

THE BEHAVIOR AND ECOLOGY OF
Pacific Salmon & Trout

THOMAS P. QUINN

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www.fisheries.org

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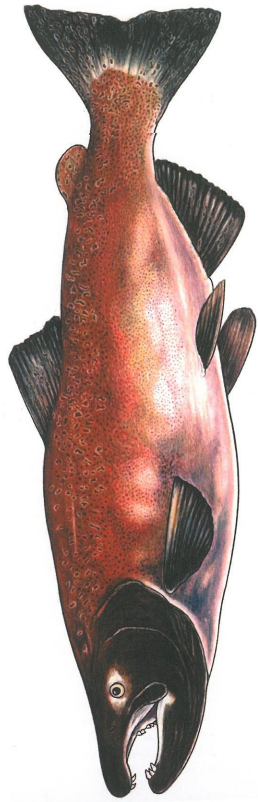


PLATE 12. Illustration of a mature male chinook salmon at the height of sexual maturity. Olive-brown color is typical of those from southern areas but chinook salmon from northern populations may be more red in color. Copyright: Charles D. Wood, Ph.D.

7

The Ecology of Dead Salmon

After reproducing, female Pacific salmon guard their nests until they become too weak to hold position and eventually drift away and die. Males, too, become increasingly listless, scarred, and emaciated, and they also die. Streams and lakes in temperate and northern latitudes are generally unproductive, limited by phosphorous (P) or nitrogen (N). This is a result of the geology that dominates much of the region, and the inevitable downstream flow of nutrients to the sea. The upstream migration of salmon, followed by their death, is a very important source of nutrients. The quantity of rotting fish flesh (photo 7-1) could not have escaped notice by humans, nor did they fail to see the congregations of animals feeding on the live and dead salmon. Still, research in this subject was quite limited until the past 2 decades, when interest in this subject increased greatly. This research has revealed that the entire ecosystem—from insects to bears and trees, including the salmon themselves—benefits in complex direct and indirect ways from decomposing salmon.

Salmon as fertilizer in aquatic and terrestrial food webs

Early in the twentieth century, scientists studying Karluk Lake, Alaska (known for its especially dense populations of sockeye salmon), pointed out the importance of P and N from decomposing carcasses in otherwise nutrient-poor freshwater systems (Juday et al. 1932). Appreciation of the importance of these nutrients (especially P) in lake and stream productivity grew during the middle of the century, and Donaldson (1967) estimated the P budget of Iliamna Lake. This is the largest lake in Alaska, with an area of 2622 km² and a volume of 115.3 km³. The lake and its associated tributaries had a record escapement of 24.3 million sockeye in 1965, weighing about 2–3 kg each. Donaldson



7-1 Decomposing male chinook salmon, exposed by lowering water levels, Adams River, British Columbia. Photograph by Andrew Dittman, National Marine Fisheries Service.

estimated that they delivered 169.3 metric tons of P to the ecosystem, the primary source in such years of great salmon abundance. The fishery took another 17.8 million salmon that year, so the total run would have brought 42.1 million carcasses to the region, with a concomitant increase in nutrient contribution. Donaldson (1967) pointed out that the smolts migrating to sea constitute a loss to the system, as they weigh about 6–10 g and can number in the hundreds of millions. On balance, sockeye salmon were a major source of nutrients in this system, at least in some years.

Many lakes inhabited by sockeye salmon are nutrient limited. The fertilization of some of these ultra-oligotrophic lakes in coastal Alaska and British Columbia (Koenings and Burkett 1987; Stockner and MacIsaac 1996) shows that addition of nitrates and phosphates increases primary production, zooplankton biomass, and sockeye salmon growth (see chapter 10), though there is increasing variation with each trophic step, so the clearest results are for increases in primary production. However, are the inorganic nutrients from salmon carcasses actually incorporated into the various trophic levels?

Scientists can take advantage of a characteristic of N to trace this element from adult salmon through the aquatic and terrestrial ecosystems. Nitrogen normally has a molecular weight of 14 but some atoms contain an extra neutron, increasing the molecular weight to 15. The proportion of the heavier isotope is greater in marine ecosystems than in freshwater and terrestrial ecosystems. Most salmon put on at least 99% of their total weight at sea, so the bodies of adults reflect the ratio of isotopes in marine waters. By examining the ratio of heavy “marine-derived” N isotopes to lighter atmospheric isotopes in various organisms—including producers (phytoplankton in the water column, rooted aquatic plants, and periphyton on rocks), primary consumers (insects, zooplankton), and higher trophic levels such as planktivorous and piscivorous fishes—one

can determine the proportion of N that is marine derived. Similar analyses can be conducted on trees along the riparian corridor, as well as the birds, mammals, and insects that might feed on salmon, indicating the extent to which salmon contribute to the terrestrial ecosystem (Kline et al. 1990, 1993). There are some complexities in the interpretation of such data, owing to the presence of nitrogen-fixing plants such as alder, fractionation of isotopes, seasonal changes in baseline values, and so on (Kline et al. 1990; Bilby et al. 1996). For carbon, marine ecosystems have a higher proportion of ^{13}C relative to ^{12}C (the most common isotope) than do freshwater ecosystems. Unfortunately, there is no marine isotope of P, and it is often the limiting nutrient.

Kline et al. (1990) collected samples from periphyton, insects, and fishes from sections of Sashin Creek, in southeast Alaska, that were within and beyond the range of pink salmon. By comparing the isotope ratios, they estimated that substantial fractions of the N and C in all trophic levels were derived from salmon carcasses. Similar work at Iliamna Lake (Kline et al. 1993) indicated uptake of marine-derived nutrients in juvenile sockeye salmon, especially in years following large escapements of adults to the lake. This supported Donaldson's (1967) hypothesis that the productivity of the lake for sockeye salmon depends, in part, on the carcasses of large numbers of adults. Most of the nutrients from salmon were found in the limnetic zone, but coast range sculpins (*Cottus aleuticus*) apparently derived a significant portion of their diet from salmon eggs and fry. Later work by Foote and Brown (1998) showed that both coast range and slimy sculpins (*C. cognatus*) eat sockeye salmon eggs, and that a single large sculpin can eat almost 50 eggs at one meal and 130 eggs in a week.

Subsequent observation and experimental research has shown that salmon carcasses enhance the abundance of algae in streams and the density of insects. Wipfli et al. (1998) reported that reaches of a creek in southeast Alaska accessible to pink salmon had fifteen times more “biofilm” (microbes covering rocks) and twenty-five times higher densities of macroinvertebrates than reaches of the creek not accessible to salmon. Working in western Washington, Bilby et al. (1996) used stable isotope ratios to estimate that marine-derived N made up about 20% of the N in biofilm and about 15–30% of the N in stream insects. Juvenile salmon eat primarily insects during much of their lives in streams, and it is reasonable that some of the nutrients from carcasses might reach the fish via insects. Bilby et al. (1996) showed that carcasses contributed about 20–30% or more of the N and C in juvenile stream-rearing salmonids (cutthroat and steelhead trout and coho salmon). This uptake might be a case of substituting one source of the element for the other with no net benefit to the fish if the elements are not in short supply. However, juvenile steelhead and coho salmon congregated at sites where carcasses were deposited, and they showed dramatic increases in condition factor (weight for a given length) relative to sites without carcasses (Bilby et al. 1998). Stomach content analysis revealed that the young salmon not only ate insects (hence an indirect link to carcasses) but salmon eggs and even the flesh from dead salmon. The size of juvenile salmon in streams is positively correlated with survival over the winter (e.g., Quinn and Peterson 1996), so a plausible case can be made that large runs of salmon enrich otherwise unproductive streams, to the benefit of the salmon.

There is thus a growing body of evidence that salmon carcasses fertilize aquatic (lake and stream) systems, with direct and indirect feedbacks to salmon populations via

various trophic pathways. However, there is also evidence for complex pathways of nutrient transfer to terrestrial ecosystems as well. Bilby et al. (1996) showed that about 20% of the N in foliage from terrestrial vegetation along salmon streams in western Washington had been derived from carcasses, and Helfield (2001) corroborated these findings in southeast and southwest Alaska. Thus trees take up marine-derived nutrients, but do such nutrients contribute to tree growth? Helfield and Naiman (2001) cored and measured trees in areas of the Kadashan River basin in southeast Alaska, above and below a barrier to salmon migration. There are many factors that affect the growth rates of trees, but Helfield and Naiman concluded that the presence of salmon carcasses had a stimulating effect on Sitka spruce growth. Trees within 25 m of the stream in areas with salmon grew 22.9 cm³ per year versus 6.4 cm³ at sites without salmon, and the researchers estimated that trees in areas with salmon would grow to a diameter of 50 cm in 86 years compared to 307 years at areas devoid of salmon. They pointed out that trees play several important roles in salmon ecology, such as maintaining stream habitat complexity, retaining gravel, providing structural cover, and trapping finer organic material. Thus there may be a feedback between salmon densities and the habitat conditions that maintain such densities.

How might the nutrients from salmon carcasses be transferred to trees? One pathway is the hyporheic water that flows beneath and alongside the visible stream. Water not only flows down the conventional streambed but also percolates through the ground between bends in the stream and along the edges of the stream, and O'Keefe and Edwards (2002) demonstrated the importance of this pathway in transporting and storing salmon-derived nutrients. In addition to hyporheic flows providing subsurface transport of nutrients from salmon to trees, floods can transport carcasses from the stream and deposit them along the banks. Ben-David et al. (1998) used stable isotopes of N and C to show both the dispersal of carcasses adjacent to streams from floods and uptake of nutrients by vegetation. However, not all streams that support salmon are flood-prone, and the distribution of carcasses from floods is unlikely to extend very far from the stream, so this is probably not a major pathway. Sites with predators (chiefly bears) showed a much wider distribution of carcass-derived nutrients in terrestrial vegetation than sites where they were absent (Ben-David et al. 1998). Eagles and otters consume salmon but are too small to transport large quantities of salmon from streams. However, brown (*Ursus arctos*) and black bears (*U. americanus*) have the means and the motive to move large quantities of carcasses from streams (Reimchen 2000; Gende and Quinn 2004), and there seems to be a very special linkage between bears and salmon that affects both the ecology of these organisms (predator and prey, respectively), but also other components of the ecosystem (photo 7-2).

Bears and salmon

W. K. Clark (1959, 337) noted, "One can walk along almost any Alaska salmon stream in bear country during the summer spawning season and see jaws, heads, and other parts of salmon left by bears." It is common knowledge that bears kill and eat salmon, but what factors determine the magnitude and consequences of the predation for the bears and for the salmon? Records of the numbers of live and dead sockeye salmon, and

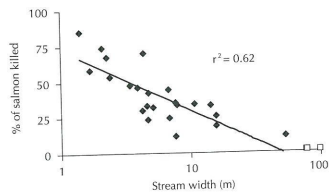


7-2 Brown bear with a ripe female pink salmon in Pack Creek, southeast Alaska; note the area on the bank that has become worn by the bear's activity, and the small size of the stream. Photograph by Scott Gende, U.S. National Park Service.

categorization of the dead as bear-killed or senescent in twenty-three different streams within the Wood River lake system, Bristol Bay, Alaska, over more than 10 years (Quinn, Wetzel et al. 2001; Quinn et al. 2003), revealed that the percent of the sockeye killed by bears was strongly related to the size (especially width) of the creek: the smaller the creek, the higher the predation (fig. 7-1). Some rivers were too big for accurate surveys but all indications were that predation there was negligible. Variation in predation among years within streams was related to density, though the strength and shape of these relationships varied among streams. In general, as the number of salmon in the creek increased, the number killed rose toward an asymptote, approximated in some cases by a log relationship (fig. 7-2).

Beyond our interest in how many salmon are killed, there is a growing appreciation of the complexities of bear predation. First, all the salmon will die at the end of a few weeks in the spawning stream, regardless of the presence of bears. Therefore, predation (i.e., salmon killed by bears) does not constitute evidence of an effect on the dynamics of the salmon populations. As indicated in the previous chapter, females tend to spawn within a few days of entering the stream and thereafter defend redds. Pre-spawning predation on females would therefore have much greater consequences for the population than postspawning predation. Predation on males would have little or no effect on the overall production of juveniles because males are essentially always surplus (in a numerical sense) to the needs of the females (Mathisen 1962). However, the reproductive success of an individual male

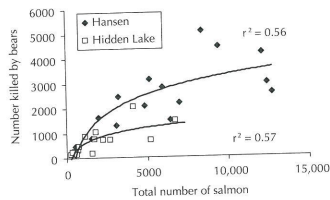
FIGURE 7-1. Relationship between the width of the stream and the percentage of adult sockeye salmon killed by bears in twenty-three streams in the Wood River system, Alaska (Quinn, Wetzel et al. 2001, Quinn et al. 2003, and unpublished data). Three larger rivers, indicated by open squares, have so little predation that it cannot be quantified and they were not used in the relationship.



might be reduced by predation, depending on whether the salmon was killed early or late in his natural life in the stream, and his breeding opportunities. Whether the salmon are killed pre- or postspawning depends on several factors.

Bears are omnivorous, eating a wide variety of plants and animals. However, Hilderbrand, Schwartz et al. (1999) showed that the density, size and productivity of bears were correlated with the availability of meat (especially salmon). There is no source of nutritious food that is as easily acquired and predictably available (in space and time) for bears as salmon. During the late summer and fall, bears need to deposit the fat that will sustain them through the winter period of fasting and parturition (Hilderbrand, Jenkins et al. 1999; Hilderbrand, Schwartz et al. 2000). Accordingly, they congregate along streams with salmon at the appropriate time of the year. Bears feed very selectively on salmon, tending to eat the body parts (chiefly eggs from females and brains) that provide the

FIGURE 7-2. Relationship between the number of sockeye salmon spawning during a season and the number killed there by bears, in two small creeks in the Wood River system, Alaska (from Quinn et al. 2003 and additional unpublished data).



7-3 Male sockeye salmon attacked by a brown bear; note the bite on the salmon's dorsal hump. Photograph by Susan Johnson, University of Washington.

most concentrated amount of fat (Gende et al. 2001; Gende et al. 2004). Salmon lose fat and protein very rapidly after they enter streams (see chapter 4), especially females after egg deposition. Thus bears should prefer to eat newly arrived salmon. In shallow streams, they indeed selectively kill these "fresh" fish rather than older ones, despite the fact that the older, senescent fish are presumably easier to catch as they become weak (Gende et al. 2004). However, in larger streams or ones with more complex habitat, the bears must "take what they can get" and they forage at random or tend to kill older fish. Only in very small streams, where fishing is easy, and when salmon are scarce, do bears seem to kill a large fraction of the ripe females.

Besides tending to kill newly arrived salmon, bears also tend to kill large salmon (e.g., Ruggerone et al. 2000). This may be because larger salmon provide more food for similar capture effort, because they are less maneuverable in small streams and so are easier to catch, or because they are simply more noticeable. Regardless of the mechanism, this selective predation on large salmon from populations in small streams where predation is intense can lead to the evolution of salmon that are younger and smaller than larger streams nearby with lower predation rates (Quinn, Wetzel et al. 2001).

Putting aside this evolutionary force exerted by bears on salmon life history, we return to the carcasses. Given that bears tend to feed selectively, how much salmon is left over? Intensive examination of carcasses over 5 years on daily surveys of Hansen Creek, a small stream with dense populations of sockeye salmon in Bristol Bay, Alaska, revealed an average of 4829 salmon that died of senescence and 3609 that were apparently killed by bears each year (Gende et al. 2001; Quinn, unpublished data). Of those killed, there was only minor consumption (bitten and dropped with no tissue eaten, or consumption of only the brain or skin) in 30%, and another 31% of the fish were partially consumed (typically the belly in females or dorsal musculature in males; photos 7-3 and



7-6 Male sockeye salmon carcass being consumed by fly maggots. Photograph by Thomas Quinn, University of Washington.

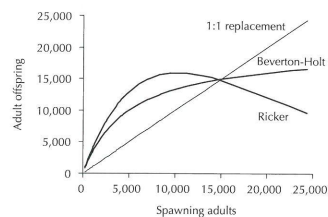
flies to rapidly locate carcasses, the patterns of maggot growth and development, and the effects of elevated invertebrate densities as a result of the presence of salmon carcasses are fruitful, if unappetizing, areas for further research.

Thus bears seem to play a special role in the ecology of dead salmon. They can kill far more salmon than any other terrestrial predator, and their patterns of partial consumption, carcass deposition, and excretion of wastes transfer nutrients from the stream to the nearby forest or grassland. People living in urban areas may doubt the ecological and evolutionary importance of bear predation. However, the range of black and brown bears was extensive until hunting and human development extirpated them from much of their range, and bears consumed salmon in these regions (Hilderbrand et al. 1996). The vast majority of salmon are (and always were) produced in small streams where bears would have had easy access to them. The densities of bears in coastal Alaska and British Columbia, even in the face of some hunting, and their levels of predation on salmon suggest a strong and long-standing linkage between these organisms.

Salmon as keystone species and the management of salmon abundance

Recent reviews (e.g., Willson et al. 1998; Cederholm et al. 1999; Gende et al. 2002; Naiman et al. 2002; Reimchen et al. 2003) have pointed out the importance of salmon in nutrient cycling, for both aquatic and terrestrial ecosystems, and the feedbacks to salmon's own abundance through algae, insects, and trees. Willson and Halupka (1995) termed salmon

FIGURE 7-3. Relationship between the number of spawning parents and the production of offspring, as modeled by Ricker (1954) and Beverton and Holt (1957).

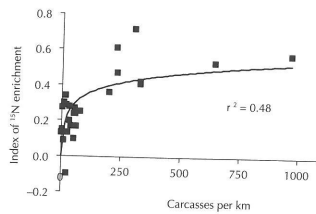


"keystone species" in recognition of salmon's special role enriching otherwise nutrient-poor systems. This new view of salmon as not merely part of a region's biodiversity but as a critical influence on many other species as well has stimulated concern for the adequacy of salmon runs from an ecological perspective. The natural dynamics of salmon populations return more adults to freshwater than the spawning grounds and rearing habitats can support. Competition among females for good nest sites, nest disturbance by other females, and competition among juveniles for food and space all limit the capacity of streams and lakes to produce salmon.

As salmon abundance approaches the carrying capacity specific to each site, the population is increasingly less productive (i.e., fewer surplus salmon are produced per spawner). The primary models for the relationship between numbers of spawning adults and their offspring are those of Ricker (1954) and Beverton and Holt (1957). As illustrated in figure 7-3, the Ricker curve predicts lower production of offspring at very high densities than at intermediate densities, whereas the Beverton-Holt curve predicts that the production of offspring will approach an asymptote. In either case, at low densities, the population produces several times more adults than the number of spawners. From the perspective of fisheries, these are "harvestable surplus" because catching them will maintain the population's productivity rather than diminish it. The general goal of salmon management is to allow the number of salmon to spawn in each river that will produce the maximum number of surplus offspring for fisheries to catch. If this escapement goal is achieved the population should not only sustain itself but support fisheries forever, a kind of biological perpetual motion machine. In this view, any salmon in excess of the number needed to maximize surplus production should be caught because they are otherwise wasted. However, the view of salmon as critical sources of nutrients for freshwater and terrestrial ecosystems makes us wonder whether long-term productivity is reduced by inadequate density of carcasses in streams.

Bilby et al. (2001) explored the idea of using nutrient levels to assess the adequacy of escapement goals. They surveyed a number of streams in western Washington that

FIGURE 7-4. Relationship between the density of adult salmon carcasses and an index of enrichment of juvenile salmonids with nitrogen derived from the carcasses (from Bilby et al. 2001).



varied in salmon-carcass density and then determined the levels of marine-derived N in juvenile coho salmon. By comparing the isotopic ratio of N in cutthroat trout in the same watersheds, but in areas without salmon, and the ratio in adult salmon, they produced an index of nutrient enrichment that was related to carcass density (fig. 7-4). Bilby et al. (2001) modeled the growth of coho salmon as a function of N and concluded that in these streams the benefits of carcasses would plateau at escapements over about 120 salmon per kilometer. However, many western Washington streams fail to reach this level.

There are many reasons for low escapements, and some of the variation is natural. However, many rivers, especially in the southern part of the range of salmon, have seen great reduction in salmon abundance over at least the past century. First, the fisheries all but guarantee that fewer salmon return to spawn than would have otherwise returned. Many fisheries are managed at about 50% exploitation rate and in some cases at least 75% of the adults are caught. Beyond the effect of fishing, impassable dams have eliminated runs of salmon in parts of many rivers. In much of the remaining habitat, the numbers of salmon being produced have been diminished by factors degrading the streams and lowering their carrying capacity (e.g., logging, mining, agriculture, water diversions, dams, and urbanization; NRC 1996). Thus the streams are less productive than in the past and we catch many of the salmon. The total numbers of salmon in recent years include a large number (sometimes the majority) produced in hatcheries, and until very recently, these carcasses were not returned to the streams.

Gresh et al. (2000) estimated the reduction in carcass deposition over the twentieth century in North America. They took records of the number of salmon caught at the earliest period of efficient Euro-American fisheries as estimates of the "historical" levels of salmon abundance and then obtained records of salmon escapements to rivers during the present period, excluding hatchery populations to the extent possible. Their summary revealed striking variation among areas in the historical and present numbers of carcasses. In the past, the majority of salmon were produced in Alaska (60.5% by number) and British Columbia (23.7%), with smaller numbers farther south. This imbalance

TABLE 7-1. Estimates of the current numbers and biomass of salmon escaping fisheries to spawn in rivers, and the percentage of historic levels that they represent. Data are from Gresh et al. (2000), using the average values given or the average between high and low estimates. Adjustments were made for differences in species composition among regions and differences in weight among species.

Area	Number of salmon (thousands)		Biomass (thousands of kgs)	
	current	% of historic	current	% of historic
Alaska	187,466	107.0	388,554	93.4
British Columbia	24,800	36.2	59,312	30.7
Puget Sound	1,600	8.0	4,123	7.1
Washington coast	72	1.8	197	1.2
Columbia River	221	1.7	1,201.5	1.3
Oregon coast	213	6.9	662.5	4.3
California	278	4.7	1258	4.7

has greatly increased recently. The researchers estimated that Alaska has roughly the same total number and biomass as before (within 10% of historical levels) but this now constitutes about 87.3% of the total escapement in North America. All other regions have seen dramatic reductions (table 7-1). British Columbia's escapement is on the order of 30–35% of the past, and Washington, Oregon, and California all have less than 10% of their former levels. The researchers did not report data for Idaho but the same would likely be true there as well.

The study of nutrient cycling from salmon and the ramifications of carcass density are likely to be fascinating and controversial areas of research and policy for some time to come. To what extent have the carrying capacities of streams been reduced by decades of low escapements, and how reversible might these effects be? Do feedbacks tend to magnify or reduce effects of carcass limitation? Should we incorporate carcasses and nutrients into the calculation of escapement goals, and how might the calculations differ between stream-rearing species like coho and those migrating to sea such as chum and pink? More broadly, what are the ramifications of salmon density for the health of terrestrial and aquatic communities?

Summary

Salmon achieve at least 99% of their final body size at sea and so, despite the mortality that takes place there, there is a tremendous net influx of biomass from the ocean to relatively unproductive stream and lake ecosystems. The millions of adult salmon are preyed upon, scavenged after death, and decomposed by a wide variety of organisms from bears to gulls, fly maggots, and bacteria. Recent research using stable isotope ratios has demonstrated that these "marine-derived" nutrients in the salmon carcasses are an important contribution to the aquatic and terrestrial ecosystems, affecting the growth

and density of bears, growth of juvenile salmonids, productivity of lakes, biofilm and insects in streams, and even the growth of trees in the riparian zone. Bears seem to have a particularly strong ecological connection with salmon, as they can not only kill a significant number of salmon but also transfer them from the stream to the riparian zone for scavenging and decomposition by other organisms. Capture of salmon in fisheries, even when well managed, reduces the number of salmon carcasses in streams, and the effect of this reduction on the ecosystem and the long-term productivity of salmon is an area of active research and controversy.

8

Incubation Rate and Mortality of Embryos

The months that young salmon spend below the surface of the stream are an important period for them. During this time they develop from unicellular fertilized eggs to complex organisms ready to emerge into open water and make their way in the world (photos 8-1 through 8-6 show chinook from the eyed egg stage through yolk absorption). Over their entire lives, from fertilization to maturation and spawning, the majority of mortality takes place during this period in the gravel. This critical phase is difficult to study because everything takes place out of our sight and often at times of the year that hinder research. Field observations are difficult at best and laboratory experiments are artificial. However, there have been many important discoveries about the rate of embryo development and the factors causing their mortality.

Spawning date, temperature, and development

Embryonic development begins when the egg is fertilized, and the timing of reproduction is among the most critical adaptations of salmon populations to their environment. Developmental rate and metabolism of salmon increase with temperature, as in all ectothermic organisms. Within the tolerable range, warmer water leads to faster development. The working hypothesis is that adults spawn at the time of year which, given the long-term average thermal regime, results in emergence of fry at a date that optimizes their opportunities for growth and survival. There may be other constraints on spawning date, including physical factors like flooding or freezing in the river, lake level in populations spawning on beaches, and biological factors such as predation on adults (e.g., by bears) or eggs (by sculpins). The relationship between temperature and development is so strong that most biologists assume that this is the dominant factor.