SALMONID FISH: BIOLOGY, CONSERVATION STATUS, AND ECONOMIC IMPORTANCE OF WILD AND CULTURED STOCKS

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Summary

Salmonids: the trout, salmon, and char, are of utmost economic and cultural importance to many people along the coasts of both the Atlantic and Pacific Oceans. They are also remarkable biologically due to their astounding abilities to perform long migrations and navigate accurately back to the streams where they were born. As anadromous fish, they utilize many habitats in both fresh and marine waters and in evolutionary and ecological terms, must be considered extremely successful animals.

In recent decades, however, many salmonid populations, including genetically distinct groups of fish, have been eliminated or severely threatened through over-fishing and habitat damage. Over the same period, salmonid farming has become a large international industry producing a greater weight of fish than the wild harvests combined.

1. Introduction

1.1 Classification

Here, we introduce the terms “family Salmonidae” and “sub-family Salmoninae.”

It is commonplace to use the term “salmonid” as a synonym for the well known and valuable salmon, trout, and charr—the groups treated here—but the family Salmonidae also includes the European genus *Hucho* and the whitefish (Coregoninae). Hucho is not discussed in this article and the white fish are treated elsewhere. The three genera dealt with here, comprising sub-family salmoninae, are: (a) Genus *Oncorhynchus*: the seven species of Pacific salmon, rainbow trout, cutthroat trout, and related species all with native ranges in the North Pacific Ocean or land masses adjacent to the Pacific; (b) Genus *Salmo*, the Atlantic trout, Atlantic salmon, and brown trout, all with native ranges in the North Atlantic Ocean and surrounding land masses; and (c) genus *Salvelinus*, the charr (lake charr, brook charr, Arctic charr, Dolly Varden charr, and bull trout), many of which are either Pacific shore species or circumpolar in their distributions. This is how the term “salmonid” will be used here. (See also *Coldwater Fish: Whitefish and Smelt*)

The three genera and species noted above comprise most of the commercially valuable salmonids as well as those important for recreation and aquaculture. There are many genetically distinct sub-populations (strains) within each species and much debate over classification with some taxonomists, suggesting the erection of many other species. The term “strain” is used here to denote a population sharing a common gene pool. For salmonids, strains are denoted by fish spawning together in well-defined spawning areas (see below). The term “stock” is very similar and is often used by fisheries scientists; it is a somewhat more flexible term and may not be used with the same precision as strain. The term “run” refers to a group of salmon returning to a river, but this is still more general and a run may include many separate strains. Runs may be bounded by narrow time frames or may be extended over months in which case they are sometimes referred to as fall runs, spring runs, or winter runs. Salmonid strains usually show very distinct biological features within a species. Some strains and even some species are endangered, some are supported wholly by hatchery production, and many strains have become extinct.

The preservation of salmonid species and strains is generally a high profile topic throughout the native salmonid ranges in the Northern Hemisphere. Salmonids have an enormous value as commercially caught fish and in recent years the sports fishing industry has grown to rival or exceed the commercial catch industry in value in many parts of the world. Aquaculture of salmonids has several faces including food production on salmon and trout farms, ocean ranching (release of hatchery fish into ocean environments for later capture), and conservation hatcheries designed to preserve threatened strains (see *Aquaculture, Principles and Prospects*). Some hatcheries produce fish for sports fishing alone. Farmed salmon and trout production has sharply risen over the last 20 years and now is approximately equal to world wild harvest in biomass and with a significantly higher value (see below).

Native, or original, distributions are referred to below, but it must be noted that salmonid species have been taken to many locations throughout the world. Often these populations have successfully colonized in new areas (successful introduction or naturalization), meaning that they have formed naturally reproducing populations in the new territory. In other instances they are held in captivity for aquaculture. The rainbow trout has formed the greatest number of naturalized populations and is found in both hemispheres and in all regions where the water temperature stays below about 16 degrees Celsius and above freezing in winter. This includes the high altitudes of many tropical countries such as Sri Lanka and Ecuador. The brown trout has also been naturalized in many countries but its congener, the Atlantic salmon has proven very resistant to colonization, especially the anadromous strains. The more complex the life cycle of a species and the more specifically it is adapted to local conditions, the less likely it is colonize. If anadromous species and strains have a genetically based component to their ocean migration patterns, then they are least likely to colonize in foreign oceans. (See *Environmental Impact of Introduced Alien Species*.)

All salmonids studied to date have strong “homing” tendencies; that is, they come back to specific geographical areas to reproduce. This naturally leads to the formation of sub-populations or strains as defined above, which are the population units of evolution. As discussed below, strain formation is a result of the inherent adaptability of the salmonids so that the many variations within one species allows a close tuning to the specific environment of each strain. All of the strains of a species within a region, for example a large watershed or several nearby watersheds, form a “meta-population” within which minor straying from one strain’s spawning beds to another’s results in a composite of genetic variation allowing the populations to evolve and adapt to changes in environmental conditions. These many strains should be preserved just as separate species should be preserved, because they represent a unique set of genetically determined traits that have evolved over many hundreds to thousands of years. Also, the strains, in the aggregate, provide an evolutionary resilience for the salmonids that is all the more important in the face of increasing anthropogenic environmental changes and threats. (See *Fisheries and Aquaculture: Towards sustainable Aquatic Living Resources Management*.)

Strain formation is so pronounced in salmonids that generalizations about any species are difficult. Mean body size within a species may vary over two to three orders of magnitude and habitat utilization (e.g. lakes, streams and rivers, oceans) is equally variable. Thus the descriptions offered here will focus on the more typical examples of species with brief notes on significant variations.

Most salmonid species are anadromous or have some strains showing anadromy, that is, most species have strains that can be found in salt water for some parts of their life cycle, but return to breed in fresh water. Some species or strains have very large ocean migrations and spend very little time in fresh water (e.g. chum and pink salmon) while other species spend only a short time in the ocean (e.g. the anadromous cutthroat trout and some Arctic charr which go to sea only for the summer and stay in coastal waters near the home stream). A few species or strains never swim in ocean waters, for example the lake charr and the resident (fresh water) rainbow trout.

2. Nomenclature and Distributions of the Salmonids.

The nomenclature and distribution of the three genera of salmonids is presented in Table 1.

Genus *Oncorhynchus*

Scientific **and Common Names**	**Native distribution**
Oncorhynchus nerka (sockeye salmon)	North Pacific Rim: Japan: – Columbia River
O. gorbuscha (pink salmon)	North Pacific Rim: Korea to California
O. keta (chum salmon)	North Pacific Rim: Korea to California
O. tshawytscha (chinook salmon)	North Pacific Rim: Northern Japan to California
O. rhodurus (amago salmon)	Southern Japan
O. masou (masu salmon)	Japan, parts of Russia
O. kisutch (coho Salmon)	North Pacific Rim: Northern Japan to California
O. mykiss (steelhead and rainbow trout)	North Pacific Rim: Mexico to Russia and Interior of N. America mainly east of Rocky Mountains.
O. clarki (cutthroat trout)	West Coast of N. America, Alaska to California. Some interior western strains.

Genus *Salvelinus*

Scientific **and Common Name**	**Native Distribution**
Salvelinus alpinus (Arctic charr)	Circumpolar, and southward as relict populations
S. malma (Dolly Varden charr)	Western North America and Eastern Asia
S. confluentus (bull trout)	North Western North America
S. fontinalis (Eastern brook charr)	Northeastern North America
S. namaycush (lake charr or lake trout)	Northern Canada and southward relict populations

Genus *Salmo*

Scientific **and Common Name**	**Native Distribution**
Salmo salar (Atlantic salmon)	North Atlantic Ocean and surrounding land masses and water bodies
Salmo trutta (brown trout)	European continent, U.K, Ireland

Table 1. Distribution and nomenclature of salmonids.

3. General Life History and Biology

Early rearing and embryological development (the development of the egg from fertilization to hatching) almost always takes place in fresh water, although some Pacific salmon strains may spawn in the intertidal zone of estuaries where the eggs and larvae are exposed intermittently to salt water. The period of fresh water rearing may vary from a few hours or days for pink salmon to several years for steelhead trout or Atlantic salmon. This is taken by many scientists to indicate a fresh water evolutionary origin for salmonids.

Salmonids are carnivores feeding on a wide variety of insects, marine invertebrates, and other fish. A large percentage of their body weight is muscle and most of this is "white" muscle designed for burst speed swimming. This muscle is often pigmented pink, red, or orange-red with carotenoids. This combined with the firm texture, long shelf life, and small number of bones creates the very high value of these fish. Salmonids are streamlined fish with wide, teeth filled mouths, large soft-rayed fins, and are capable of high swimming speeds. They can navigate, by unknown mechanisms, over vast distances with great accuracy. For example, a sockeye salmon in the North Pacific Ocean may travel 14 000 kilometers over three years of marine life and arrive back at the river of origin with quite precise timing, usually within a week or two of the annual mean arrival date. They have a keen sense of smell used to home in on the final approach to the ancestral spawning grounds. In streams and rivers, they usually have dark colors and often parr marks (vertical dark lateral markings) as camouflage, while in the pelagic zone (open waters of lakes and oceans) they are usually silvery with green or blue backs. When near breeding, they display dramatic color and body shape changes often looking like completely separate species.

The size of adult salmonids varies greatly—50 grams to 50 kilograms. Even within the same species there may be great variation. For example, Chinook salmon are the largest of the North American salmonids, sometimes reaching over 50Kg (110 pounds), but some Chinook males may mature as precocious parr at a size of 10 to 30 grams and these fish may even spawn with much larger adults returning from the ocean migration. Most ocean run salmonids are from 2 to 10 kilograms in weight, while fresh water residents are usually much smaller (.5–2 kg). But again there are many exceptions to all general rules about salmonids.

Salmonids, as noted, spawn in fresh water, either in the fall-winter months (Pacific salmon, charrs, Atlantic salmon) or in the spring (rainbow and cutthroat trout). Usually the female digs a depression in well-aerated gravel beds in fast flowing sections of streams and rivers where she is joined by one or more males. Eggs and sperm (milt) are extruded simultaneously and fertilization of eggs is immediate and usually very successful. The female then buries the eggs in the gravel "nest" and moves just upstream to begin the process again until all eggs have been deposited in 3–6 nests collectively called a redd. Courtship involves much intricate behavior and mate selection is complex.

Salmonid eggs are large (usually 3–8mm in diameter) and filled with yolk, which is about 50% water and 50% lipid (oils) and protein. The egg develops slowly in the low temperatures of the redd where inter-gravel water flow brings them a supply of oxygen and removes wastes. After some weeks (the exact period varies with temperature), the egg hatches and the developing embryo emerges to become a larval fish known as the alevin which has a large yolk filled sac on its lower surface. Alevins are very adaptable and can live at lower levels of dissolved oxygen than the eggs. They can move through the tight spaces in the gravel to find optimum conditions, but their preference is to remain in one place, propped upright, large yolk sac down, in the dark interstitial spaces of porous gravel beneath flowing streams. After several more weeks, the yolk sac is nearly used up and the alevin is ready to begin exogenous feeding (taking in food from the environment as opposed to living on its yolk). By this time it will have increased its size by several-fold and may weigh between .2 and 5 grams. It will now be called a salmonid fry.

When the fry first emerges from gravel beds, it is still somewhat photophobic, and will hide under rocks and in the gravel until dusk or night. Salmonids are physostomes, having an external connection to the gas bladder so on emergence they swim to the surface to take small "bites" of air to fill the gas bladder (a small air sac located along the dorsal region of the viscera). When the gas bladder is filled, the small fish becomes nearly neutrally buoyant and is ready to begin feeding on small insect larvae or other invertebrates. This may be a critical time with exposure to predators, floods (freshet), and uncertain food supply.

As noted above, the next stages of salmonid life histories are very diverse. For example, pink salmon will head downstream very quickly and utilize the shallow waters of estuaries for several weeks before heading out to sea for another 18 months before returning to spawn. Chum salmon fry may be similar to the pinks, or they may spend a few days to a few weeks in streams and rivers before entering the estuaries. They will feed in the marine environment for 2 to 5 years before returning to spawn. Steelhead trout will remain in the streams and rivers for up to five years before smolting at a size of about 160mm fork length and heading out to sea for a very long ocean migration. High latitude Atlantic salmon may require up to eight years in fresh water before becoming smolts beginning a complex and variable marine life history (see below). On the other extreme, some fresh water resident fish (for example resident cutthroat trout living above waterfalls) may move little more than a few meters from their section of stream.

Another variation noted among salmonids is the number of spawnings per individual. The five main species of Pacific salmon (chum, pink, Coho, sockeye, Chinook) all die after spawning. There seems to be no exception to this rule (except possibly for some of the precocious male Chinook parr). This is called semelparity—spawning once only. Other species such as the charrs, (genus *Salvelinus*), brown trout and Atlantic salmon, (the genus *Salmo*), and rainbow and cutthroat trout, (genus *Oncorhynchus*) may spawn more than once. These species may spawn every year after the first spawning, or they may spawn every other year. In many strains (e.g. steelhead), few fish actually survive long enough for a third or even second spawning. Repeat spawners are said to be iteroparous.

There are several sub-species or varieties recognized within the above categories. For example, the kokanee is a genetically distinct variety of sockeye salmon that has probably evolved many times, and both cutthroat trout and rainbow trout are divided into at least two sub-species each. Classification at this level is highly variable from author to author with considerable disagreement. As noted above, the native distribution differs greatly from the contemporary distribution due to introductions, aquaculture stocks, and extirpations.

The ocean migration of the anadromous species, especially the steelhead trout, the five species of Pacific salmon, and the Atlantic salmon, is a spectacular phenomenon. For example western Canadian salmon going to the high seas from British Columbia rivers, tend to migrate outward along the British Columbia coast in a “ribbon” 20 to 40 kilometers wide all the way to the Aleutian islands in Alaska. They then move offshore with many variations to their exact routes, swimming from 10 to 30 km per day, moving in the southward summer and northward in the winter. This is a feeding migration—there is much more food in the ocean than in fresh waters—and these fish grow rapidly. Some stay in the ocean several years while others return after only a few months. Even within one strain of one species, there may be great variation with several year classes (fishes of the same age) in the ocean at any one time.

For many species, the transition from early fresh water life to the oceanic phase is demarcated by a dramatic transition called smolt formation (or the parr-smolt transformation). Although this varies from species to species, it generally involves great changes in physiology mediated by hormonal changes that in turn are orchestrated by changes in day length (usually increases in day length.) The smolt is quite different from the darkly colored, camouflaged parr and is known for its bright silvery and blue/green coloration. There are many other changes in anatomy, physiology, and behavior, but, in brief, the smolt becomes a schooling fish with a preference for salt water, downstream migration, a slimmer, more buoyant body, a higher metabolic rate, and a new ability to hypo-osmoregulate (regulate blood salt content in water saltier than the blood). In salt water, the fish looses water through the gills, but replaces it by drinking. This creates a large influx of salts that are actively secreted across the gills by the same salt cells that have now proliferated in number. The environmental and genetic influences on the smolting process are complex. Usually there is a critical size to be attained in the late summer or autumn before the spring transformation takes place. The size differs from species to species.

Some species do not form smolts (e.g. resident rainbow trout) but can still be acclimated to salt water if they are over 40–50 grams in size. Most species can be grown in salt water if they are large enough and if they are introduced to salt water slowly.

During their ocean migration, most species swim in the upper few meters of oceanic surface waters, rising somewhat closer to the surface at night and descending a little deeper during the day. Food includes squid, small fish like herring or sand lance, euphausid shrimp, and other large plankton animals.

When the fish begin to mature in response to a genetic influence, age and body size, they begin to migrate back toward the coast at speeds higher than those seen during the feeding migration. They continue feeding and growing on their way back, but now they also begin to develop ovaries and testes in preparation for spawning. It is not known how they navigate, but it is assumed that they use a bi-coordinate system of navigation (that is they locate themselves in latitude and longitude as does a modern ship). This may be accomplished through celestial observations, the earth's magnetic field and an internal clock, but the mechanism is not known. Their accuracy and timing of arrival at the home stream is quite precise, and it is known that as they enter the home river estuary they begin to use olfaction (smell) to complete the return to the spawning area. This topic is discussed in detail in the section below on Atlantic salmon.

Bouquets of smell from the home stream and even home spawning beds in some cases, appear to have been learned at critical periods during fresh water rearing by a process called imprinting, and these are now remembered and used to find the home stream. Salmon can detect water-borne odors in the parts per billion range, and each stream has its own particular range of odors including some that may originate from the salmon populations themselves (see discussion below under Atlantic salmon). Straying (going to the "wrong" stream) is relatively rare and as noted above, this tendency to home to the stream of birth (or rearing) creates strains of related fish that can adapt closely to the characteristics of their stream or lake. This has many implications for management and enhancement.

4. Environmental Requirements

4.1 Temperature

As noted above, salmonids are coldwater fish. They do well in water temperatures from 1C to 20C, but usually grow most rapidly between temperatures of 10C and 18C depending on the species and strain and life stage. They also require high levels of dissolved oxygen—ideally close to saturation, concentrations ranging from 8 parts per million to 12 parts per million depending on temperature and altitude.

The hemoglobin in the salmonid's red blood cells is designed to work well at high levels of dissolved oxygen, but not at lower levels that create stress. In this respect, salmon are very different from eels, carp, bass, and many other fish.

4.2 Salinity

Salmonids are, as a group, euryhaline: they can withstand and do well over a wide range of salinity, but they cannot venture into marine waters unless certain conditions are met (this may involve smolt status, fish size, and temperature). As noted before, most species have anadromous strains or life stages. In fresh water, there is a constant influx of water through the gills into the fish's tissues.

This is pumped back out by the kidney (located near the backbone of fish), which produces copious amounts of dilute urine (up to 1/3rd of the salmonid's body weight per day). Special cells on the gill filaments move salts into the bloodstream to make up for salts washed out in the urine.

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Bibliography

Baum E. (1997). Maine Atlantic Salmon, A National Treasure. *Atlantic Salmon Unlimited*, 224 pp. Maine: Herman. [A superb review of Atlantic salmon biology on the N.E. coast of the United States with emphasis on Maine stocks. Reviews species biology, historical records, and current efforts to save endangered strains.]

Barton B. A. (1996). General Biology of Salmonids. *Principles of Salmonid Culture* (eds. Pennell W. and Barton B. A.), pp. 29–96. 1039 pp. Amsterdam: Elsevier Science. [A general and complete review of salmonid biology stressing anatomy and physiology]

Behnke R. J. (1992). *Native Trout of Western North America*. American Fish Society Monograph. 6, 275 pp. [The most exhaustive review of the many strains and species of western North American trout.]

Groot C. (1996). Salmonid Life Histories. *Principles of Salmonid Culture*, (eds. Pennell W. and Barton B. A.) pp 97–230. 1039 pp. Amsterdam: Elsevier Science. [A broad view of the life histories of salmonids with emphasis on behavior and ecology. There is a general account followed by reviews of specific species.]

Heard W. R. (1996). Ocean Ranching: An Assessment. Principles of Salmonid Culture (eds. Pennell W. and Barton B. A.) pp. 833–870. 1039 pp. Amsterdam: Elsevier Science. [A review of Pacific Ocean enhancement activities with emphasis on Japanese and Alaskan programs. Includes economic analysis].

Groot C. and Margolis L. (eds.) (1991). *Pacific Salmon Life Histories*, 564 pp. Vancouver: UBC Press. [An extremely detailed and scientific review of the life histories of the Pacific Salmon including two Japanese species. Extensive literature reviewed.]

Groot C., Margolis L, and Clarke W. C. (eds.) (1995). *Physiological Ecology of Pacific Salmon*, 510 pp. Vancouver:U.B.C. Press. [A review of Pacific salmon ecology from a physiological perspective. Includes chapters on growth, osmoregulation, and feeding among others. Very extensive literature review. Intended for a scientific audience.]

Jorstad K. E. and Naevdal G. (1996). Breeding and Genetics. *Principles of Salmonid Culture*, (Pennell W. and Barton B. A. eds.) pp. 655–726. 1039 pp. Amsterdam: Elsevier Science. [A comprehensive scientific over-view of the principles governing genetic change in salmonids including principles of breeding programs and conservation hatcheries. Extensive literature review.]

Kalleberg H. (1958). Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and Salmo trutta L.). Rep. Inst. Freshwat. Res. Drottningholm, 39, 55-88. [One of the early important studies on the behaviour of salmonids.]

MacKeown B.A. (1984). *Fish Migration*, 284 pp. Beckenham, UK: Croom Helm. [A general review of fish migration including that of salmonids. Theories of navigation are reviewed.]

Meerburg D. J. (1986) Salmonid Age at Maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89:118 p. [A discussion of age at maturation and the ecological and physiological factors that influence it. Includes discussion of evolutionary benefits to varying age-size-maturation combinations.]

National Research Council. (1996). *Upstream, Salmon and Society in the Pacific Northwest*, 451pp. Washington, D.C: National Academy Press.. [A detailed case history of the salmonid populations in the Columbia River drainage and nearby systems in the Pacific North West states. A very important book for managers of salmonid species and stocks. Full discussion of genetic principles and salmonid strain conservation.]

Nordeng H. (1971). Is the local orientation of anadromous fishes determined by pheromones? *Nature* **233**, pp. 411–413. [A research report on pheromone research on the homing mechanism of salmonids and other fish.]

Nordeng H. (1977). A pheromone hypothesis for homeward migration in anadromous salmonids. *Oïkos*, **28**, pp. 155–159. [Further research reported on pheromone studies on the homing mechanism of salmonids.]

Nordeng H. (1989). Salmonid migration: hypotheses and principles. *Salmonid migration and distribution symposium* (E. Brannon and B. Jonsson eds.), School of Fisheries, University. of Washington, 1–8. [A broad and inclusive examination of migration issues in the migration of salmonids including pheromones, high seas navigation mechanisms and others.]

Quinn T. P. and Groot C. (1984). Pacific salmon (Oncorhynchus) migrations: orientation versus random movement. Can. J. Fish Aquat. Sci., 41, pp. 1319-1324. [A research paper discussing alternative concepts in navigation. Although the discussion is specific, there is a useful literature review.]

Biographical Sketches

William Pennell graduated from Bowdoin College (BA) and McGill University (Ph.D., Biological Oceanography). He has been in the Department of Fisheries and Aquaculture at Malaspina University-College for the last 20 years teaching in a combined technology and degree program for both aquaculture and fisheries. Before this, he worked for native groups in British Columbia to develop fisheries management and aquaculture programs. In aquaculture his work has focussed on salmonid rearing in both salt and fresh water and invertebrate culture. In fisheries he has been involved in salmonid biology and marine and fresh water zoo-plankton. He is currently doing research on the copepods of British Columbia. Dr. Pennell has also been involved in many overseas projects in aquaculture. Currently he is working in a CIDA (Canadian International Development Agency) project to develop shellfish aquaculture in the artisinal fishing communities of coastal Brazil. He is a past President of the Aquaculture Association of Canada and sits on various boards and committees at both the local and national level.

Patrick Prouzet graduated from University of Western Brittany (PH.D., Biological Oceanography). He has been in the Aquaculture Department at CNEXO (National Center for the Exploration of the Sea) from 1975 till 1982 then at IFREMER (French Institute for the Exploitation of the Sea) in the Department of Fisheries. He worked on the Atlantic salmon restoration program of Brittany rivers from 1975 till 1984 and on sea ranching program during the period 1985-1987. From 1988, he has been involved in dynamic population of amphihaline species, in some studies of estuarine fisheries of Adour river and in the assessment of Bay of Biscay anchovy population. He represented France at the International Council for the Exploration of the Sea in the framework of the Anacat Committee since 1977 then in the framework of the Living Resources Committee since 1997.

Presently, he is working in an European project to evaluate the migratory behaviour and abundance of glass-eel in the Adour estuary and he is currently doing research on the impact of anthropogenic effects on the future of amphihaline species in France.