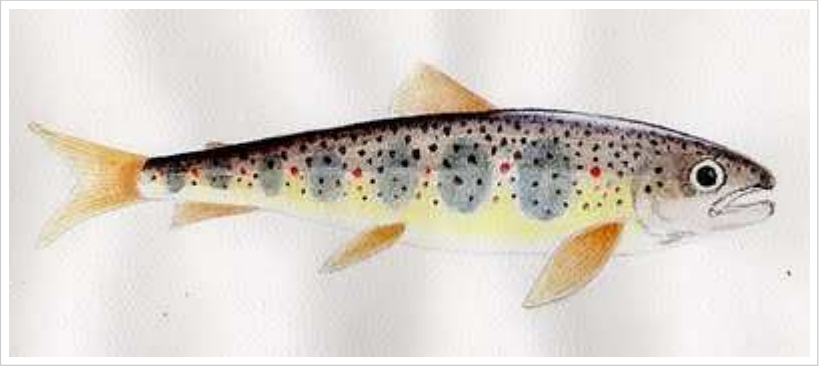
MONDAY, SEPTEMBER 28, 2009

Revenge of the Nerds: The Story of Precocious Atlantic Salmon Parr



Native Atlantic salmon parr, Bond Brook, Kennebec River, Augusta, Maine. Watercolor, gouache and pencil. Douglas Watts, 1999.

By Douglas Watts
Augusta, Maine
September 2009

A fascinating aspect of Atlantic salmon is the existence of precocious parr.

Atlantic salmon live in the streams where they were born until they are two years old. In the spring of their third year, when they are 6-7 inches long, they turn bright silver, their kidneys and other organs undergo a profound change to let them live in saltwater, and they head out to sea for two years, whereupon they return to their natal stream to mate and spawn as 8-15 pound adults.

But some male Atlantic salmon take a different path. In the fall of their second year, they become sexually mature while still only the length of a dollar bill. Because baby salmon in freshwater are called "parr" (a very old Scottish word), these prematurely sexually mature males are called precocious parr.

In any given Atlantic salmon river, only a small number of the baby male salmon become precocious. Most do not develop testes and sperm (fish sperm is called "milt" and looks much like human semen) until they are 4 years old and have spent two years at sea.

The existence of precocious Atlantic salmon parr offers an

The existence of precocious Atlantic salmon parr offers an insightful window into the mechanics of evolutionary biology. To look into this window, we need some background on the basics of the Atlantic salmon's life history.

Atlantic salmon are anadromous fish, which means they are born in freshwater but spend most of their adult life in saltwater, returning only to freshwater to mate and spawn. Atlantic salmon adults have developed an amazing ability to return from their two year stint in the ocean to almost the exact river or stream (or river and stream section) where they were born in order to mate and spawn. How salmon do this is still not known, but smell is considered the most likely candidate. Somehow, salmon can remember the "smell" of their birthplace and unerringly follow it back to where they were once babies. Other anadromous fish such as alewives and shad also share this "homing" ability.

Most Atlantic salmon return to their home rivers in the spring and summer of their fourth year, having spent two years in freshwater and two years in saltwater. In the late fall, the female salmon select nesting sites in the shallow tails of large pools in their natal rivers. These sites are chosen with great care because the fertilized eggs of salmon must remain in the riverbed for 5 months, from late fall to the next spring, before hatching into baby salmon. To build the nest for her eggs (called a "redd," another Scottish word), the female turns on her side and vigorously flaps her tail and body to create a powerful current of water directed at the stream bottom. The force of this jet of water causes the stones on the stream bottom to become momentarily suspended in the water column, whereupon the stream current carries them a short distance downstream. As you can imagine, for this technique to work, the female must choose a nesting site with just the right sized stones (about the size of tennis balls) and with enough current to carry them a small distance downstream once they are dislodged by the shaking of her tail. These sites are invariably located at the end of a pool, just above a small riffle or rapids, where the water becomes shallow and current begins to accelerate before it spills over the riffle just downstream.

This photo shows a 30 inch female Atlantic salmon turning on her side and digging her second redd in Bond Brook, Kennebec RIver, Augusta, Maine. Her first redd is visible at the far right.

After many hours of turning on her side and fanning the water vertically, the female creates a depression in the stream gravel that is roughly 1.5 - 2 feet in diameter and 1 foot deep, with excavated stones in a loose pile just downstream. It is at this point that she selects a male salmon as her partner. The male and female salmon, positioned alongside each other, pointing upstream with their sides touching, then go into a series of brief, quivering mutual orgasms which culminates in the female discharging her eggs into the depression in the gravel and the male simultaneously discharging his milt onto them. Both the eggs (which are the size of small peas) and the milt are somewhat heavier than water, and if everything goes right, the sexual act ends with a kettle-sized depression in the gravel filled with several hundred eggs blanketed and covered in pearlescent milt. This is repeated until the female determines that the depression is sufficiently filled with eggs. She and the male then break off and the female swims a few feet upstream of her nest and repeats the digging process with vigorous beats of her tail. But this time, the female is not trying to dig a nest, she is instead dislodging the stones so that the current will carry them downstream and fill in her egg-filled nest. By repeating this process for several hours, her nest becomes a humped pile of river stones with the eggs safely nestled at the bottom of a sizeable pile of loose, clean gravel. Because most female salmon carry 7-10,000 eggs, far more than one nest can accommodate, the female then digs a second nest and spawns again until she has laid all her eggs.

This photo shows a female Atlantic salmon at left, on her side digging her redd, while a large male (34-36 inches) in the center of the photo "guards" the female and her redd from other males. At the moment this photo was taken, the female had curved her body into a horseshoe and made a powerful downthrust with her tail to dislodge stones from the stream bed. The cloud of sediment from her downthrust can be seen just to the left of the male. Close examination of the male shows his distinctive pink and brick red coloration along his flanks. Large male salmon take on this color only when they are spawning. Just to the right of the male salmon is a 12 inch brown trout, which illustrates how big the male salmon is. Bond Brook, Kennebec River, Augusta, Maine, Nov. 1, 1996.

The 30 inch female salmon fully on her side at the beginning of her digging thrust. A 12 inch male brown trout can be seen in the lower right hand corner of the photo. Brown trout and Atlantic salmon are very closely related species and for this reason, male brown trout respond to the pheromones released by spawning female Atlantic salmon and will try to mate with them.

Like many animals, male Atlantic salmon aggressively compete with each other for the right to mate with females. Male salmon compete by "claiming" a female as she is digging her nest and then trying to drive all other interested males away from the nesting site. While male salmon do not bite each other, they will use their heads and snouts (which become curiously enlarged and curved at spawning season) as battering rams to "head butt" a particularly obstinate competitor. As a rule, the larger male tends to win these competitive displays and the smaller male (or simply less aggressive male) moves away to find another available female or to wait on the sidelines for a rematch. In cases where three or more males are vying for one female, these competitive matches are tumultous, with the male salmon chasing each other up and down a pool and in the shallows. This frenzy can continue for several days, especially if additional males arrive in the area after being driven off by other males at nests up or downstream, or as fresh males arrive from the ocean. The male battles only end when all the females in the area have spawned.

Enter stage right our little friends, precocious parr. Precocious parr are sexually mature male Atlantic salmon, but are only the length of a dollar bill. They are only two years old (rather than four), and have never gone to the ocean. Adult male salmon which have gone to sea and back are big fish, anywhere from 28-44 inches long and weighing from eight to 40 pounds. They have swam from their home rivers more than 2,000 miles to their marine feeding grounds near Greenland and back, growing from 7 inches long to nearly 3 foot long in just two years. Most of their compatriots on this long migration did not survive, but were eaten by larger ocean predators at some point in their journey. These large males are the veterans, the survivors, are in the peak of condition, have a tummy full of milt and only one objective: to win a female salmon against all competitors and to pass along their genetic legacy.

So how does a precocious salmon parr that weighs a few ounces and is barely the length of an adult salmon's tail have any chance of competing for and winning a female? Isn't this totally wacky?

Precocious male salmon parr do this by using their tiny size as an asset. Their secret weapon is as comical as it is effective. Here's

the secret: during all of the time the big, giant male salmon are chasing each other around, fighting and vying between each other for "possession" of the female salmon and her nest, the precocious parr wait in the wings for the big males to be preoccupied with fighting other and then stealthily swim into the nest itself and sidle up alongside and underneath the female's abdomen, much like how a remora swims underneath the belly of a shark. Then they wait.

The only time I have seen precocious parr mate with a female salmon is when there were also large males around, and a large male with the female. In these cases the precocious parr sidles up underneath the female's belly, waits for the female and large male to simultaneously emit eggs and milt and then the precocious parr emits his (much smaller) package of milt at the same time, which then settles into the nest with the eggs and the large male's milt. Interestingly, even though the tiny parr has a lot less milt to squirt onto the eggs than the large male, his abdomen is much closer to the eggs, because he positions himself underneath the female which places him just a few inches above where the eggs are deposited.

Sunrise on the Kennebec River at Hallowell, Maine.

Evolutionary Persistence of Precocious Parr

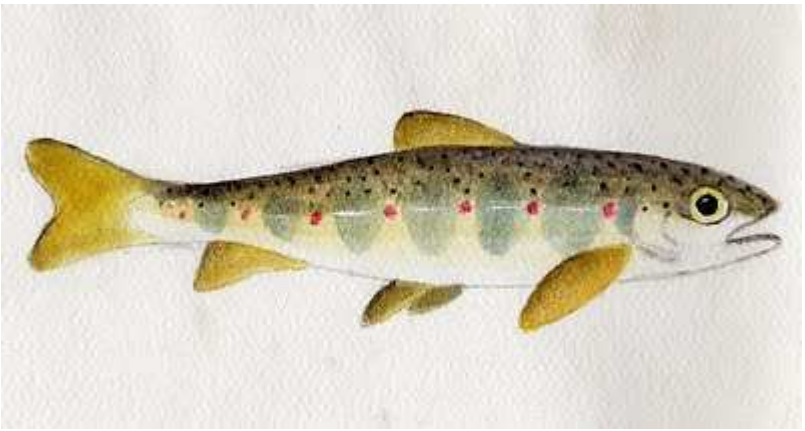
The reasons why and how precocious salmon parr exist must be viewed from the perspective of the selfish gene (Dawkins 1976) and not to their utility to the species as a whole. From a "selfish gene" perspective, the precocious parr have only one aim: to ensure their genetic legacy is passed onto the next generation.

The most obvious advantage of precocious parr-ness is that they can avoid waiting until they are 4 years old to spawn, and instead spawn when they are only two years old. As important, the male parr does not have to undertake a 2,000 mile journey in the open ocean before it spawns, as must its larger male competitors.

The drawbacks of precocious parr-ness are several. First, the precocious parr is so tiny that it cannot compete for females with the large adults by driving off smaller competitors (although precocious parr will aggressively drive other precocious parr away from a spawning nest). Second is that during the spawning season, precocious parr lose their secretive nature and swim around the stream in the open during the day with wild abandon, exposing them to being eaten by kingfishers and other streamside predators. This is a threat that large males do not face because there are virtually no streamside predators large enough to attack and carry off a full-sized male salmon. A second threat is that to become sexually mature, male 2+ year old salmon parr must devote approx. 20 percent of their body weight to growing testes and developing sperm and spending the fall of their second year attempting to spawn, rather than conserving their body mass and saving their stored "fitness" to survive the oncoming winter in preparation for swimming to the ocean the next spring. Several studies (listed below) show that the over-wintering survival rate of precocious parr is lower than parr of the same age which do not become sexually mature.

We know the trade-offs of precocious parr-ness must outweigh the risks because precocious parr do exist. This means that whatever genetic proclivity toward making some male parr precocious is at least successful enough to persist in the gene pool. If the disadvantages of precocious parr greatly outweighed the benefits, the genetic recipe for making them would long ago have disappeared. By corollary, we can assume there is some sort of ongoing "stalemate" between the advantages and disadvantages of precocious parr-ness because most male salmon are large four year old adults. If the advantages of precociousness greatly outweighed the disadvantages, contemporary salmon populations would be wholly or mostly made up of small males that never went to the ocean.

Two other facets of salmon behavior contribute to the persistence of precocious male parr. First is that female salmon do all of the nest building work. If males had to contribute to the nest-building effort, the precocious parr would be in bad shape, because their tiny body size keeps them from moving even the smallest river stone, while the large males can move stones just as easily as the largest females. Second is that female salmon do not seem to actively select one mate and then drive off all other suitors. Instead, females spend all of their time building their nest, while the males around them are fully occupied with trying to drive one another away from the female. The female is only "ready" to spawn when she decides her nest is finished and is large enough and deep enough to successfully hold her cargo of eggs. It is only at this time she acknowledges or interacts with the jostling males around her.



One-year-old native Atlantic salmon parr, Worromontogus Stream, Kennebec River, Randolph, Maine. Watercolor, gouache and pencil. Douglas Watts, 1999.

Why no female precocious parr?

The reason precociousness in male salmon works -- and doesn't work for female salmon -- lies in the enormous difference in size between salmon sperm cells and eggs. Salmon eggs are the size of a small pea. A 7 inch female could only hold in her a dozen or so eggs. A 7 inch male can hold in him thousands of sperm cells. In contrast, a full grown female salmon can hold from 5,000 to 15,000 eggs. From the perspective of the selfish gene, the female has a much better chance of passing along her genetic legacy by going out to sea for two years, feeding in the rich ocean environment, growing to 28-36 inches long and being large enough to carry 10,000 eggs instead of becoming sexually mature

enough to carry 10,000 eggs instead of becoming sexually mature at age two, not going out to sea and carrying only 12 eggs. There is also the issue of nest building. The female salmon builds her nest without assistance from males, and it is an arduous task. A 7 inch female could only build a nest the size of a tea cup for her 12 eggs; and few if any males would be willing to use up their sperm supply fertilizing such a tiny amount of eggs. Under the selfish gene concept, the goal of the males is to use their sperm supply to fertilize as many eggs as possible, thus increasing the chance that their genetic legacy will be passed on. The more eggs you fertilize, the greater chance that at least one of the fertilized eggs lives to spawning age itself and passes on part of your legacy. Given that precociousness in male salmon is quite common and precociousness in females is unknown, we can assume that if there ever was a genetic proclivity that created precocious females, it has blinked out of existence every time it arose because it did not "work."

30 inch long, two sea-winter adult male Atlantic salmon after spawning, Bond Brook, Augusta, Maine, October 1996. Held by Nate Gray, fisheries scientist of Maine Dept. of Marine Resources.

Do females benefit from precocious parr?

In Atlantic salmon, as humans, each fertilized egg gets one half of its chromosomes from its mother and the other half from its father. From a selfish gene perspective, the female's sole interest is in the welfare of her half of the chromosomes in her fertilized eggs. While she needs a male to mate with, this is only because she

needs male sperm cells to ensure that her half of the chromosomes is passed on to her children. In this sense, the female doesn't really care whether her eggs are fertilized by a 24 inch, 36 inch, 40 inch or 6 inch male, as long as they all get fertilized. This is shown by the fact that female salmon do not appear to overtly select certain males as mates and refuse to mate with other males. From a purely statistical standpoint, female salmon benefit from having their eggs fertilized by multiple males because it increases the chance that at least some of the eggs will carry beneficial genetic adaptations from the male and have a better chance of living to adulthood and spawning. The idea is the same as betting on 6 numbers on the roulette wheel rather than putting all your money on one.

Second breach of Edwards Dam, Kennebec River, Augusta, Maine, August 12, 1999.

Kennebec River at Augusta, Maine, July 2000, one year after removal of the Edwards Dam. The dam was located in the upper center of the photo.

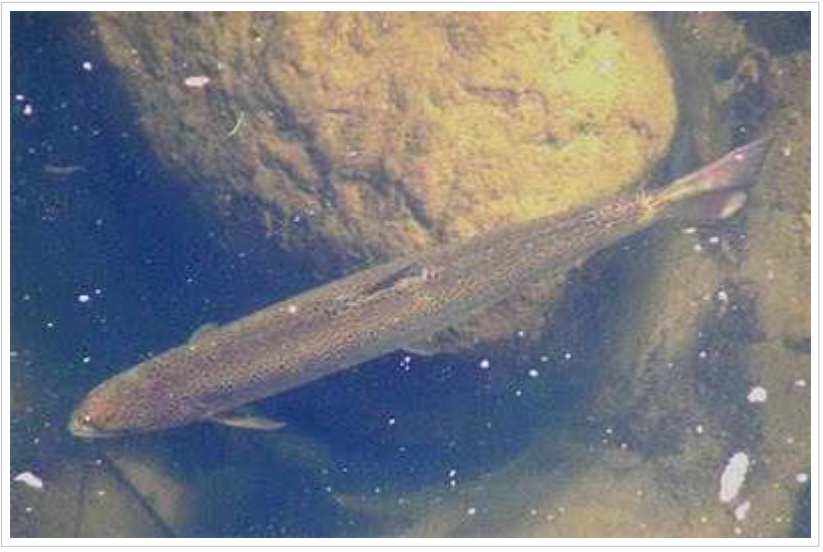
Male vs. Female salmon Imperatives

A large male Atlantic salmon contains millions of sperm cells, enough to fertilize all of the salmon eggs deposited by every female in a salmon river. A female, in contrast, carries between 5-10,000 eggs. From a purely statistical standpoint, it is in the female's interest to have her eggs fertilized by multiple males, which allows her genetic legacy (half of the chromosomes in each egg) to benefit from any potential genetic advantages contained in the various males in the river.

Male salmon have a powerful motivation to prevent other males from spawning with females, because every egg fertilized by another male is one that he did not fertilize. The female, on the other hand, benefits from having multiple males fertilize her eggs. This helps to explain why males devote all their time on the spawning beds to driving away other males from a female; and why females show little interest in selecting one male and spurning others.

This also helps to explain the existence of precocious salmon parr. Under the rules described above, the female benefits from having a precocious parr sneak under her belly just as she emits her eggs and casting his small cargo of milt onto them, even as the large male is next to the female doing the same thing. The large male does not want the precocious parr anywhere near the female when she is releasing her eggs because he wants to make sure that only his milt touches and fertilizes all of her eggs. By hiding underneath (or on the opposite side) of the female as she emits her eggs, the

(or on the opposite side) of the female as she emits her eggs, the precocious parr stands a good chance of not being noticed by the large male and is able to eject his milt at about the same time as the large male ejects his milt, creating the opportunity that at least some of the parr's milt will reach an egg and fertilize it, thereby thwarting the large male's efforts to fertilize all of the eggs himself.



30 inch Atlantic salmon at mouth of Bond Brook, Kennebec River, Augusta, Maine, July 2005.

Species benefits of precocious parr

An important rule of evolutionary behavior is that individuals of a species do not do things to benefit the species as a whole. Each individual is trying to pass on their own individual genetic legacy and that is it. To the extent that one individual's efforts to pass along his or her own genes creates inherited adaptations that are spread through a population, you can (very cautiously) examine how adaptations that help one individual pass on their genetic legacy can ultimately increase the fitness of a larger group of individuals. This is especially true where some type of calamity has

caused a drastic reduction in localized population size.

Female Atlantic salmon digging her spawning nest in upper Bond Brook, Kennebec River, Augusta, Maine, October 1998.

This fact was made apparent to me in 1998 in Bond Brook in Augusta, Maine. Bond Brook is a very small (25 square mile) watershed which enters the Kennebec River just below the site of the Edwards Dam, an impassable structure built in 1837 that almost completely wiped out the Kennebec River's Atlantic salmon population. The dam was removed in 1999. For several decades prior to 1999, Bond Brook was one of the only places below the Edwards Dam that contained quality Atlantic salmon spawning and nursery habitat, and for this reason, a dozen to several dozen adult salmon would swim up the brook each fall and spawn. These few salmon represented the last, tiny struggling remnant of the Kennebec's original salmon population, which exceeded 100,000 adults prior to the construction of the Edwards Dam in 1837.

In 1996 I located a previously unknown Atlantic salmon spawning area several miles up Bond Brook in a remote, roadless area that required a long, muddy walk to reach. In this reach, the habitat was nearly pristine and ideal for spawning salmon and their young. In late October 1998 I hiked into this habitat and was very pleased to find a large female digging her nest, accompanied by two large males, who fought and chased each other constantly for control of the lone female. Hiding in the tall grass next to the brook bank, I was able to spend several hours observing the stream and the salmon without being noticed, even though the

stream and the salmon without being noticed, even though the salmon were only 15 feet away from me. During this time, I noticed a dozen precocious male salmon parr swimming all around the female's nest, constantly chasing each other away from the nest and vying for "ownership" of it, even as the two large males did the same thing to each other. The precocious parr behaved exactly toward each other as the two large males toward each other. They all viewed each other as competitors and rivals for possession of the nest and the female salmon building it.

What struck me was that in such a depauperate, remnant salmon population (with only one female and two large males in this stretch of brook and a total population of perhaps 30 adults), the addition of the dozen precocious parr I saw darting about greatly increased the effective breeding population of the brook. From the female's perspective, a fertile male is a fertile male, even if one is 30 inches long and the other is only 6 inches long. It is in the female's interest to have her eggs fertilized by as many different males as possible. If there were no precocious parr in the stream reach I observed in 1998, the female's eggs would at best be fertilized by two males, and perhaps only one, if the larger male was successful at driving the smaller male away and fertilizing all of the female's eggs. With the dozen precocious parr present, and because of their sneaky way of swimming underneath the female's belly without being noticed by the large males, the female's eggs had the opportunity of being fertilized by as many as 14 different males. While each baby salmon that hatched in spring 1999 from this site would have the same mother, they would have perhaps as many as 14 different fathers.

Large male and female Atlantic salmon just above the female's spawning redd in Cobbosseecontee Stream, downtown Gardiner, Maine, November 1997. I took this photo 25 feet up in a red maple tree. On this same afternoon, I observed several precocious male salmon parr occupying the redd below.

Precocious Parr, Genetic Drift and Bottlenecking

Animal populations reduced to extremely small sizes must mate with closely related members of the population or go extinct. They have no choice. This fact is especially pronounced in Atlantic salmon, which display a tightly focussed homing instinct to the stream and river of their birth and in doing so increase the chance of mating with close relatives. In a large, healthy salmon population with hundreds of fertile males and females in a short reach of river, the chance of a full sibling mating is quite small because it requires, by pure chance, a male salmon selecting his sister even in the presence of dozens or hundreds of other females who are more distantly related. But in a very small, impoverished salmon population, where only a handful of males and females spawned, there is a very high likelihood that many of the males and females returning four years later are full or half siblings. Given the choice of spawning with a sibling or not spawning at all (and not passing on their genetic legacy), the salmon must spawn with "who they brought." Over time, such a pattern of repeated sibling mating can have a very negative effect, which is well known in humans via cases of human incest. Sibling mating is bad because many diseases and birth defects are caused by the mother and father sharing the same rare, debilitating gene which is only activated when an offspring inherits it from both its mother and its father. When distantly related males and females mate, the chances of both having this debilitating gene are very low. But if the mating pair are siblings, the chance that both have the defective gene can be quite high.

Large Atlantic salmon trying leap over an impassable 1850s dam on Cobbosseecontee Stream, Gardiner, Maine, Nov. 11, 1996. The dam is still impassable.

An analogy is a deck of cards. Let's say you play a card game where each player draws a card and places it on the table. If the cards match exactly, both players "die." If the cards don't match both players "live." In such a game the risk of living and dying is dependent on the number of cards in the deck. With a 52-card deck, the players might have to go through many full decks to each throw down the same card at the same time. But now add a variation. Each time the players go through a full deck without getting a match, each has to remove some cards from their deck (say, remove all the kings, then the queens, then the jacks, and then all the 10s, etc.) With every round of the game, the chance that the players will throw down the exact same card increases because they always share the same set of cards but the total number of cards decreases. As the deck grows smaller and smaller, the chance that both players will throw down the same card approaches unity. This is a rough analogy to the effects of genetic "bottlenecking" due to a greatly reduced population size where genetic variation is sharply reduced because of the need for close relatives to mate with each other or not mate at all.

Now let's add precocious parr to our card game. Let's assume that each time a male and female "player" goes through a full deck without losing (ie. throwing down a matching card) is equal to one spawning season for Atlantic salmon. Because our game assumes a rapidly declining population of adult salmon (due to losses of adults and juveniles at dams, from human capture), we invoke a penalty after each game where each player removes all of the cards of one number before starting the next round, leaving them with fewer cards, and fewer chances of a mismatch (and their offspring living) and a greater chance of an exact match (and their offspring having a genetic defect and dying). Because an adult

female having her eggs fertilized by a precocious male parr eliminates the chance of sibling mating (by definition a 2 year old precocious parr is not a sibling of a mature 4 year old female), the addition of precocious parr to the spawning stream decreases the chance of a female mating with a sibling male.

We can approximate this change in our card game by reducing (by some number) the amount of cards each side loses after each round of the game from what it would be if precocious parr were not present and available to mate with adult females. This is because, without precocious salmon parr, the chance that a 4 year old female and 4 year old male being siblings in a very depressed salmon population approaches one, and the increase in the chance of deleterious genetic defects and diseases due to sibling mating increases dramatically.

Using our card game as an analogy for the genetic shuffling between male and female Atlantic salmon, precocious parr are an important buffer against the tendency of a declining salmon population to enter a genetic bottleneck where siblings increasingly tend to mate with direct siblings, resulting in a continued reduction in genetic variation and an increase in harmful defects caused by the mother and father each having copies of the same harmful gene.

Precocious parr cannot mate with their siblings

Due to the two-year separation between precocious male parr and their 4-year-old female mates, it is impossible for precocious parr to ever mate with their sisters. This is because only male salmon are precocious and all of their sisters must reach age 4 before they reach spawning age. When the precocious males are trying to spawn at age 2, their sisters are nearby in the same stream, still two years away from reaching sexual maturity. In contrast, nonprecocious male parr and their sister parr each spend two years in the ocean before returning together to spawn at age 4. This creates a fairly high chance (especially in small, impoverished populations) that brothers and sisters will mate. In a large, healthy population the chance of direct sibling mating is greatly reduced by the large number of available, unrelated male and females in any river reach. While sibling mating in a large river population is statistically possible (and undoubtedly

happens), the number of matings between unrelated salmon is much larger. In a very depressed salmon population where most of the juveniles arise from a handful of closely related adults, sibling mating becomes the rule rather than the exception.

Precocious parr and newly established salmon populations

Precocious parr should assist the establishment of persistent Atlantic salmon populations in unoccupied habitat (in contrast to the "the last survivors model" described above, this model would be the "first pioneers" model). While Atlantic salmon have an acute homing instinct which causes them to return to the river reach where they were born, some Atlantic salmon break from this instinct and explore and colonize suitable habitat where few, if any, salmon are present. This "straying" instinct is well documented in Atlantic salmon, although it is adopted by only a small (1-5 percent) of salmon, with most (95 percent) returning to the same river, stream and even gravel bar where they were born (Baum 1997).

A pioneer group of Atlantic salmon colonizing an uninhabited stream is comprised of just a few spawning males and females. The success of this colonization effort depends on the progeny of the first pioneers surviving in the stream to adulthood and returning to the same stream to spawn. In such a nascent population, sibling and half sibling mating is practically guaranteed.
Precocious salmon parr provide a unique opportunity for newly established salmon populations to "mix-up" their mating combinations by allowing cross-generational spawning between 4 year old females and 2 year old males. This greatly reduces the chance that all of the offspring in an early spawning generation are produced by the mating of siblings or half siblings.

The needs of the "selfish genes" of Atlantic salmon

In this era of Atlantic salmon populations approaching extinction, the primary focus of Atlantic salmon biologists and conservationists is on the preservation of Atlantic salmon populations rather than the welfare of any one individual Atlantic salmon (although obviously the former is completely dependent on the latter). Evolutionary biology requires us to examine Atlantic

the latter). Evolutionary biology requires us to examine Atlantic salmon strictly through the lens of individual salmon trying to preserve their legacy by surviving to spawning age, mating, and giving birth to salmon that also spawn. This is especially true in the case of precocious male salmon parr. While we can theorize or surmise that precocious parr increase the fitness of a local population, stave off the extirpation of depressed populations, and increase the chance that newly established populations will persist, we cannot forget that the genetic adaptations which allow 2+ male salmon parr to be sexually mature two years earlier than most of their cohorts was not "designed" for these purposes. A more appropriate way of characterizing this genetic adaptation is that it has persisted in Atlantic salmon populations because in some statistical way it confers a neutral or positive survival advantage to those salmon who are born with it; and that the "success" of this peculiar life history strategy can be estimated by its prevalence or absence in the gene pool of Atlantic salmon today. Presumably, in Atlantic salmon populations decimated by long-term anthropogenic effects (as in the U.S.), if precocious parr provided a neutral or negative benefit to survival of their offspring, it would have disappeared from the remaining gene pool of U.S. salmon. By an admittedly speculative analytical basis, the adaptation of precocious parr seems to provide individual Atlantic salmon in highly depressed remnant populations an important hedge against the environmental and genetic forces which conspire to drive remnant populations to increased dimunition and extirpation.

Precocious parr mitigate against harmful environmental effects face by young salmon as they try to migrate downstream as smolts and live in marine waters for two years before they return to spawn. This is accomplished by allowing some male 2+ parr reaching sexual maturity in their own natal stream without having to live to age 4 or survive a perilous 2 year journey back and forth across the Atlantic Ocean to their feeding grounds near Greenland.

The adaptation of precocious parr mitigates against the harmful effects of genetic bottlenecking and genetic drift in small, declining, remnant Atlantic salmon populations by reducing the chance that most or all returning adult salmon are forced to mate with their sisters and brothers or not mate at all. Precocious male salmon parr have a unique life history because they mate at age two with females that are age four or older. This guarantees that

they will not mate with their siblings or close relatives. The presence of numerous precocious parr in an impoverished Atlantic salmon spawning stream greatly increases the effective population size of the stream by greatly increasing the number of potential fathers for the available females' egg cargo. Due to their young age, precocious parr have different mothers than the females they try to mate with and the adult males they compete with. This means precocious parr increase the effective population size of mothers in a given stream because they do not share a mother with any of the adult males and females. In contrast, in a very depressed and small population, it is possible that most of the adult male and female salmon have the same mother.

A Theory Explaining Precocious Male Atlantic Salmon Parr

It is likely that all male Atlantic salmon carry the necessary genes to allow them to become precocious, ie. to become sexually mature prior to migrating to sea as smolts. It is also possible that this gene for precociousness tends to be triggered by the relative presence or absence of male salmon testosterone in a salmon spawning stream. A spawning stream occupied by a large number of adult males carries a much higher "signal" of male salmon testosterone than a stream with very few adult males. If the presence of salmon testosterone inhibits the genetic expression of precociousness in 2+ male salmon parr, the number of male parr in the stream displaying precociousness would be higher if there were few adult males.

Such an environmental triggering would explain why recent field research shows a higher incidence of precociousness in small, depressed Atlantic salmon population lacking adult males and a lower (observed) incidence of precociousness in salmon populations with a large number of adult males. Support for this theory is shown by the fact that male brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) typically become sexually mature at age 2-3. Two sea-winter Atlantic salmon become sexually mature at age 4, three sea-winter salmon at age 5 and male grilse at age 3. In contrast, sexually mature female anadromous Atlantic salmon less than age 4 are extremely rare. Among brook trout and brown trout, its closest cousin species, sexual maturity for male Atlantic salmon at age 2 is the norm, ie.

the age at which precocious salmon parr become sexually mature. Only in healthy anadromous Atlantic salmon populations do males tend to delay their sexual maturation until age 3, 4 or 5. This suggests an environmental inhibiting factor keeps most anadromous male Atlantic salmon from exhibiting their "normal" sexual maturity at age 2 and delays it until age 3, 4 or 5; the existence of precocious parr suggests a relaxing of this inhibition; and this relaxation is expressed most prominently when a local population lacks adult males. From this we can deduce an inverse relationship between the number of precocious parr in a spawning stream and healthy survival conditions for those male Atlantic salmon which go to sea before spawning.

Large Atlantic salmon, Cobbosseecontee Stream, Kennebec River, Gardiner, Maine. Nov. 11, 1996.

UPDATE: A recent research study of southern European salmon populations (Garcia-Vazquez et al. 2001) seems to confirm the above theories of species benefits in depressed Atlantic salmon populations from the presence of precocious male parr. The study states in part:

> "Mature juvenile males may have saved south European Atlantic populations from extinction, given the depressed size of populations for a number of decades. This point suggests that these populations may be under intense selection for maturation of juvenile males, and hence that the relative preponderance of mature juvenile males in the southern populations may be an adaptive response to anthropogenic depletion of anadromous salmon numbers

.... In conclusion, precocious Atlantic salmon parr contribute to balance the sex ratio, enlarge the effective population size, and increase outbreeding. In addition, they fertilize most eggs in the interspecific matings between Atlantic salmon and brown trout. Sneaking behavior has not been evidenced in small maturing brown trout, this being the main reproductive difference between brown trout and Atlantic salmon in wild southern European populations."

Works Cited:

Baum, E.T. 1997. *Maine Atlantic Salmon: A National Treasure*. Atlantic Salmon Unlimited. Hermon, Maine.

Dawkins, R. 1976. *The Selfish Gene*. Oxford University Press. London, England.

Garcia-Vazquez, E., P. Moran, J. L. Martinez, J. Perez, B. de Gaudemar, and E. Beall. 2001. *Alternative Mating Strategies in Atlantic Salmon and Brown Trout*. The Journal of Heredity 2001:92(2).

Myers, R.A, J.A. Hutchings. 1987. Mating of Anadromous Atlantic salmon, *Salmo Salar L.,* with mature male parr. J. Fish Biol. (1987) 31, 143-146. PDF here.

Saura, M. et al. 2008. *Impact of precocious male parr on the effective size of a wild population of Atlantic salmon*. Freshwater Biology. Vol. 3 No. 12. pp. 2375-2384. Blackwell Science, Oxford.

Mark Kemezys (1961-2009) at the ledges and falls at the head of tide of Bond Brook, Kennebec River, Augusta, Maine in spring

2005. For more than 150 years, Bond Brook provided the only accessible habitat for Kennebec River salmon below the impassable Edwards Dam. A native of Norridgewock, Maine, Mark spent many hours cleaning up trash and debris along the Kennebec River at the "yellow stairs" in downtown Augusta.

POSTED BY