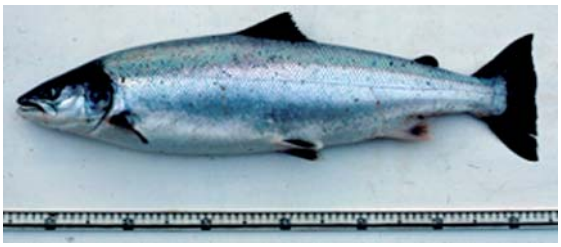
Atlantic salmon – *Salmo salar*

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Biology, ecology and genetics

Distribution

The species' range encompasses Europe, North America, and Greenland (1) (Fig. 1). Non-anadromous forms occur in Europe in a few land-locked locations in Norway and Sweden, and throughout the Neva/Lake Ladoga system and Karelia regions of Russia. In North America non-anadromous forms occurred throughout most of the species' historical range, as far west as Lake Ontario, and remain common throughout Newfoundland, Labrador and northern Quebec. Over the last 150 years anadromous stocks have become extinct in many rivers. Native stocks are no longer present in the Elbe and the Rhine, two of Europe's largest rivers, or in many rivers draining into the Baltic and in southern England, France and Spain, which previously had abundant salmon runs (1), and have become extinct in many rivers in the US and southern Canada (1, 2, 3). The species has been introduced in a number of locations, both within its range and elsewhere (1) but its native range has contracted and fragmented. Most remaining stocks, particularly in the southern part of its range and in the Baltic Sea region, are depressed and many no longer self-sustaining; detailed information, however, is lacking for most river systems where the species still occurs.

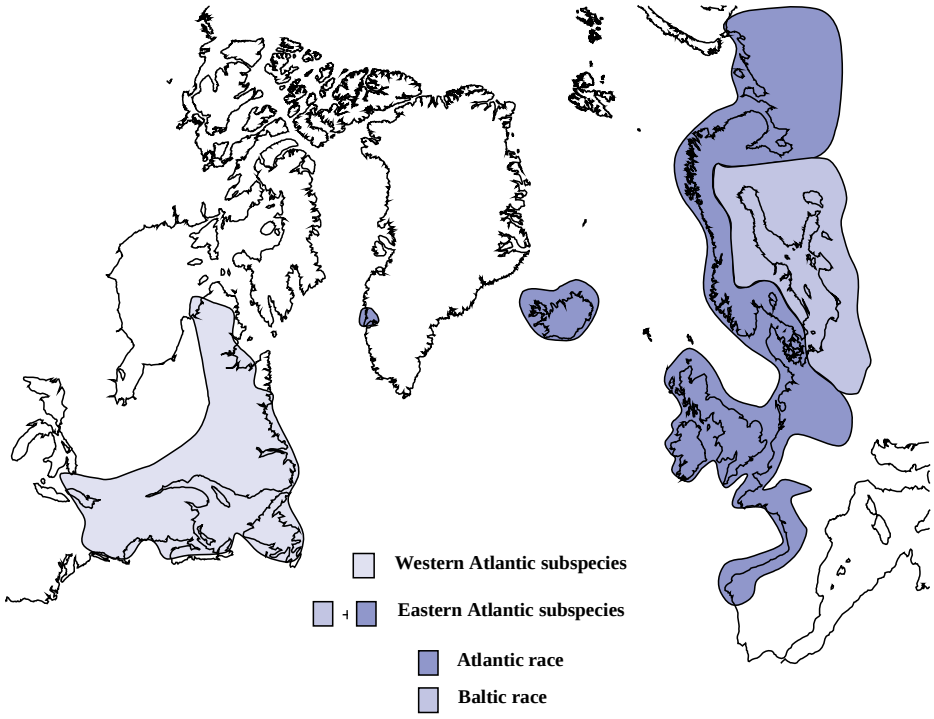


Fig. 1. *The historical distribution of Atlantic salmon and its main evolutionary divisions.*

Biology

Atlantic salmon, *Salmo salar,* are salmonid fishes of the temperate and subarctic regions of the North Atlantic (4). They show strong homing to natal areas to spawn and are highly variable in their biology within and among locations. Fertilization is external with eggs generally deposited in gravel nests in rivers and covered by the female. Over 70% of natural mortality occurs from the egg to fry stage. Juveniles feed on small invertebrates and adults on crustaceans and fish. Most stocks are anadromous - egg and juvenile development occur in freshwater, as smolts they migrate to the sea, where they feed, mature, and they return to rivers to spawn and complete their life-cycle (Fig.2); migrations in rivers may exceed 1 000 km and in the sea 2 000 km. Some salmon are non-anadromous, completing their entire life cycle in freshwater (Fig.2), and migrate from spawning rivers to lakes, or are locally resident in either rivers or lakes. Anadromous forms spend 1-7 years in freshwater and 1-4 years at sea; variable proportions of male parr mature in fresh water and contribute to spawning, and some spawners survive, migrate back to sea, and return to spawn again. Adults range from ~50-120 cm and ~2-30 kg; females produce ~2 000 – 15 000 eggs. Their marine phase is poorly understood as is, to a lesser degree, the ecology of eggs and alevins in river gravels (4). Resident fish mature at age 2-5, can live for 10 or more years, growing to ~12-120 cm and ~20 g to 20 kg, depending on location, with spawning in consecutive years common. Small females produce as few as 33 eggs and some populations are lake spawning.

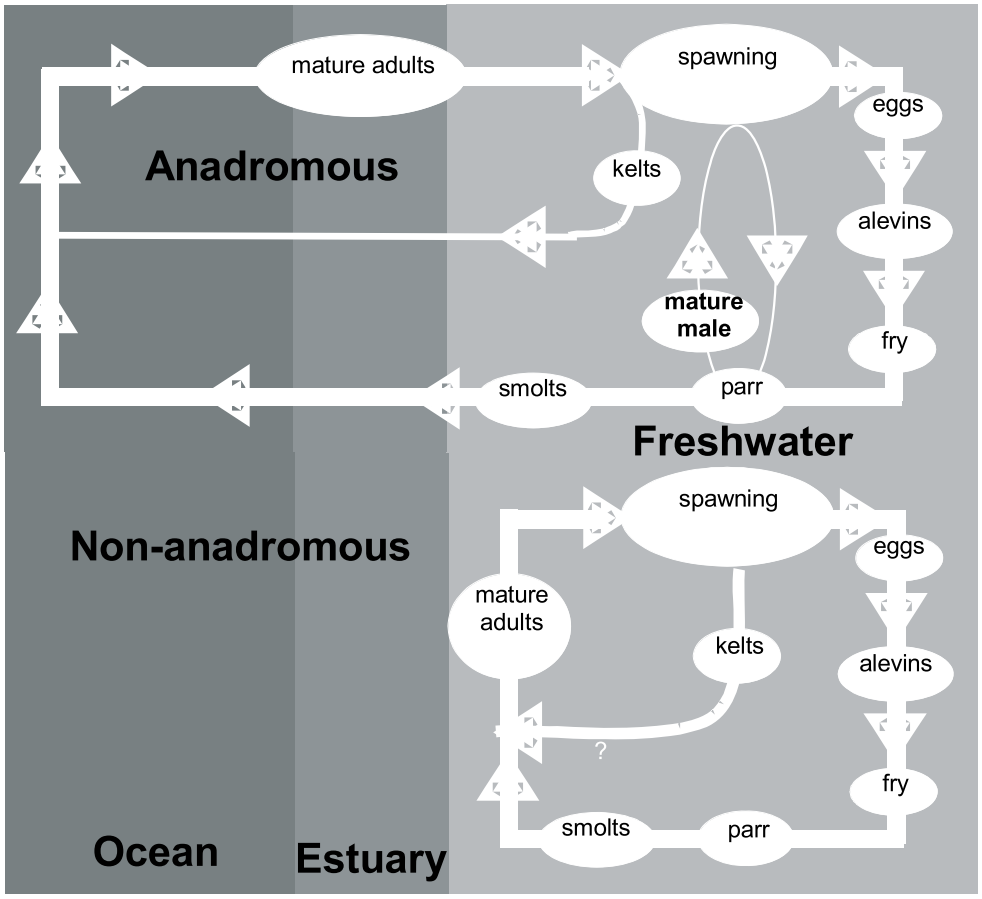


Fig. 2. *The basic life cycles of anadromous and non-anadromous Atlantic salmon*

Capture

Exploitation in the North Atlantic, in decline over the last half century (5) (Fig.3), encompasses high seas, coastal, river mouth fisheries, and in-river recreational fishing, with the latter making up to 80% of regional catches and 17-87% of fish caught in rivers released after capture. In the Baltic Sea coastal and river fisheries have become relatively more important than sea fisheries, but overall fisheries catches have declined and only ~1 000 tonnes of wild fish were caught in 2004(6).

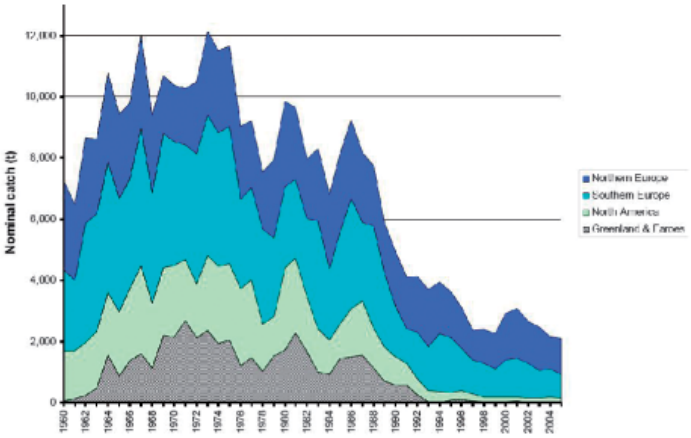


Fig. 3. *The nominal North Atlantic catch of Atlantic salmon since 1960 - excludes Baltic Sea (5).*

Population genetics and local adaptation

Conditions necessary for population structuring exist: homing to natal rivers to spawn, a naturally fragmented distribution of spawning and juvenile habitat, and a capacity for local adaptation. The existence of structuring and highly restricted contemporary gene flow, even among tributaries within many rivers, is indicated by observed molecular genetic differentiation (7). Limited but sporadic gene flow among populations may locally link populations within or among rivers into evolutionarily connected meta-population groups, but this is poorly understood. Genetic isolation has been sufficient for phylogenetic and evolutionary divergence at all spatial scales (7) and divides the species into two distinct subspecies (Fig. 3), *Salmo salar salar* Linnaeus 1758 and *S. salar sebago* Girard 1854, respectively, which have been largely isolated for >500 000 yrs (7); these encompass, respectively, salmon in the eastern Atlantic and the other salmon in the western Atlantic. The former are further divided into two less divergent, more recently evolved "races", one associated with Atlantic and the other with Baltic drainages (Fig. 3). Further regional evolutionary divisions occur within these three groups, and non-anadromous stocks have evolved independently in most river systems (7).

Stocking of fish has been carried out across the species European range, to supplement depressed river stocks, e.g. where spawning grounds have been lost through hydroelectric developments, and to restore extinct stocks, but is in decline and increasingly tightly controlled. Increased abundance is seen in some cases but most attempts to restore self-sustaining salmon populations have failed and its value appears variable and is in many situations questionable at best.

Conditions for local adaptation of Atlantic salmon exist and the evidence it occurs is compelling, though largely circumstantial (8). High heritability values are seen

for variation in fitness-related traits such as growth and body composition, and to a lesser extent for health traits such as disease resistance, and for survival and life history traits. Also, genotype-environment interactions and genetic correlates occur for many traits, translocations of salmon generally fail, performance of domesticated stocks in the wild is poor, performance differences occur among wild stocks in common-garden experiments, and there are non-random patterns of inherited resistance to some parasites in the wild. Through the process of domestication cultured stocks become adapted to a culture environment. A major component of local adaptation is likely to involve a genetic response to water quality, photoperiod and related variables, and disease vectors, as they are of particular biological importance and can vary spatially in a predictable way, likely to promote adaptive evolutionary change. However, local adaptation most likely varies spatially and can be expected to be lower within meta-populations.

Breeding and culture practices

Production

European farming started in 1969 and was >800 000 tonnes in 2004 (5) (Fig.4), ~60% of world and > 90% of North Atlantic production, is valued at US$ 141 billions (9) and is 300-600 times the nominal catch of wild salmon. Norway is Europe's biggest producer (565,902 tonnes) followed by the UK (158,099 tonnes) and the Faeroe Islands (37,296 tonnes). Ranched production in the Baltic involved the release of 5.28 million in 2004 (4.6-6.5 million/yr from 1987-2004) and contributed ~50% of the Baltic fisheries catch (6), though data show significantly lower survival to fishery for ranched smolts. Elsewhere in Europe, only ~10 tonnes of ranched salmon are now harvested (5).

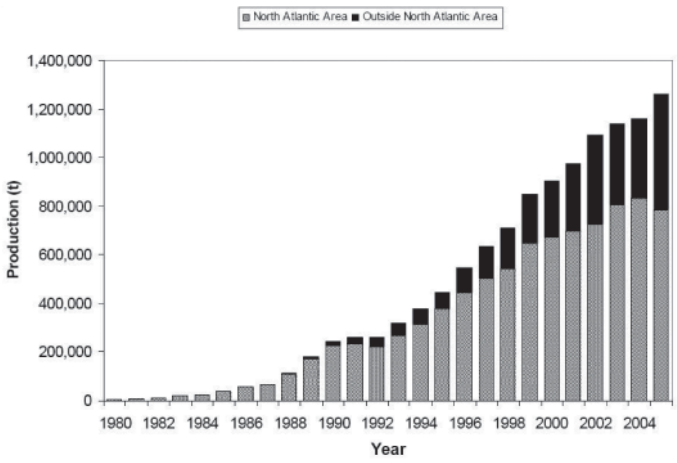


Fig. 4. *Farm production of Atlantic salmon since 1980 (5).*

Hatchery practices

Broodstock are normally moved from sea cages into freshwater tanks in autumn prior to stripping, producing ~1,600 eggs per kg body weight (10). Eggs are stripped, fertilized with milt, hardened in water, and disinfected prior to placing in hatchery trays or silo systems for incubation. Following eyeing, they are "shocked" to remove unfertilized and dead eggs. Hatching occurs in trays or, following transfer, in tanks. Both eggs and alevins are normally reared in water at <9 °C.

Grow out

Late alevins are transferred into tanks with flow-through or recirculation systems, and fed on inert feeds until smolts; this takes 1½ years on ambient temperature and light regimes, but as is now normal, light and temperature regimes are manipulated to reduce this to 6-8 months; in some areas parr are transferred for on-growing to cages in lakes. Production densities may be up to 50 kg/m^3 or higher (10). When smolts, at 40-120 g, fish are transferred to marine net cages anchored to the seabed, where temperatures are 6-16 °C and salinities near oceanic levels (33-34‰), with stocking densities of up to 20 kg/m^3; cages of 40 m in diameter and 20-30 m depth, and ten or more grouped together at a site, with most sites having only a single generation of fish. Rearing in pump-ashore seawater tanks is the exception. On-growing in cages lasts 1-2 years before harvesting at 2+ kg by netting and live transfer to slaughter plants by well-boats. Location of farms is regulated to ensure current speeds are sufficient to eliminate waste and supply well oxygenated water (~ 8 ppm), and takes proximity to other farms and/or wild fisheries into account. Sites are generally fallowed for 6 or more weeks before a new generation of fish is introduced.

Selective breeding

The European industry is now largely based on a few selectively bred strains of mostly Norwegian origin. The first, established in the early 1970s (10) with 190 males and 430 females from 40 Norwegian river, encompassed four distinct strains to deal with the species' 4-year generation interval in culture. There are now four breeding programmes in Norway providing ~80% of Norwegian farms with smolts. Two utilise combined family and within-family selection programmes and each comprises a breeding station, several commercial farms and fish labs, and commercial multiplier hatcheries to produce smolts for farms. Trait selection started with growth and now encompasses sexual maturation, disease resistance, and carcass quality. Such broad breeding goals result in a low selection pressure across a wide spectrum of alleles. Programmes involve testing 300-400 families per year with effective breeding populations of 33-125 individuals, sufficient for short-term inbreeding avoidance. Little genetic exchange occurs between Norwegian programmes but fish are widely exported within and outside Europe. Similar family based breeding programmes exist in Iceland, Ireland, Faeroe Islands and Scotland.

Differentiation from wild stocks

Genetically differentiation from wild populations is expected due to: 1) the effects of limited numbers, non-random selection and sourcing of wild founders, 2) domestication selection, 3) loss of variability by genetic drift (increased by using small numbers of brood fish), and 4) selective breeding for economic traits (11). Differences have been reported with regard to variation at protein genes, and at mitochondrial and nuclear DNA loci as well as for phenotype variation (6). Molecular studies show reductions in numbers of alleles and mean heterozygosity of up to 50% and differentiation between strains and wild founder populations 2-6 times higher than among wild populations in general. Changes due to domestication and trait selection exist for growth rate, body size, survival, delayed maturity, stress tolerance, temperature tolerance, disease resistance, flesh quality and egg production. Unintentional correlated changes also occur for fitness-related traits including survival, deformity, spawning time, morphology, fecundity and egg viability, aggression, risk-taking behaviour, and growth hormone production. A >100% and 20% genetic gains have been recorded for growth and feed conversion

efficiency, respectively after 5-6 generations in one Norwegian farm strain (12); not surprisingly, farm salmon outgrow wild salmon both in culture and the wild (11).

No commercial production of triploid or transgenic salmon occurs in Europe. The former produce sterile fish but there is concern over the use due to reduced growth rate and deformities, and marketability is hindered by consumer perception that they are GMO´s. Salmon transgenic for a growth hormone gene have been engineered and are awaiting US FDA approval, and a transgenic freeze-resistant salmon is under development for aquaculture in low temperatures.

Interaction studies

Around 0.5-2 million salmon (0.5-1.6% of production) escape each year into the North Atlantic, ~50% of the wild pre-fishery abundance in the region (9), despite close regulation of farming. Numbers of sexually mature farm salmon returning to rivers in the 1980s and 1990s ranged from 200 000-300 000 and composed up to 80% of salmon in some Norwegian rivers (9). Escapes generally enter rivers, near to their farm of origin, but some may do so hundreds of kilometres away, where many interbreed with wild fish, with farm females generally more successful than farm males and more hybrid than pure offspring produced. Escapes of juveniles from hatcheries and freshwater cages occur in some areas but their numbers and impact are poorly documented.

Both can cause direct genetic effects on wild populations (9).

Predictions of impact based on modelling vary, depending on the assumptions made. In field studies indirect effects are seen due to behavioural, ecological, and disease interactions which can reduce effective sizes of wild populations and increase genetic drift; in particular, competition with farm fish and hybrids, which are larger, may depress wild smolt production (11). Direct effects occur due to interbreeding. Farm and farm-wild hybrid offspring show substantially reduced lifetime success with poorer survival in freshwater and at sea, causing reduced recruitment of wild fish (11). When farm escapes are re-occurring, fitness reductions may accumulate and can lead to the extinction of already depressed populations. Change may also occur in the character of wild populations. For example, increases may occur in multi-sea-winter salmon in predominantly grilse populations. However, though more fecund, given their reduced lifetime success, such hybrids do not compensate for the loss of wild recruitment, and still decrease overall population fitness. Such negative consequences may not occur in all situations, but are likely to be widespread. Impacts are expected even if all wild populations were genetically identical as domestication appears to be the main reason for the genetic differences between farm and wild populations.

Conclusions/Implications

Conclusions

- The basic biology and distribution of the Atlantic salmon are well understood.
- Two distinct forms occur – anadromous and non-anadromous, both highly but variably, structured into populations and meta-populations with little gene flow.
- Evolutionary structuring, due to historical isolation, is seen at all spatial scales, including within rivers, and between defines Eastern and Western Atlantic stocks as distinct subspecies.

- Population and meta-population structuring, and the spatial boundaries of these genetic groups, within and among river systems, remains to be resolved in detail.
- Compelling, but largely circumstantial evidence, indicate genetic populations and meta-populations are generally locally adapted, though its degree and spatial scale remain unclear.
- Maintaining evolved adaptive population and meta-population structuring, and historical habitat conditions, is essential for healthy, self-sustaining wild stocks.
- Production of farm salmon is well documented and 300-600 times wild production.
- The biology of farm stocks is well understood, rearing practises well defined, and breeding programmes and culture highly standardised and carried out at a sophisticated level, and farming occurs in a well defined regulatory environment in Europe.
- Production is largely based on a few breeding strains largely established from wild Norwegian populations and developed using family based selection programmes with large effective population sizes, but showing genetic shifts due to founder effects; there is no commercial farm production of triploids or GMO salmon in Europe.
- Selective breeding for economic traits has focused on growth, disease resistance, delayed sexual maturity, and carcass quality.
- Farm salmon are genetically different from wild fish with respect to a range of molecular and phenotypic traits, and display reduced genetic variation though the majority of additive genetic variation for phenotypic traits has been retained.
- ~0.5-1.6% of farm salmon (0.5-2 million) escape, equal to ~50% of pre-fisheries abundance of wild fish, of which ~10% enter rivers where many interbreed with wild salmon and trout.
- Farm escapes can have significant direct and indirect negative impacts on wild populations by reducing productivity, though the range of scenarios producing significant impacts is unclear; interbreeding can directly impact by reducing mean fitness and indirect effects occur through competitive, disease and parasite interactions; studies show farm fish in the wild have severely reduced life-time fitness compared to wild fish with intermediate hybrid fitness.
- Modelling suggests the impact will depend on the magnitude and frequency of escapes, the "health" of the wild populations and the specific genetic differences between the farm and wild stocks involved, and that in the extreme may lead to extinction of wild populations.
- Effective containment and considered location of farms, involving epidemiological zones and vaccination programmes to control disease and parasites, as well as maximising domestication of farm strains, is the best ways to ensure avoidance of direct and indirect genetic impacts.
- The ability to identify farm fish has significant potential to help understand the extent of fish escapes, their causes, and their impacts.



Research priorities

- Detailing the evolutionary diversity and the spatial boundaries of genetic populations, the extent to which they are dynamically linked into meta-populations and are conditioned by historical and contemporary factors environmental influences, including understanding of the extent of genetically effective straying among populations through juvenile and adult dispersal.
- Developing roboust, cost-effective methods for monitoring diversity, abundance, and effective breeding size (N_e) of local populations and metapopulations, taking into account overlapping generations and mature male parr; obtaining historical data to assess change.
- Understanding the degree and scale of local adaptations, and selective forces and how these vary spatially, by measuring the heritability of fitness related traits in the wild and carrying out, common garden/reciprocal transfer experiments.
- Increasing knowledge of the marine ecology of anadromous populations and metapopulations, and how this varies, as increased marine mortality, underlies recent declines, in abundance.
- Resolving the genetic basis of local adaptation and domestication, and how the former can vary, to understand the basis of outbreeding depression when farm and wild stocks mix.
- Developing low-cost genetic and non-genetic methods for ID of farm fish.
- Building realistic working simulation models to assess impact risk across interaction scenarios, define research priorities, and assess the efficacy of different management strategies.
- Field research to "proof" simulation models, including studies of indirect genetic and ecological impacts from disease introduction and of density dependent population dynamics.

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