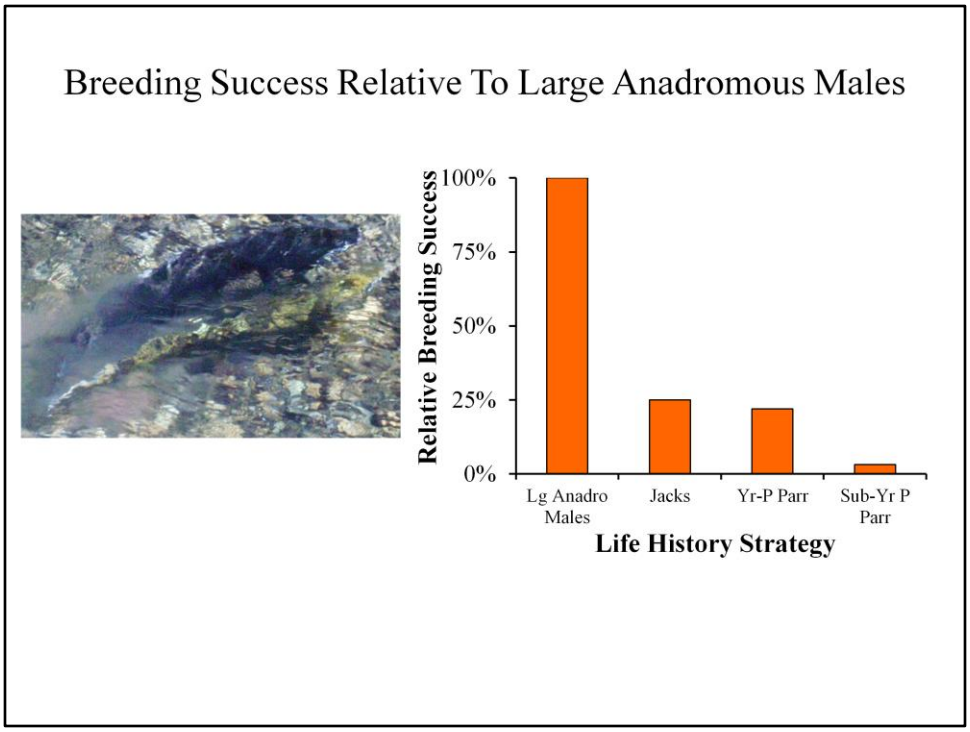
The satellite strategy does work, if a satellite male can participate in a spawning they will on average fertilize about 25% of the deposited eggs.



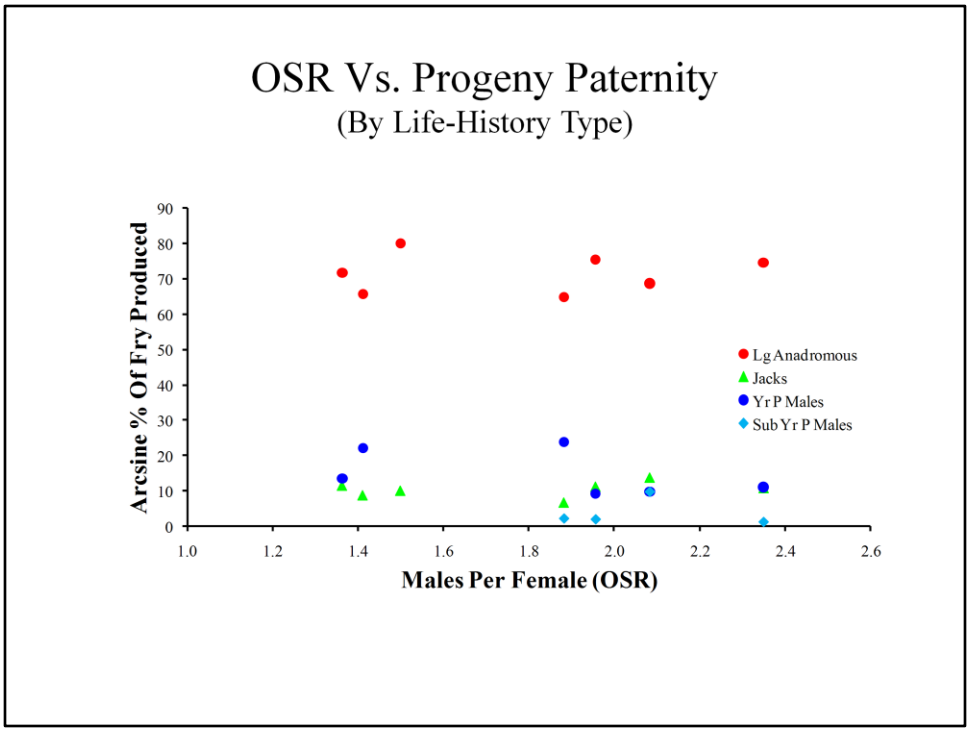
Males may also use different life-history strategies to fertilize eggs and produce offspring. In upper Yakima spring Chinook four male history strategies exist, two of which are anadromous, in one, males spend two or more years at sea returning at age 4 and 5. In the other anadromous strategy "jacks" spend a year at sea. Two non-anadromous strategies also occur, in one males rear in freshwater for 16 to 18 months before becoming mature while in the other they rear for just 6 to 7 months before reaching maturation.



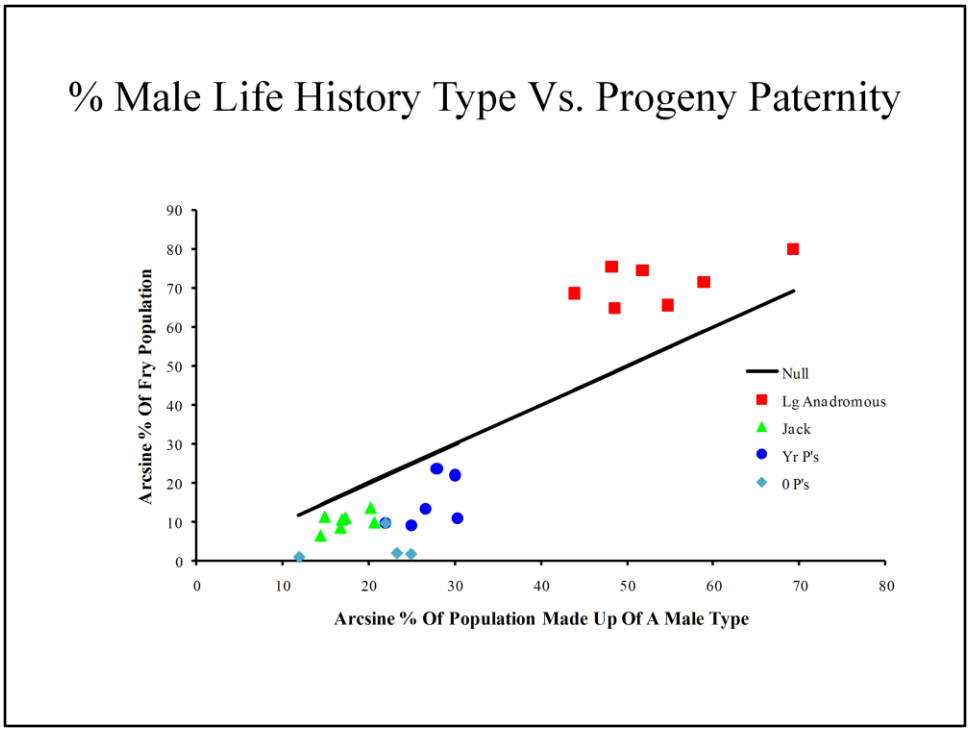
There are differences in the breeding success of males using each of these life history strategies. Breeding success is directly related to the number of females each male is able to spawn with and the number of progeny they produce per mate. Here you can see that Large Anadromous males mate with more females and produce more offspring per mate than any of the other life history types.



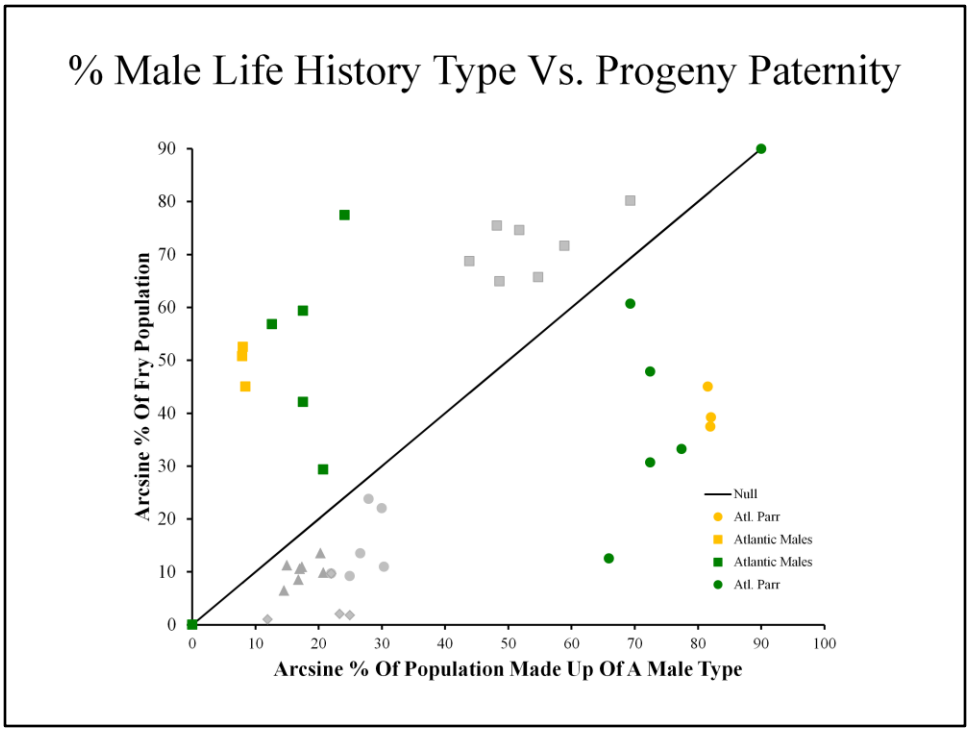
Taking the information just seen it is possible to compare the relative breeding success of each male life history type. In our studies, jacks and yearling precocious parr had equivalent breeding success values which were about 25% of that achieved by large anadromous males. Sub-yearling parr are about 3% as effective at producing fry as the large anadromous males.



So how many offspring might these different types of males produce in a spawning population? One factor that will influence how many progeny males in a life history strategy produce is the OSR that exists on the spawning ground. At very low OSRs every male type is expected to be equally successful. In the OSR ranges we examined, large anadromous males consistently produced about 90% of all the progeny.



Another factor that can influence the proportion of offspring produced by a male life history type is their prevalence in the population. If each male life history type was equally successful at producing offspring then we would expect the percentage of fry fathered by males of each type would be the same as their occurrence in the breeding population (which is represented by the black line). As you can see this is not the case. Instead, even when over 50% of a population was made up of jacks and precocious parr, Large Anadromous Males still produced about 90% of the offspring. This graph begs the question, what would happen if fewer and fewer males on a spawning ground were large anadromous individuals?



Data from studies on Atlantic salmon suggest that even when just 2% of all the males in a spawning population are large anadromous males they were still able to produce up to 50% of the offspring from a population. Our data suggest that when at least 50% of the males present on a spawning ground are large males they will produce about 90% of the offspring.