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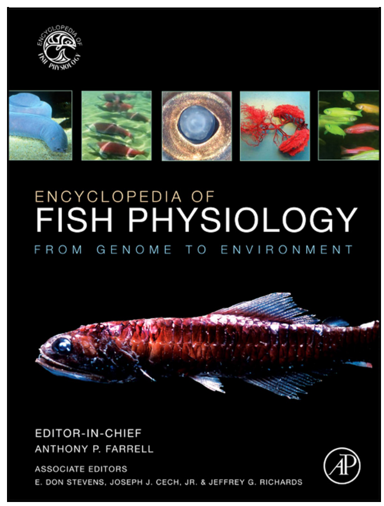

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Cooke S.J., Crossin G.T., and Hinch S.G. (2011) Pacific Salmon Migration: Completing the Cycle. In: Farrell A.P., (ed.), *Encyclopedia of Fish Physiology: From Genome to Environment*, volume 3, pp. 1945–1952. San Diego: Academic Press.

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Pacific Salmon Migration: Completing the Cycle

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Glossary

Anadromy Life-history strategy entailing reproduction and early rearing in freshwater followed by a significant growth phase in seawater.

Natal homing The phenomenon whereby animals return to the site where they were born to reproduce themselves.

Osmoregulation The maintenance of consistent cellular or organismal fluid composition and volume.

Pacific salmon Fish of the genus *Oncorhynchus* in the family Salmonidae.

Semelparity A reproductive strategy whereby an individual reproduces only once within its lifetime.

Smoltification Series of physiological and morphological changes a fish may undergo when migrating from freshwater to seawater.

Introduction

Pacific salmon (*Oncorhynchus* spp.) are well known for their large-scale migrations that can take them thousands of of kilometers from inland freshwater systems, where they begin their lives, to rich and fertile ocean habitats for feeding. Ultimately, they return to their natal stream to reproduce, before this lifecycle is repeated by their offspring (see **Figure 1**).

The migratory strategy of reproducing in freshwater, yet feeding primarily in marine waters is known as anadromy. Of the ~35 000 species of fish, ~2.5% are known to undertake migrations, and of that small percentage only 16% participate in anadromous migrations. Unlike Atlantic salmon (*Salmo salar*), Pacific salmon are semelparous, meaning that they die after spawning (**Figure 2**). The dead adults provide energy and nutrients for stream ecosystems, which benefit their own offspring after they hatch and begin to feed independently. This means that a fish that fails to mature and reach spawning grounds and reproduce will have zero fitness, contributing no genetic information to future generations. Indeed, not all fish that hatch return to spawn. Typical success rates are less than 1% for alevins. Even during the upriver migration phase, significant mortality can occur (e.g., up to 90% mortality from river entry to spawning grounds for some stocks in some years).

As described in **Fish Migrations**: The Biology of Fish Migration, migration represents a complex interplay of behavior and physiology. This interplay is perhaps best exemplified by the Pacific salmon (genus *Oncorhynchus*) given the many natural challenges that these fish encounter during migration including predators, dynamic river flows and ocean currents, diseases, parasites, variable temperatures, and dramatically variable salinities. In addition, migrating salmon face additional anthropogenic challenges, such as fisheries exploitation, habitat alteration, and physical barriers (e.g., dams, climate change, and other ecosystem alterations).

There are three aspects of Pacific salmon migration that make them particularly remarkable. The first is their navigational ability, which enables them to migrate from the high seas to the exact steams where they themselves were spawned. Such natal spawning fidelity is rare among fish and among other animals. Even so, fidelity for home stream does vary among Pacific salmon species. Sockeye salmon (*O. nerka*), for example, tend to exhibit low rates of straying (<1%) whereas pink salmon (*O. gorbuscha*) tend to show less preference for natal sites.

Encyclopedia of Fish Physiology: From Genome to Environment, 2011, Vol. 3, 1945-1952, DOI: 10.1016/B978-0-1237-4553-8.00260-4

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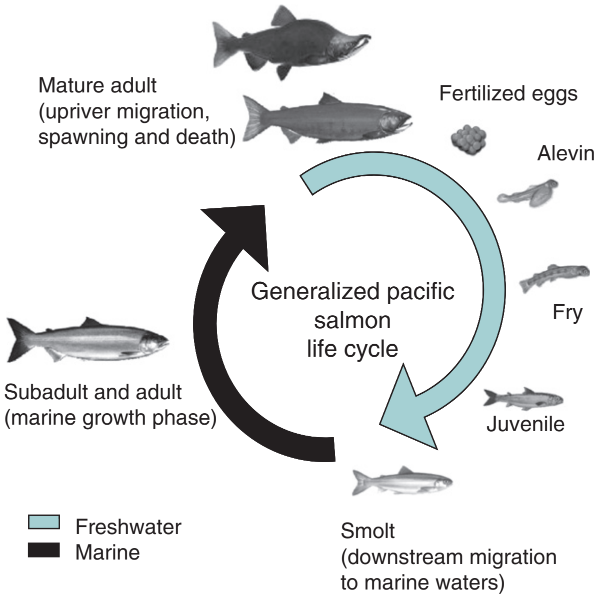

Figure 1 Generalized life cycle for Pacific salmonids.

Figure 2 Dead sockeye salmon on spawning grounds. After reproduction, most Pacific salmonids die, a characteristic of semelparity. The carcasses provide nutrients for the developing offspring as well a wide variety of plant and animal life (e.g., bears, bald eagles).

The second remarkable aspect is their ability to transition from freshwater to saltwater during their seaward migration in a process known as smoltification. When they return as adults, they reverse the process, transitioning from saltwater to freshwater. Many fish species would die when exposed to such a challenge, yet this is the norm for Pacific salmon, despite the need to remodel gill functions as well as their entire osmoregulatory apparatus (**see also Osmotic, Ionic and Nitrogenous-Waste Balance**: Osmoregulation in Fishes: An Introduction).

The third remarkable feature is the homeward river migrations of spawning adult salmon. Before they enter the river, they stop feeding and then complete a freshwater migration, sometimes in excess of 1000 km, using stored body energy, principally fat. Not only is this body fat used to fuel the entire spawning migration, but the energy must also be in sufficient quantities to support the maturation process: development of secondary sexual characteristics, the production of sperm and eggs (**see also The Reproductive Organs and Processes**: Vitellogenesis in Fishes and Regulation of Spermatogenesis), and the act of reproduction itself. Given these challenges, it is remarkable that any individual Pacific salmon is successful. Yet, every year, millions of Pacific salmon continue returning to natal spawning grounds throughout the north Pacific rim, extending from Japan and Russia in the western Pacific, northwards to Alaska, the Yukon, British Columbia, and south into Washington, Oregon, and California. Pacific salmon, however, are not found south of the equator except as an introduced or cultured species.

Although the most remarkable and notable migrations are the large-scale seaward and spawning migrations, Pacific salmon make their first migrations within hours of hatching! To fill their swimbladders for the first time, they must migrate from the gravel, where they are hatched to the water's surface to take this first gulp of air, otherwise they die. Other small-scale migrations include the day–night vertical migrations taken by juvenile salmon in rivers, lakes, and coastal seawater, usually for foraging and predator evasion. There are many other examples of specific small- and large-scale migrations made by Pacific salmon, but because there is immense variation within and among different species, we will generalize the various migratory phases of salmon and focus on what we will term the 'generic Pacific salmon'. By so doing, we will describe seven principal migratory phases that occur throughout the lifetime of a generic salmon.

Given that the vast amount of research that has focused on the downstream smoltification migration and the upriver spawning migration, we provide an in-depth description of these two particular phases. Just because the bulk of research efforts have been directed toward the larger-scale and relatively conspicuous migrations such as upriver migrations, this does not mean that the smaller, less conspicuous migrations are not important. All migratory phases of salmon are important for the survival of the species. Indeed, for an animal with only one life-time opportunity to reproduce, all migratory phases could perhaps be considered essential, irrespective of scale. Furthermore, sockeye, coho (*O. kisutch*), Chinook (*O. tschawytscha*) and pink salmon are the most well-studied salmon, particularly with respect to migration and physiology. However, other Pacific salmon including chum and masu salmon, as well as the Pacific salmonid steelhead (henceforth regarded as a Pacific salmon), make the same migrations during their lifetime and should not be overlooked. Although we have structured this article around the migratory life history of a

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generic Pacific salmon, we will provide examples and data from all species where available.

Larval Developmental Migration

The fertilized eggs of all Pacific salmon (including steelhead) hatch into young alevin in the gravel and rocky substrates where the mother laid them. These small salmon fuel early development using endogenous energy stored in their yolk sac. As swimming muscles develop and the yolk sac becomes nearly depleted, the alevin must forage. However, the first step is to obtain neutral buoyancy (**see also Buoyancy, Locomotion, and Movement in Fishes**: Buoyancy in Fishes) and to do so they must migrate from the safety of the gravel to the surface to fill their swimbladder. From the moment this first migration begins, the fish are exposed to a variety of threats including swift water currents and various predators.

Although the timing of this migration is critical, researchers know little about the specific environmental cues or physiological processes that mediate the initiation of this first migration. The endocrine system, and in particular the thyroid hormones, appear to be associated with photic sensitivity, which may serve as a proximate control for the timing of migration; alevins typically attempt the migration at night rather than day to minimize exposure to predators. Gas exchange occurs almost exclusively at the skin surface rather than at the gills during this phase of life (**see also Ventilation and Animal Respiration**: Respiratory Gas Exchange During Development: Respiratory Transitions), facilitated by dense capillary networks surrounding the yolks sac and a high surface area to body mass ration. The primary role of the gills at this phase, before they eventually are used for gas exchange, is for ionoregulation (**see also Osmotic, Ionic and Nitrogenous-Waste Balance**: Osmoregulation in Fishes: An Introduction).

Migration to Larval Feeding Grounds

River spawning is, by far, the most common strategy among salmonids. Alevins of many species of Pacific salmon then migrate to a nursery area (the river itself or a nursery lake) by either passive drifting or sometimes volitional swimming. During this period, they are termed fry. Sockeye salmon more typically migrate to a nursery lake, unless they were spawned in a lake.

The motivation for migration by sockeye fry to a lake-nursery environment is to take advantage of the growth potential offered by the productive lake environment, but getting there successfully from the natal stream requires important behavioral decisions to minimize energy use and avoid predators while migrating. Several physiological and behavioral adaptations facilitate this process, which vary depending upon whether the young fry move downstream or upstream to reach the nursery lake (i.e., moving with or against the water flow). The locomotory capabilities, muscle development, and anaerobic capacities of salmon fry can differ based on whether they migrate upstream to larval feeding grounds or downstream; upstream migrants have better swimming performance, muscle development, and anaerobic capacity. With regard to navigation to the lake environment, it is likely that rheotaxis (i.e., orientation against the water current) is the dominant orienting mechanism by which fry find their way upstream to a nursery lake, although olfaction may also play a role in fry, which must cross a tributary on the way to the nursery lake, or when fish must first swim down one river and then up another to reach the lake. These migrations generally occur at night, presumably to further minimize predation risk. Furthermore, life in nursery lakes involves diel vertical migrations associated with prey searching.

Smolting and Migration to Sea

The transition by salmon from freshwater to seawater is undoubtedly the best studied of all fish migrations. The principal motivation for seaward migration is the massive feeding and growth potential afforded by the nutrient-rich, open ocean compared with the nutrient-limited freshwater systems where salmon spawn. The smoltification (i.e., the transition physiologically into seagoing forms) process is an inherently stressful and risky period in the life cycles of salmon, and this phase is often considered a survival bottleneck, in which mortality is high. To survive this period, the smolts must carefully time this event to arrive at the ocean at an optimal time when ocean currents are favorable for their movement into coastal areas and when food resources are available. They must also overcome the challenges associated with the transition between hypoosmotic freshwater and hyper-osmotic marine environments, which imposes significant physiological stress (**see also Osmotic, Ionic and Nitrogenous-Waste Balance**: Osmoregulation in Fishes: An Introduction). The smolt process involves a suite of physiological, morphological, biochemical, and behavioral changes, which all require sufficient food energy intake as well as efficient energy use. Superimposed on all of this are new predation risks, as there are many animals that feed on young salmon in the new marine environment. All of these factors contribute to the survival bottleneck effect.

Increasing photoperiod in spring seems to be the key environmental factor that synchronizes the endogenous changes occurring seasonally. Long before smolting takes place, individual fry must make a decision as to when they are going to smolt. Most Pacific salmon species complete smolting within a few months after hatching. However,

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some species such as sockeye wait up 1 or 2 years after hatching. The factors controlling the subsequent down-river migration, however, are not well understood. Current evidence suggests that an innate, endogenous circannual rhythm is the primary controlling factor, one that is trigger by changes in photoperiod. Temperature regulates the rate of physiological processes and is also involved as a modulating factor, just as food availability is. What is clear, however, is that the process of smoltification is directly linked with initiating this migration.

Smolts tend to eat little during the downstream migration. In fact, upon entering the ocean, smolts are often malnourished and in a catabolic state, a condition that is similar to adult salmon during upriver migrations to spawning areas. There is some evidence that the size of the heart increases disproportionately during this time, which may enhance metabolic capacity and efficiency. Although downstream migrants tend to drift passively with the flow, they can and do actively swim, which enables them to attain remarkable migration speeds of 10–20 km or more each day. In river systems, such as in the Columbia River, hydro-electric and other dams can prolong migration by several weeks, and such delays can increase energetic costs and physiological disturbances, thus exacerbating patterns of mortality at a time when mortality is already high (i.e., the survival bottleneck) (**see also Swimming and Other Activities**: Applied Aspects of Fish Swimming Performance).

Smolting is a prerequisite to anadromy and must be regarded an important component of the downstream migration. The associated changes in body shape and metabolism facilitate active downriver migrations, and complex changes to gill, kidney, and intestinal functions occur to optimize ion- and water-exchange systems (**see also Osmotic, Ionic and Nitrogenous-Waste Balance**: Mechanisms of Gill Salt Secretion in Marine Teleosts and Mechanisms of Ion Transport in Freshwater Fishes). The suite of endocrine processes (**see also** The **Hormonal Control of Metabolism and Ionic Regulation**: The Hormonal Control of Osmoregulation in Teleost Fish) that underlie these physiological restructurings for a life in saltwater also have many co-evolved effects of migratory behavior. These include a migratory restlessness, which occurs in the days and nights before downriver migration begins, which is important for initiating the migration, as well as increases in general activity level (i.e., increased metabolic rate). The hypothalamus and possibly the pineal gland likely receive information about environmental light and temperature levels, which provide important information about the time of year (i.e., seasonality), and via the pituitary gland, a cascade of hormones are then released to direct physiology, behavior, and morphology along migratory lines. Hormones also elevate metabolic rate and alter the alertness of the fish to different stimuli, thus bolstering the probability of surviving the many challenges of migration.

Experimental studies have provided clues to the roles of many different hormones. During the pre-migratory season, some species of fry are negatively rheotatic, but experimental treatment with the thyroid hormone (T3) made them positively rheotactic. Thus, the natural surge of thyroxine (T4, a derivative of T3) that occurs prior to downstream migration is likely a key trigger for downstream migration. In addition to thyroxine, growth hormone, insulin-like growth factor, and cortisol are other hormones, which increase during smoltification and contribute to the development of gill chloride cells. Chloride cells on the gills represent the primary site for ion regulation in fish in saltwater (**see also Osmotic, Ionic and Nitrogenous-Waste Balance**: Osmoregulation in Fishes: An Introduction). When fish first enter seawater, cortisol concentrations in the blood increase widely and ion concentrations are temporarily elevated. It is worth noting that not all smolts successfully adapt to seawater. In fact, mortality rates among salmon are generally highest during this migration phase, largely due to osmoregulatory unpreparedness. Furthermore, one important hormone for saltwater preparedness is cortisol, which is also a principal stress hormone (**see also Hormonal Control of Metabolism and Ionic Regulation**: Corticosteroids and **Hormonal Responses to Stress**: Hormone Response to Stress). Though the transition to saltwater is inherently stressful, undue stress or stress beyond some threshold level can provide a conflicting physiological motivation, which can adversely affect migratory behavior and survival. For example, high cortisol could lead to early entry to the marine area, before physiological systems have had a change to fully prepare for saltwater, which would put the smolt at risk of mortality. Moreover, additional stressors can lead to further elevations in cortisol, and fluctuations in hematocrit and ionic status also correlate with mortality. All of this information serves to highlight the sensitivity of smolts to a number of factors during the fresh-to-salt water transition, which ultimately affect migration, survival, and fitness.

Migration to Ocean Feeding Grounds

Pacific salmon undertake directed coastal migrations to seek out rich food sources. Some species congregate in sheltered bays, where they exploit food resources that concentrate as a result of eddies and tidal shear forces. Consequently, their speed of migration varies greatly among species. Thus, salmon migrate from near-coast environments to the open ocean after several months to a year.

Many Pacific salmon feed in the Alaskan Gyre, a productive region of the northeast Pacific Ocean (i.e., Gulf of Alaska). Modeling studies suggest that the swimming speeds

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required for fish to override the influence of ocean currents in this region are prohibitively costly. Consequently, sockeye salmon, for example, are known to complete two large counter-clockwise loops of the northeast Pacific during 2 years, riding on the Gyre currents, while attaining a mature size and mass prior to homeward migrations. Nonetheless, most of the Gulf of Alaska is considered unfavorable for fish growth based on temperature suitability and prey availability. Salmon prefer cold water, and even small increases in surface water temperatures can dramatically reduce growth potential. To obtain sufficient energy to fuel the homeward migration to natal streams and enable reproduction, salmon in the ocean must feed optimally (i.e., near maximum ration) and continually, searching for zones of positive growth potential. To locate and exploit patchy food resources and areas with optimal thermal conditions, perhaps avoiding areas of high temperature, salmon must have finely tuned physiological systems that enable them to detect and evaluate subtle differences in growth potential conditions. Few physiological studies have been undertaken on Pacific salmon in the high seas to examine these mysteries.

Directed Migration to the Coast and Natal River

Pacific salmon start their impressive migration toward natal streams after 1–3 years of feeding in rich ocean waters. They typically gain about half of their adult mass in their last 6 months at sea and therefore continue feeding as they migrate towards the coast. What triggers salmon to make the decision to initiate homeward migrations is poorly understood, but is presumably linked to reproductive maturation and the endocrine system (**see also Hormonal Control of Reproduction and Growth**: Endocrine Regulation of Fish Reproduction). When researchers manipulate gonadotropin-releasing hormone (GnRH) in salmon, it triggers the growth of gonadal tissue and such growth is associated with a shift from foraging to homing in salmon.

Testosterone is an end-product of GnRH release and this hormone is believed to be the direct link to migration behavior. Masu salmon that were castrated to eliminate testosterone production stopped migrating, but resumed migration when subsequently injected with testosterone. Testosterone also influences the speed at which salmon return to their natal rivers – higher testosterone levels lead to faster swimming into natal rivers. The trigger for initial for GnRH release is likely associated with both exogenous factors such as changing photoperiod (i.e., changing seasons) and endogenous factors such as nutritional condition and body size. It is possible that GnRH will only trigger homeward migrations if fish which exceed certain growth or energetic thresholds. Thus, sometimes some Pacific salmon species vary in their abundance from year to year, sometimes spending an extra year in the ocean (with the exception of pink salmon which have a 2-year life cycle; **see also Hormonal Control of Reproduction and Growth**: Endocrine Regulation of Fish Reproduction and **The Reproductive Organs and Processes**: Vitellogenesis in Fishes).

After triggering a homeward migration, immense navigational challenges ensue as fish must find their way from the Alaskan Gyre to their natal coastal river. Natal homing represents one of the most remarkable characteristics of Pacific salmon migrations and one of the greatest feats of any animal. There is still much debate about the sensory cues and physiological systems used by salmon to direct homeward migration. In general, it is believed that while in the open oceans, salmon should swim with small vertical and horizontal oscillations, which would enable them to sample odors from different water layers. It is believed that salmon are able to recognize four major odorants (amino acids, bile salts, steroid hormones, and prostaglandins) at minute concentrations (**see also Smell, Taste, and Chemical Sensing**: Morphology of the Olfactory (Smell) System in Fishes). Collectively, these odorants from natal streams create what is known as the 'home stream olfactory bouquet', and these are apparently detectable even in the open ocean. Beyond detecting natal odors, salmon must use other sensory systems to help fish move toward natal streams. Vision seems to be of paramount importance for migratory salmon, and they may use a sun compass, polarized light patterns, or even landmarks to guide them homewards (**see also Vision**: Adaptations of Photoreceptors and Visual Pigments and Behavioral Assessment of the Visual Capabilities of Fish). Studies have revealed that even experimentally blind salmon can find their way home, slowed by days of random swimming. Presumably, the fish rely solely on olfactory cues when visual cues are unavailable. Water temperature and salinity levels (i.e., less saline waters) may also serve as orientation cues, particularly as they approach the river mouth.

Physiologically, preparation for transition to freshwater and reproduction also occur during homeward migration. Timing is critical. Salmon must position themselves at the mouth of the river at a time that coincides with an appropriate level of osmoregulatory preparedness and when river conditions such as flow and temperature are suitable for initiating upriver migration. Physiological sampling of fish between 700 and 250 km away from river entry shows that they are pre-prepared for the transition to freshwater well before arrival at the river mouth. For example, gill Na^{+}/K^{+}-ATPase, an important ionoregulatory enzyme (**see also Osmotic, Ionic and Nitrogenous-Waste Balance**: Mechanisms of Gill Salt Secretion in Marine Teleosts and Mechanisms of Ion Transport in Freshwater Fishes), is downregulated in preparation for freshwater despite the fish still being in full strength seawater.

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In addition, reproductive hormone concentrations are also elevated (**see also Hormonal Control of Reproduction and Growth**: Endocrine Regulation of Fish Reproduction). At some point during this phase, salmon stop feeding, with the exact time and location varying by stock and species.

Adult Upriver Migration to Natal Stream

One of the most conspicuous, well-studied animal migrations is that of the upriver migrations of Pacific salmon. These migrations are perhaps the best known because they present a rare opportunity to visibly see large numbers of salmon, and because the numbers of returning salmon can reach into the millions. The distances that salmon swim to reach spawning areas vary among populations within species, and among species, and can range from as few as 10–100 km to well over 1500 km. At times, salmon must leap over barriers (Figure 3). Regardless of the relative difficulty of a migration, energy reserves are limited and must be allocated carefully and conserved wherever possible. Energy stores are needed to fuel migration, complete sexual maturation, and support behaviors and morphological changes associated with courtship and spawning. At the onset of upriver migration, salmon populations differ in their somatic energy store in an adaptive way; long-distance migrants starting the migration with higher somatic energy (their gas tank is fuller for the journey ahead). A trade-off for long-distance migrants is that they have fewer and smaller eggs than short-distance migrants. This type of reproductive trade-off is common in other animals that make arduous migrations. To conserve energy further, long-distance migrants have smaller and more compact bodies making them more hydrodynamic when swimming. Furthermore, because long-distance migrants often encounter more difficult river hydraulics, they typically have a higher maximum metabolic rate.

As in coastal migrations, high testosterone levels are associated with fast river migration speeds, and also with high levels of aggression in spawning fish. Aside from its influence on behavior, testosterone and other sex steroids (e.g., estradiol, 11-ketotestosterone) are responsible for the production of gametes and the development of secondary sexual characteristics – the morphing from a sleek chrome colored ocean salmon into the hooked nosed, humped backed, and brightly colored form found on spawning grounds (Figure 4). Gamete production and morphological change generally occur over a period of weeks to months, and reach their peaks toward the end of upriver migration, which is necessary because both processes negatively affect hydrodynamic efficiency in homing salmon. Once migration is finished and salmon are on spawning grounds, swim efficiency is no longer important and spawning forms can be modified for reproductive combat.

Figure 3 Jumping sockeye salmon en route to spawning grounds. Pacific salmon have remarkable jumping abilities needed to negotiate natural and artificial barriers encountered during spawning migration.

Figure 4 Mature male sockeye salmon on spawning ground. The pronounced hump on the back, curved jaw (known as the kype) and red colouration are reflective of sexually selected traits that are desired by females.

Anthropogenic Threats Involving Salmon Migrations

Because of their migratory life style, Pacific salmon face a myriad of threats to their existence. Barriers to migration represent the single largest problem faced by anadromous Pacific salmon because an inability to physically proceed to a subsequent life stage can, in a short time, extirpate a population. Large dams and associated water diversions to store and divert water for hydroelectricity, agriculture, land reclamation, and human consumption have caused widespread extinctions. For example, in the Columbia River basin, 35% of Pacific salmon stocks are extinct and 40% are endangered. Some dams have been fitted with bypass structures (e.g., fish ladders or fishways; see Figure 5) to enable smolts to migrate downstream and adults upstream. Small barriers are also problems. The residential and industrial development has annihilated most salmon in the lower mainland in and around

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Figure 5 Fish passage facility to enable Pacific salmon to pass a dam in the Fraser River basin. Fish passages (also known as fishways or fish ladders) are engineered structures built to facilitate passage of fish around natural or artificial barriers.

Vancouver and bordering on Canada's greatest salmon watershed, the Fraser River. The most common type of stream crossing in the Pacific Northwest are corrugated pipe culverts which number in the hundreds of thousands on salmon bearing streams. Many have been installed improperly and are undersized resulting in streambed erosion at the downstream end and the culvert outfall perched above the stream thereby isolating upstream areas from downstream ones effectively eliminating adult migrants from many small creeks and streams. The replacement of perched culverts with larger diameter or open natural bottom arch culverts has shown to be an effective response to this problem (**see also Swimming and Other Activities**: Applied Aspects of Fish Swimming Performance).

Mortality can also occur due to physiological stress, delay, and physical injury. Migrations are inherently stressful periods of life, particularly those involving transitions between freshwater and saltwater. Anthropogenic stresses add to this.

Exacerbating these stresses are the environmental challenges associated with climate change. Warming rivers are now pushing some populations of adult salmon beyond their optimal temperature such that they have reduced or no aerobic scope for migration. In addition, disease and illness have become more apparent in these warmer migratory environments affecting spawning fish. Less productive and warmer oceans are reducing growth rates and energy reserves and changing migration timing (**see also Integrated Response of the Circulatory System**: Integrated Responses of the Circulatory System to Temperature and **Temperature**: Effects of Climate Change).

Because adult salmon migrate in high numbers and at predictable locales and times, humans have been able to effectively exploit this resource. For centuries, First Nations relied on salmon for food, trade, and as part of their mythology and spirituality. European settlers established coastal communities in North America, which relied heavily on the fishery. Though overfishing has led to several stock declines in the past, large fisheries still exist today. Depending on the type of fishing gear, large numbers of fish can escape from capture or are released after capture. Though research is limited, stress and delayed mortality of escaped or released fish can be high, especially in warm rivers. Thus, fisheries and a warming climate may put Pacific salmon in a double jeopardy.

Conclusions

Pacific salmon are a relatively well-studied group of animals compared with other fishes, and their migrations have been focus of considerable investigation. Researchers have learned that migrations are a complex interplay of behaviors and physiology, involving an integration of sensory and locomotory systems, mediated by endocrine and osmoregulatory systems. Pacific salmon have also served as key models for addressing questions related to fish orientation, mating systems, and evolutionary biology. Yet, there remain many large gaps in our knowledge. For example, we know relatively little about the biology of Pacific salmon in the ocean. In addition, even what appears as simple questions are difficult to address: e.g., why do some individuals die and some survive migrations, why do all migrants die after spawning? New technology such as the use of biotelemetry transmitters and archival data loggers, and the integration of these approaches with physiological bioassays show promise for illuminating the biology of salmon throughout their lives, but particularly in the ocean. In addition, functional genomics has the potential to dramatically improve our understanding of the physiological basis for different migratory strategies. Given the anthropogenic threats faced by Pacific salmon during their migrations, improving our understanding of the behavior and physiology of their migration will be essential to ensure appropriate management and conservation strategies.

See also: **Buoyancy, Locomotion, and Movement in Fishes**: Buoyancy in Fishes. **Fish Migrations**: The Biology of Fish Migration. **Hormonal Control of Metabolism and**

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Ionic Regulation: Corticosteroids; The Hormonal Control of Osmoregulation in Teleost Fish. **Hormonal Control of Reproduction and Growth**: Endocrine Regulation of Fish Reproduction. **Hormonal Responses to Stress**: Hormone Response to Stress. **Osmotic, Ionic and Nitrogenous-Waste Balance**: Mechanisms of Gill Salt Secretion in Marine Teleosts; Mechanisms of Ion Transport in Freshwater Fishes; Osmoregulation in Fishes: An Introduction. **Smell, Taste, and Chemical Sensing**: Morphology of the Olfactory (Smell) System in Fishes. **Swimming and Other Activities**: Applied Aspects of Fish Swimming Performance. **The Reproductive Organs and Processes**: Regulation of Spermatogenesis; Vitellogenesis in Fishes. **Ventilation and Animal Respiration**: Respiratory Gas Exchange During Development: Respiratory Transitions. **Vision**: Adaptations of Photoreceptors and Visual Pigments; Behavioral Assessment of the Visual Capabilities of Fish.

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