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Perspectives on Salmon Aquaculture: Current Status, Challenges and Genetic Improvement for Future Growth

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Abstract

With an estimated global value of US\$15.6 billion, farmed salmonids represent a precious food resource, which is also the fastest increasing food producing industry with annual growth of 7% in production. A total average of 3,594,000 metric tonnes was produced in 2020, behind Chinese and Indian carps, tilapias and catfishes. Lead producers of farmed salmonids are Norway, Chile, Faroe, Canada and Scotland, stimulated by increasing global demand and market. However, over the last 2 years, production has been declining, occasioned by effects of diseases as well as rising feed costs. Over the last year, production has declined sharply due to effects of covid-19. This chapter reviews the species in culture, systems of culture, environmental footprints of salmon culture, and market trends in salmon culture. Burden of diseases, especially Infectious pancreatic Necrosis, Infectious salmon anemia and furunculosis, as well as high cost of feed formulation, key challenges curtailing growth of the salmon production industry, are discussed. A review is made of the international salmon genome sequencing effort, selective breeding for disease resistance, and the use of genomics to mitigate challenges of diseases that stifle higher production of salmonids globally.

Keywords: salmon, smolts, salmon genome, fish meal, parr, anadromous

1. Introduction

Salmonids constitute a large group of teleost fishes thriving in the cold-water fisheries and aquaculture. Salmonids belong to the family Salmonidae, comprising 11 genera, including the salmon, trout, charr, ciscos, grayling, hucho and the freshwater whitefish [1]. The sub-family Salmoninae groups three well known genera: *Onchorynchus*: rainbow trout, cutthroat trout, Pacific salmon, all with native ranges in the North Pacific Ocean. The genus *Salmo* groups the Atlantic salmon, Atlantic trout and the brown trout, all with native ranges in the North Atlantic Ocean. *Salvelinus* comprises the charr, with native ranges in the Pacific shores. The Pacific salmon has 5 species: chinook (*Onchorynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*),

casu (*O. masu*), pink (*O. gorbuscha*) and sockeye (*O. nerka*) [2]. Pacific salmon are basically anadromous (migrate to sea water after spending early life in streams and rivers), semelparous (reproduce only once in a life time) and exhibit accurate homing. Atlantic salmon which inhabits the eastern coast of North America, are homing and iteroparous (reproduce more than once in a life time) [3].

Salmonids are the third largest farmed fin fish crop, behind Chinese and Indian carps and tilapias, with a total annual production of 3,594,000 metric tonnes [4]. They however form the lead farmed carnivorous fin fish globally. Production of salmon (Atlantic and Pacific salmon) forms the fastest growing food producing industry in the world, with annual growth of 7%. Atlantic salmon, *Salmo salar*, is iconic, high value, widely traded global fish product, and natural stocks are often threatened by overexploitation and habitat degradation [5]. It contributes substantially to food, economic and employment security in many countries, especially Norway, Chile, Canada and the United Kingdom [5], which are lead producers of the species (**Table 1** and **Figure 1**).

Significant development in the farming of *S. salar* is recorded in temperate coastal regions of countries such as Norway, Canada and Scotland [6], with Chile being among the top producers. A total of 30,000 direct and over 14,500 indirect jobs are provided by the salmon industry in Chile [7], underscoring the importance of salmon industry in the country, which is also the second biggest producer of farmed salmonids globally, with annual production averages of 700,000 tonnes [8]. Farmed salmonids account for over 73% of aquaculture production in Chile and became the second largest contributor to the Chilean economy [9], with the three most intensively farmed salmon species being *S. salar*, *O. mykiss* and *O. kisutch* [10]. In Scotland, salmon farming takes place on the west coast and islands of Scotland and approximately 95% of the aquaculture industry is dominated by *S. salar*, making it the third largest producer after Chile and Norway [7]. These countries are located within certain southern hemispheres that are at a constant temperature of around 0–20°C. Salmon farming ideally requires temperature of 13°C [11], or below. But the fish's appetite for food reduces at very low temperatures, and can therefore affect growth rates. Typically, juvenile fish less than 250 g (raised in freshwater) are released in to pens or cages in the ocean, where they are grown to market size of 2–8 kg a piece, within a grow-out period of 16–24 months. Before reaching 250 g for release to pens or cages, the early forms grow in wide areas of freshwater farms and hatcheries across eastern and southern Chile [12]. Thereafter, they are released for fattening in the marine environments in the southern most Patagonian fjords [13]. These areas are endowed with ample water flow in current, protected naturally by fjords and archipelagos.

With average growth in annual production of about 9%, salmonids represent the fastest growing food production system globally over the years, highlighting the important role of the fish in food and nutrition security, as well as livelihood and income generation. Salmon is rich in protein, omega-3 fatty acids, minerals and vitamins. In this respect, the Atlantic salmon is iconic in value, distribution and conservation status. With an increasing demand globally, consumption of salmon is currently 3 times its quantity for 1980, and contributes 70% of the market for salmonids. Apart from its high global demand, the high visibility of salmon on the market is due to the high level of industrialization and low-level risk associated with its culture. Contrary to its status of a luxury commodity in the 1980s, it is a major food item in the USA, Europe and Japan, with high prices of about US\$11.9 in USA and US\$ 7.3 per kg in Europe. High demand is also driven by lucrative emerging markets in China, Russia, and Brazil [14]. Farming *S. salar* is also much more efficient, about 8 times more efficient than beef production.

Species	2017		2018		2019		2020	
	Tonnage	% growth	Tonnage	% growth	Tonnage	% growth	Tonnage	% growth
Chinese carps	19,131		19,469		20,090		21,747	
Tilapias	5881		6276		6513		6800	
Catfishes	4553	7.2	4879	2.5	5003	3.8	5193	
Atlantic salmon	2,290,000	5.8	2,423,000	7.3	2,599,000	3.5	2,689,000	
Coho salmon	171	9.6	187	8.6	203	2.5	208	
Large rainbow trout	261	1.6	265	13.1	300	0.7	302	
Small rainbow trout	582	2.5	596	2.4	610	2.0	623	
<i>Pangasius</i>	1249	13.8	1422	3.3	1468	2.6	1506	
Sea bass and sea bream	403	4.0	419	−1.7	412		387	

Table 1.
Global production of lead farmed fish species 2017–2020 (000 metric tonnes).

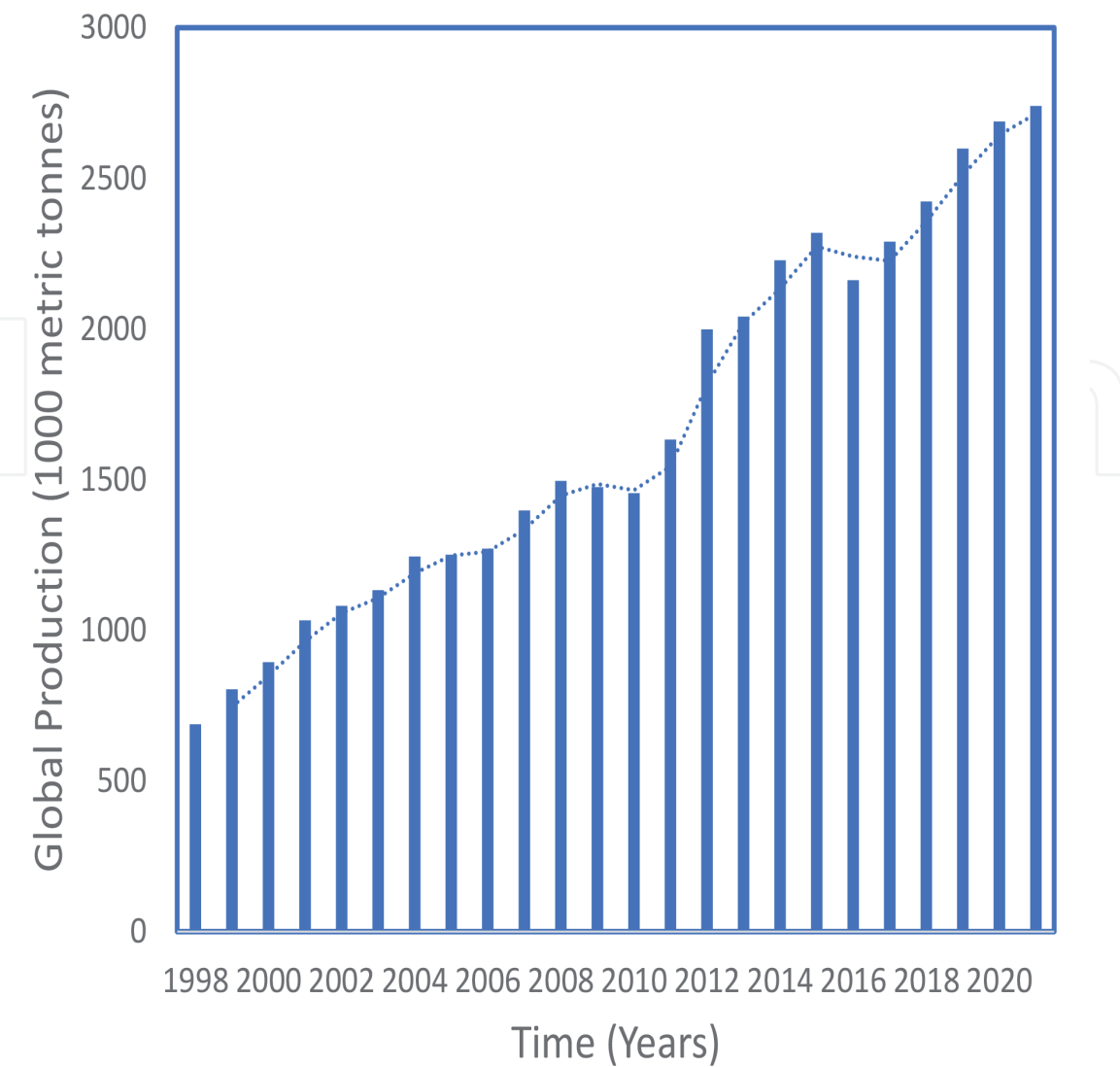


Figure 1. Global production of farmed *Salmo salar* (1998–2021), in metric tonnes. A steady increase in production is recorded annually over the years, demonstrating the importance of the species as food and source of income in main global producing countries.

1.1 Anadromy in Atlantic salmon

Most salmonid species are anadromous. Hence, they spawn in freshwaters (streams, lakes and rivers), where the young ones spend 1–3 years before juvenile stages migrate to the sea for feeding and fattening. The ability to switch lifestyle from freshwater to sea water is called smoltification, a process controlled by temperature and photoperiod. As the fish mature in the sea, they begin to return to their point of release or spawn, in a process called homing, for spawning. Most salmon are semelparous, i.e. they breed only once in their life time and then die. Death is mainly due to exhaustion from the long distances covered during homing, and the excessive energy spent during spawning. A few salmon are iteroparous, i.e. spawn severally in their lifetime. This is because they are able to migrate back to the sea, after spawning to continue feeding and rebuilding their reproductive capacity. However, some species, such as rainbow trout complete their life cycles in freshwater. Anadromous salmon shows fidelity to the freshwater site at which they were spawned, or released, and therefore when they reach sexual maturity and are about to start breeding, they migrate back to these sites for spawning. The return of mature salmon to their natal streams from the ocean is called homing, a complex process in which majority of the fish return to their actual natal streams, while a few veer off to different streams.

Suitable environmental conditions for growth of salmon include: low water temperatures of 8–16°C, clean and well aerated waters and well protected fjords, free from storms and other environmental upheavals [14]. These low temperatures reduce stress to the fish during summer, and reduce the growth rate in winter, conditions suitable for minimizing disease incidences among salmonids. Typically, these conditions are found in Norway, Chile, the North Atlantic and North Pacific coasts, as well as coastlines of Tasmania and New Zealand. These are countries of higher latitudinal ranges, often temperate regions. Although it is generally regarded that fish production increases with reducing latitudes, especially for warm water species [15], production of cold-water species nevertheless positively increases with increasing latitudes [15]. Although for warm water species, the effect of temperature on fish production in a fishery is generally boosted by the fertility of the waters [16], temperature is probably the main factor driving productivity of salmonids [15], given that most salmonid species are generally farmed in sea ranches or raceways on fish farms, systems that require clean, well aerated waters.

As high value species of global demand in the developed countries, salmonids are usually cultured in intensive systems, characterized by high fish densities, low water flow, and high concentrations of dissolved oxygen. Removal of carbon dioxide, solids and excretion end-products, such as ammonia and nitrites, are generally prioritized, in order to improve growth and health of the fish. Generally, *S. salar* has a low tolerance to a dissolved oxygen deficit, sensitive to increased concentrations of carbon dioxide, un-ionized ammonia and nitrites in freshwater.

2. Main aquaculture systems used in salmon production

2.1 Flow through systems (FTS)

Flow through systems, also called raceways or semi-closed culture systems, are culture units in which water flows continuously, making a single pass through the unit before being discharged. Raceways are mainly concrete, but some are earthen, lined with waterproof materials, yet some are fabricated from wood, fiber glass, metal, plastic and other materials, depending on the resources of the farmer. They are majorly designed for highly intensive culture and especially suitable for fish species that need constantly flowing clean water e.g. juvenile salmon and in the production of smolts. As high value species therefore, almost 80% of *S. salar* smolts globally are produced in flow through systems before being stocked in sea cages. Egg-larvae (parr) are supplied with fresh water from local sources such as rivers, lakes, ground water or natural springs at hatcheries and fish farms. Good flow rates and velocity of water is essential to the health of the stock under culture, and to flush wastes from the system. Water quality is maintained by treatment and manipulation of the flow rate of the water. The quality is then enhanced by injection of oxygen using air blowers, in order to minimize the water flow rate to 0.6 L/kg/min. Sophisticated farms heat the water to a certain temperature and manipulate light intensity [6]. Appropriate stocking density of the fish in FTS is dependent on water quality, management skills and general husbandry practices put in place, as well as the biology of the species, including the ability of the fish to tolerate crowding. FTS are capable of supporting a high number of smolts yearly, with averages of 900 million smolts in Norway alone produced under FTS [17]. Fish reared in these systems can however be highly susceptible to diseases due to stress caused by overcrowding. Raceway systems can be earthen or concrete based, majority are constructed from concrete or cement blocks.

2.2 Recirculation system (RAS)

Recirculation system was developed in the 1970s, to reduce the required amount of water and resultant waste produced from traditional flow through system. The system is highly controlled, and therefore requires substantial skills and input. In order to reduce the demand for large amounts of water, the system involves recirculation of water, which also reduces water wastage. Since water is recirculated in the system, there is enhanced biosecurity on salmon fish farms and hatcheries, and this prevents or minimizes escapee fish to the natural environment. Prevention of escapees from farms or hatcheries comes with several benefits, such as preservation of the purity of local natural populations of salmon, reduced incidences of disease and parasites to the natural populations, as well as to those within farms [18]. Wastes from fish are controlled and easily collected, which reduces pollution of the environment and the collected waste is easily aggregated for subsequent use for other purposes on the farm. Additionally, the environment for fish growth is optimized, with control of water temperature, water quality, feeds, and these maximize growth rates of the fish. Due to its ability to minimize impacts to the environment, RAS is easily and locally sited to markets, which therefore reduces transportation costs and carbon footprints, while simultaneously improving traceability and freshness of the product, and profitability of the enterprise as well.

Improved RAS systems comprise of two portions, with one part of the tank dedicated to fish rearing and trapping of particles and draining of sludge [19]. The other part is the water treatment system, composed of an additional solid removal system, submerged biofilter and an airlift for water circulation and gas exchange [19]. This therefore allows addition of oxygen and removal of carbon dioxide and ammonia gases from the water. Additional mechanical filters aid the removal of particles that would not settle. Generally, the efficiency of the RAS is enhanced, in order to reduce the amount of energy required to produce a kg of fish, while maximizing the stocking density of the fish (typically 61–122 kg/m³, but in some cases, may exceed 545 kg/m³). The system is therefore successfully applied to rear smolts in many salmon producing countries [20]. In Norway, a total of 12–20 million smolt per year are produced under RAS [21]. Averagely, 350,000 MT of salmon are produced annually under RAS [22]. High technological complexities that necessitate high costs of production and highly skilled and competent human resource is the key challenge facing salmon farmers that operate RAS.

2.3 Cage culture

Cages or pens are natural or semi-sheltered bay where the shoreline forms all but one side of the enclosure. Cages or pens are made from bamboo, wooden poles or stakes driven into the substrate, the mesh size is typically small enough to retain the cultured fish but large enough to allow entry and exit of small fish and food organisms. Its management is less complex than land-based systems, make use of existing water bodies which gives local non-land owners access to fish farming. This type of system makes the majority of the salmon grow out particularly for seawater operations, and is appealing to most farmers, for incurring the lowest production and operation costs of all the production systems.

Cages are movable and float off the bottom, range from about 1 m² to over 1000 m² in surface area, with a depth of about 20–50 m, and a maximum circumference of 157 m. The stocking density limits for post smolt *S. salar* in commercial scale culture averages 75 kg/m³ [23]. Average production volumes almost doubled in Norway, increasing from 37 to 67 million m³ from the year 2005–2009, mainly due to better quality of water, better food organisms and reduced impact of storms.

Escaped fish, predation by seals and climate change are the main challenges facing cage culture of salmon.

3. Marketing of salmon

As an iconic group of fishes, salmon is very rich in high quality proteins, and long chain omega-3 fatty acids, which reduce the risk of cardiovascular disease and other health issues. It is a good source of minerals (iodine and selenium), vitamins (D and B12) and macronutrients. Due to this important nutritional composition, salmon is a globally traded product, especially in the developed countries, where purchasing power is also high.

3.1 Processing of salmon

In order to increase safety of the product, preserve high quality characteristics, extend shelf life and enhance economic returns to the producer, salmon is processed in different forms [24]. About 47% of the EU market supply of salmon is filleted, while 12% is of whole fish form, which is also the most preferred since they are fresh and preserved through chilling and freezing. A total of 28% of the supply is smoked salmon, while 13% constitute other value-added products [25]. Smoked salmon is the most expensive, sold at €90 a kilo, while fillets cost €14 a kilo [25]. Processing plants are required to ensure that the weight, color, size, shape and packaging of the final product are of the standard desired by the final consumer. This requires well trained and skilled workers to assure product quality. In this regard, and in an effort to maintain the highest standards of safety and hygiene of this globally traded fish product, processing facilities are often certified by US and EU authorities for them to qualify to supply export markets (**Figure 2**). Some of the requirements for this certification is the maintenance of solid cold chains, international standards of germ

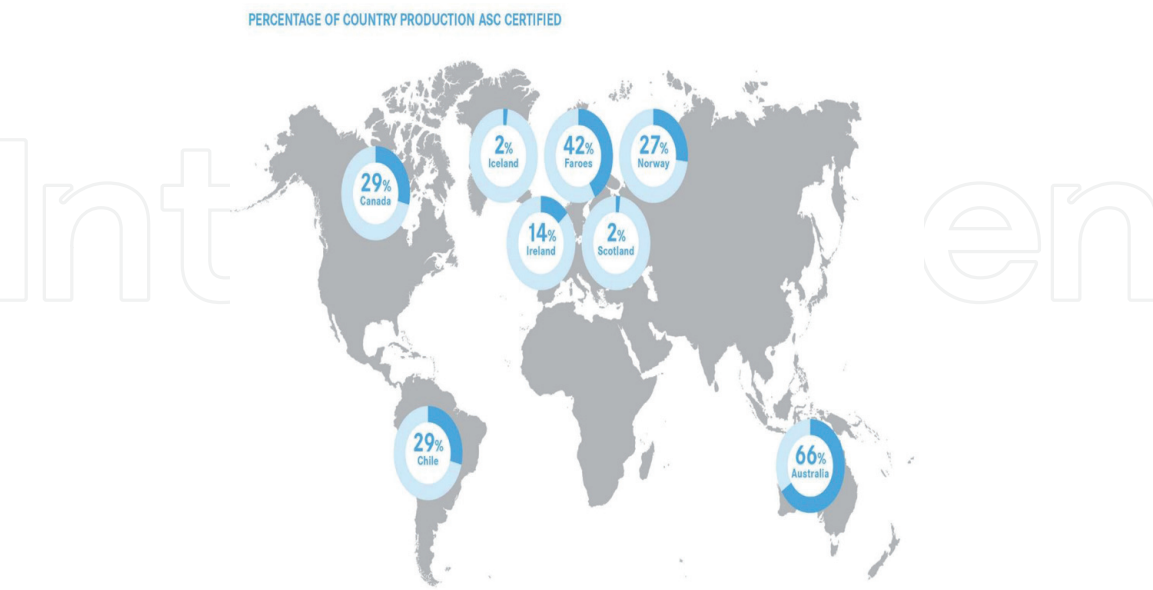


Figure 2. Percentage of salmon producing companies in each of the main global salmon producing countries that are certified by Aquaculture Stewardship Council (ASC). Some of the criteria used by the ASC for certification of production value chain includes: the amount of fish meal used in formulating fish feed and fish oil for the farmed salmon, the amount of chemicals and drugs used in control of parasites and diseases, and biosecurity or the level of control put in place on fish farms to limit escape of farmed fish to the natural environment, lethal incidents involving marine mammals, antibiotic use and viral disease mortality. Fish from certified farms should be more attractive to export markets.

control, i.e. the Hazard Analysis of Critical Control Points (HACCP) certification and efficient systems of waste management. As happens with other fish products, salmon processors also undertake value addition, to increase the shelf-life and value as well as expand the market [26]. The main value-added products of salmon include fillets, salmon bread, sushi, and smoked salmon [26]. Apart from improved purchasing power and awareness of nutritional benefits of consumption of salmon, this hygienic standards in processing the product and value addition have seen increased consumption of the product (**Figure 3**). A total consumption of farmed Atlantic salmon of 2.4 million tonnes was estimated in 2020 [4], which, when combined with those from capture fisheries rises to 3.2 million tonnes.

3.2 Packaging of salmon

Packaging is crucial for providing useful information to the consumer, such as product identity, origin, how to use and store, nutritional information among others. Well packaged fish products enhance efficient mechanized handling, distribution and marketing. Rigid materials like cans, glass container jars, plastic bags, pouches, film, sheets, jars and boxes are commonly used in packing salmon [27]. Fresh fish are usually loaded in plastic boxes that are hygienic, light and strong. The boxes are insulated to maintain the temperature of iced fish, while also allowing drainage of any melted liquid from the fish [27]. Frozen fish is commonly packed in interlocking, printed, polycoated and corrugated fiberboard cartons and expanded polystyrene and corrugated polypropylene boxes, sealed with polypropylene or metal tape. This type of boxes are also used for freezing wet fish, storing wrapped or unwrapped frozen fish [27]. Fresh, chilled or frozen fish are packed using Styrofoam, polyvinylidene chloride or polystyrene trays wrapped with cling film made from either polythene or polypropylene. Although this type of packaging can

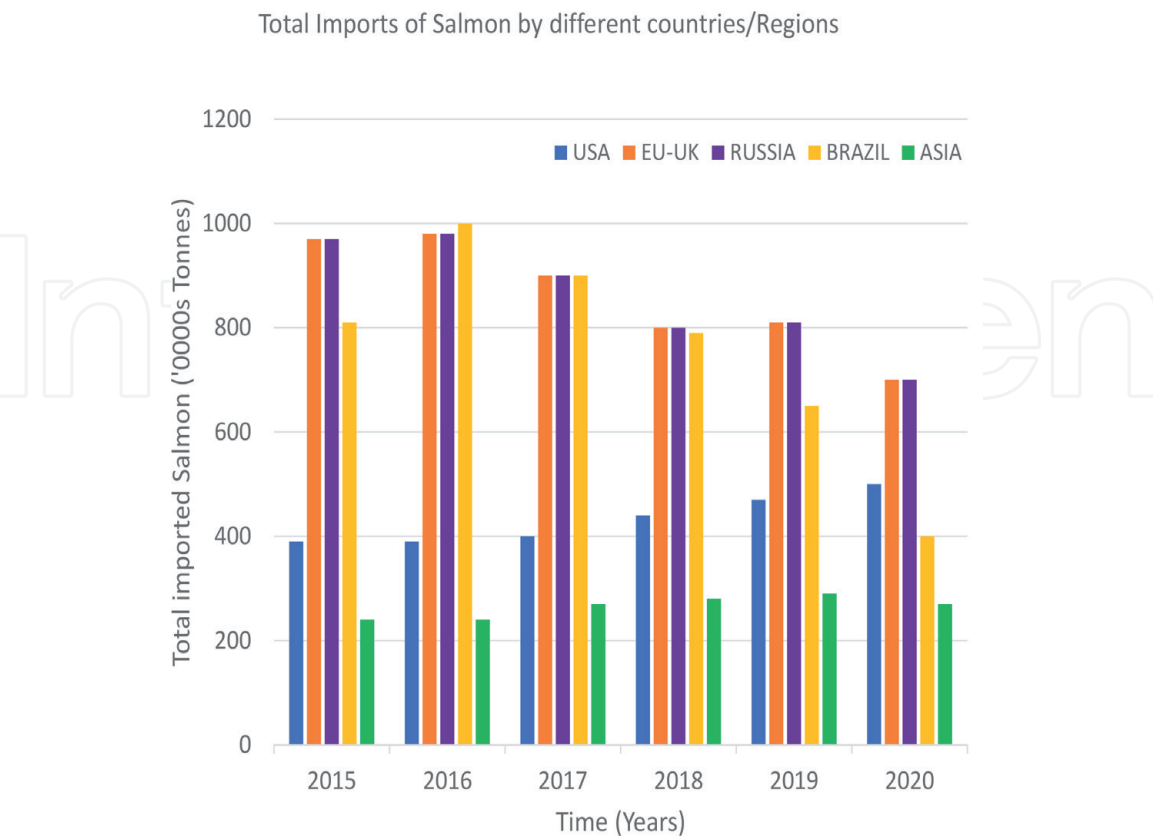


Figure 3. Total imports of salmon by major consuming countries or regions from 2015 to 2020. USA is the United States of America, EU-UK is the European Union and the United Kingdom.

be attractive to customers, they cannot protect the fish from mechanical damage, loss of moisture and aroma or even contamination from microorganisms and odor from other products [27].

3.3 Freight packaging

Fresh, frozen or live salmon for airfreight is packaged in containers made from metal, fiberglass and expanded polystyrene. Such a container is insulated, easy to handle, heavy to give physical protection to the products and watertight to protect against contamination [27].

The main importing countries or regions for salmon products include the USA, EU-UK, Russia, Brazil and Asia. Although imports or consumption of salmon has been decreasing in the EU-UK, Russia and Brazil since 2016, consumption of salmon products has been on the increase in the USA and Asia (**Figure 3**), causing an increase in imports. The decline in Russian imports is occasioned by an embargo on salmon imports from Norway following the EU's trade sanctions against Russia due to the conflict in Ukraine.

4. Main challenges in salmon aquaculture

4.1 Incidences of diseases

The main diseases in farmed salmon include infectious salmon anemia (ISA), characterized by pale gills and fish that swim close to the water surface while gulping for air. Some cases are asymptomatic, but the fish die suddenly. ISA was first reported in Norwegian salmon farms in 1984, from where it spread to other big producers of salmon, causing huge losses of up to €100 million [28, 29]. ISA is caused by a virus, the Infectious salmon anemia virus, one of the most devastating diseases of marine farmed *S. salar*, and mainly attacks the grow out stages of the fish. In Chile, the first outbreak was in June 2007, with the ISAV HPR7b variant in circulation [30]. The impact of the outbreak was devastating, and was partly responsible for the brief decline in global production of salmon in subsequent years (**Figure 4**). ISA outbreaks come with high mortality of fish, huge losses to farmers and severe restriction to production in surrounding areas. A large number of risk factors are known to predispose salmon to ISA outbreaks [32]. Presence of the ISAV receptors in the fish, the variant strain (whether virulent or non-virulent) responsible for an outbreak, rate of evolution of the strain from non-virulent to virulent, the rate of viral reproduction and shedding, suboptimal management practices at cage farms, fish stocking and fallowing routines in cages, related disease outbreak events, level of intensification in fish production on the farm, and handling and treatment of fish constitute some risk factors that fuel increased incidences of ISA outbreaks [33–35]. Increased biosecurity, advanced fish husbandry practices, as well as a better understanding of some of the risk factors constitute suitable mitigation measures for ISA outbreaks [32].

Infectious pancreatic necrosis (IPN) is a disease of young salmonids (*Salmo*, *Onchorynchus* and *Salvelinus*), attacking the pancreas and liver parenchyma of the fish. The virus responsible for IPN is an *Aquabirnavirus* of family Birnaviridae, and comprises a bi-segmented double stranded RNA. Severe necrosis of pancreatic and liver cells occurs, which extends to the intestinal mucosae [36]. Post-smolts darken in color, anterior part of the abdomen swells, capillaries around the pectoral fins engorge, the dorsal fin erodes, while the vent swells [36]. It occurs both in freshwater and marine water stages, when the fish is typically of start-feeding stage to about 20 g (after

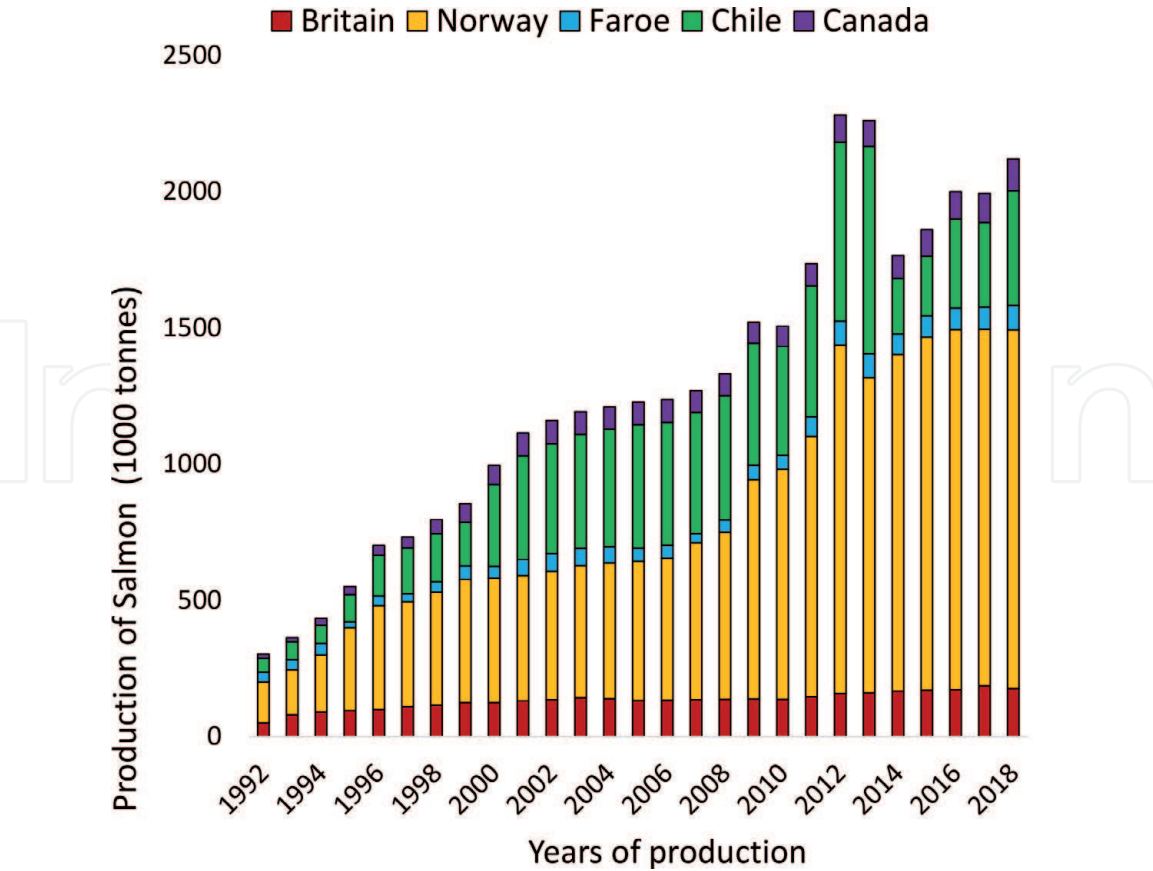


Figure 4. Production of Atlantic salmon (*Salmo salar*) in the 5 largest producer countries from 1992 to 2018. Norway remains the lead producer, followed by Chile over the years. Adopted from Iversen et al. [31].

transfer to the seas in post-smoltification stage). Therefore, the disease attacks fry and post-smolts, and becomes especially severe in the marine environments (post-smolts), causing substantial mortality [37]. Effects of IPNV outbreaks are therefore economic, ecological, and social (welfare), since the salmon that survive the attack often remain asymptomatic carriers of the virus [38]. Economic losses due to IPNV outbreaks in Norway, for instance were estimated at US\$ 30 million [39]. Apart from presence in the pancreatic cells, some of the virus cells hide and therefore multiply and persist in the leucocytes of the head kidney. This leads to recurrent outbreaks, which spread quickly across farms in a locality, especially in lead salmon producers like Norway, and Chile where farms are concentrated in a locality. Some of the host defense mechanisms against IPNV include the interferon necrosis (IFN) factor and the anti-viral protein or gene Mx [40], which suppress the persisting viral cells. Following the introduction of IPN resistant strain (IPN-QTL) homozygous in salmon producing countries, mortality now varies based on the susceptible and resistant strains of salmon during the outbreak. Therefore, mortality can vary from 5 to 10% in the resistant strains of salmon, to 70% in the genetically susceptible strains in sea cages. This suggests that considerable gains against diseases in farmed salmon production can be made by a combination of selective breeding of salmon for disease resistance and a suite of both natural and active immune responses against invading pathogens.

Apart from infecting salmonids, furunculosis is also highly pathogenic for other fish species of the wild waters as well as farmed populations. It is caused by a gram-negative rod bacterium, *Aeromonas salmonicida* subsp. *salmonicida*. The bacterium carries an external surface layer, the A-protein surface layer (A-layer), which counters the host defense mechanisms of the fish. This is boosted by a lipopolysaccharide, a protective cell envelope antigen on the surface of the bacterium [41]. As the bacteria grow, they release extracellular products, which cause lesions

on the fish. Therefore, symptomatic cases are characterized by fish with lesions that lead to mortality in severe cases [41]. Infected fish are generally lethargic, lack appetite, develop dark skins, show ventral haemorrhage at the base of anal, pectoral and pelvic fins, splenomegaly and subcapsular haemorrhage occur in the liver [41]. When liquefactive skin lesions and ulcers rupture, more bacteria are released in to the environment, and increase infection of the surrounding fish. Severe outbreaks are reported to cause economic losses in excess of US\$100 million in Norway salmon Industry [28]. Control measures during outbreaks include prophylaxis, such as use of vaccines. Drugs (antibiotics such as flumequina) against furunculosis may be administered to the infected fish through diets, while best management practices are recommended to avoid outbreaks. In case of severe outbreaks, movement of smolts may be banned (quarantining farms), and farms that suffer outbreaks are banned from sale of smolts [41]. Common risk factors that induce outbreaks of furunculosis in salmon farms include: migration of fish, water quality, sharing or transfer of staff among salmon farms and hatcheries, breach of quarantine protocols and poor husbandry and hygienic practices of hatcheries and farms [42]. Additionally, algal blooms, increasing temperatures and salinity in wild waters increase the risk of outbreak of furunculosis [43].

4.2 High cost of feeds for salmon production

As a carnivorous fish group, farmed salmonids require high quality feeds (high crude protein content) for fast growth, and to attain appropriate nutritional composition. Typically, feeds for salmon comprise of: 93.4% dry matter, 35.6% crude protein, 33.5% crude lipid, 11.0% carbohydrates and 1.3% phosphorus [44]. However, formulating and maintaining such high-quality diets is not only expensive, but also environmentally challenging, as it requires high amounts of marine fish resources to provide the ingredients for protein and oils, which invariably increases overexploitation of resources (overfishing). In this regard, formulation of suitable diets for farmed salmon requires inclusion of fish meal and fish oil in appropriate quantities, to give the final product the required nutritional quality and composition. Usually, formulated diets for salmon constitute 40–60% fish meal and 20–30% fish oil, sourced mainly from marine anchovies, mackerel, pilchards, herring and blue whiting [45]. These marine fish species are often targeted as sources of fish meal and fish oil for salmon feed production because they provide appropriate nutrients for carnivorous fish species and offer appropriate amounts of polyunsaturated fatty acids (omega 3), in the fillets of the salmon, which is beneficial for human health. Notwithstanding the benefits of using fish meal and oils in salmon diet for human health, the practice not only makes salmon diets expensive, but also increases overfishing of target marine fish species, and so runs contrary to sound principles of conservation of aquatic biodiversity. Since the mid-2000s, the prices of fish meal and fish oil rose between 50 and 130% [46]. Such increases in the costs of key ingredients, coupled with the fact that traditionally, fish feeds form the highest cost of total fish culture enterprises, feeds for farmed salmon production provide a critical challenge in the global culture of salmonids, for their high cost and unsustainability in the long term. Previous studies report an intake of 2.5 kg of marine fish to produce 1 kg of salmon [46]. Globally, 1 kg of salmon feed retails at an average price of NOK 13 (€1).

In order to address this challenge, and increase efficiency and sustainability of farmed salmon production, viability lies in diversifying the sources of protein and oils, especially plant sources, in order to reduce exploitation of marine fish species for fish meal and oils, but still retain high nutritional quality of the diets. In this regard, the composition of formulated feeds for salmon has been changing since

1990, with some of the marine ingredients being replaced by ingredients from plant sources [44]. Both fish meal and fish oil composition in salmon feed formulation have declined, with replacement by plant-based ingredients (**Figure 5**). Studies in to alternative feed resources report suitability of zooplankton, mesopelagic fish, some species of squids, and the Antarctic and North Atlantic krill as viable alternatives to fish meal and fish oils [47], as they equally supply excellent levels of omega-3 polyunsaturated fatty acids, vitamins, minerals, essential amino acids, carotenoids and nucleotides. The nutritional composition of such alternative diets is enhanced further by feed additives [47], prebiotics and immunostimulants. Another appealing alternative is the use of by-products and by-catch (non-target fish and other aquatic organisms caught during fishing) from fisheries and aquaculture. This targets the utilization of non-edible parts of fish from processing plants, as well as the discards from fishing expeditions. The use of these materials as ingredients in formulating diets for salmon is strictly undertaken in conformity with the regulations in place, such as the EU regulations on the use of animal products, to control and prevent the spread of diseases and bioaccumulation of contaminants and other undesirable substances [45]. As long as the selection of such materials is done properly, taking in to consideration their nutritional composition, they impart useful nutrients to the feeds formulated for farmed salmon, helping achieve cost-effectiveness, sustainability and high quality of diets, without the use of fish meal and oils [45].

Efforts to find viable alternatives to fish meal and fish oils in feeds for salmon have been concentrated on plant products or ingredients, since their availability, nutritional quality and prices can be achieved competitively. This is underscored by the increasing amounts of plant matter used as ingredients in formulation of feeds for farmed salmon, in comparison with fish meal and fish oils, which are on the decline (**Figure 5** and **Table 2**). In this regard, one of the most suitable and promising plant ingredients is the soy beans as the source of protein and oils, for its high

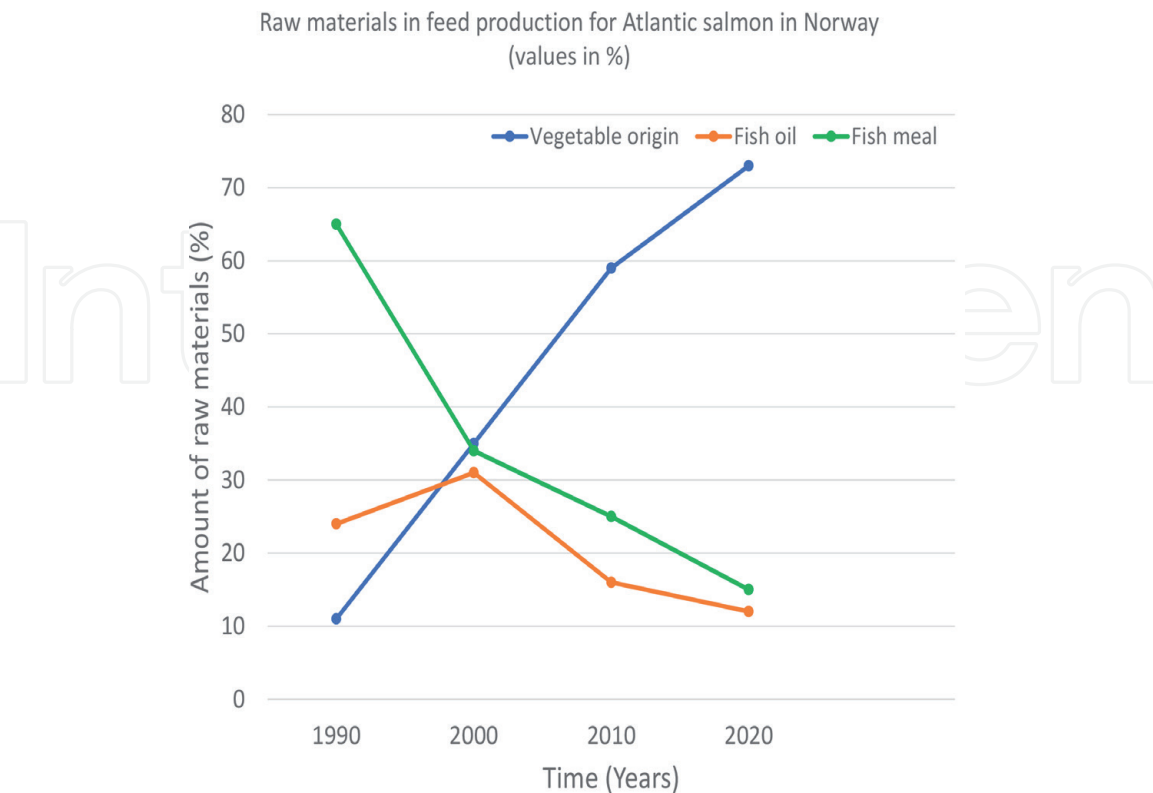


Figure 5. Trends for raw materials used in feed production for Atlantic salmon in Norway (values in %). Since 1990, vegetable-based ingredients are often used to replace fish meal in feeds for salmon, in order to reduce overexploitation of marine fish species.

Ingredient	% composition
Plant protein sources	40.2
Plant oils	20.1
Carbohydrate sources	10.7
Marine protein sources	14.5
Marine oils	10.4
Other	14.5
Total	100

Table 2.
Norwegian salmon feed ingredients used in 2016 (values in percentage %). In line with the need to reduce exploitation of marine fish meal, ingredients for feed formulation now comprise of 40.2% plant protein sources, while marine protein sources are reduced to about 14.5%.

protein content, ease of availability and affordability [45]. Other sources of plant ingredients for possible use in formulating diets for salmon include wheat gluten, barley, pea, lupin, corn maize, sunflower, linseed, olive and palm oil. Similarly, vegetable oil is a suitable replacement for fish oils in formulation of feeds for salmon [48]. However, proper attention is required in the choice of the plant material, to ensure that it meets the required amounts of protein, the high amounts of starch in plant matter is adequately reduced, meets suitable profiles for amino acids and minerals, as well as reduced levels of fiber and anti-nutritional factors [45].

The ingredients that constituted the largest portion in Norwegian salmon feed was soy protein content which was 19% and rapeseed oil together with camelina oil accounted for 19.8% while wheat and wheat gluten accounted for 17.9% [44]. The ingredients used in Norwegian salmon feeds in 2016 are as shown in the table below (Table 2).

5. Genetics and genomics to support improved breeding of salmon

Salmon is iconic not only in its ecology, life cycle, ability to oscillate among different environments, high conservation value, but also in its genomic organization. As tetraploid individuals, the genome of salmon evolved through a historical auto-tetraploidization whole genome duplication (WGD) [49], which occurred 88–103 million years ago [50]. Autotetraploidization occurs by a spontaneous doubling of all chromosomes [5], creating four pairs of chromosomes that recombine spontaneously during meiosis after WGD. Like the normal diploid gametes, there is a reduction in the ploidy state of salmon genome (halving), a rediploidization process that returns the salmon genome to diploid state prior to recombination [5]. Enormous structural re-organization occurs in the salmon genome during rediploidization, with some parts of the genome remaining tetraploid [51], mismatch in recombination rates of females and males [51], and the retention of half of the genes of the species in duplicated state from the salmonid specific 4th round (Ss4R) of WGD [52]. Apart from this reorganization of the salmonid genome during rediploidization, which creates suitable substrates for the evolution of salmonids, a fifth of salmon genes retained a pair of more ancient gene duplicates from the Teleost specific 3rd round of WGD (Ts3R) [5]. This increases the diversity and complexity of gene families in salmonids, compared to other teleost fishes, which increases evolutionary potential as well as heritability and genetic potential during selective breeding of salmon for commercial aquaculture. The overall effect of these events is a much higher variability in the gene pool, from which samples for generating F1 are drawn.

5.1 Selective breeding in salmon aquaculture

Selective breeding in support of salmon aquaculture began in Norway, a lead producer of *S. salar* in the 1990s, with the first such programme initiated in 1997, using a total of 40 strains collected across rivers country wide [53]. Concerted efforts produced 4 more strains: Mowi, Rauma, Jakta and Bolaks strains [54], which have been crossed and used extensively, including export to other salmon growing countries. The breeding programme focused on growth rate, with a substantially superior genetic gain per generation of 15% being achieved. This rate is comparatively better than tilapias, where for instance the GIFT strain achieved genetic gain of 12–17% in the fifth generation, compared to 15% in the first generation of salmon [55]. Similarly, in China, the ProGift strain of *Oreochromis niloticus* reported a genetic gain of 11.4% in the 6th generation [56], translating to increased growth of 60–90% bigger body weight at harvest [56]. The high rate of genetic gain in salmon could be attributed to selection intensity, recent history of domestication, in addition to a complex genome following whole genome duplication events [5].

With improved technology and changing interests of salmon breeders in the 1990s, the breeding objectives, moved from growth rate to other complex challenges, such as disease resistance, rationalized by increased incidences of infectious pancreatic necrosis virus (IPNV) for instance [5]. Indeed, disease outbreaks are a major challenge in farmed salmon production in some lead producer countries. To this end, marker assisted selection helped identify individuals with QTL for higher resistance to IPNV [57], resulting to reduced incidence of IPNV, and therefore better yields.

5.2 Genetic mapping

One of the major challenges facing intensive farming of salmonids is infectious diseases, which often occasion huge losses to farmers, and slows down the rate of expansion of salmon farming. Most of these diseases are caused by bacteria, viruses and parasites [58], whose severity and frequency of occurrence increases with the level of intensification of production. Infectious salmon anemia (ISA), Infectious pancreatic necrosis (IPN), Skeletal muscle inflammation (HMSI), and pancreas disease are viral diseases of salmon [36, 58], which also lower growth rates and increase costs of treatment [58]. The main bacterial disease is the salmon rickettsial syndrome, which causes huge economic losses, while the sea lice disease is the main parasitic disease in farmed salmon. On the other hand, the amoebic gill disease is the main protozoan disease in farmed salmon [59], which also increases susceptibility to other infections. Most of the conventional preventive and prophylactic measures used to control these diseases such as vaccination, antibiotics and anti-parasitic drugs, or biosecurity [58], are often not effective. To counter these losses and increase economic returns of salmon farming ventures, selective breeding for resistance to diseases is often applied, based mainly on information from relatives (sib information) [58], since the trait is difficult to measure directly on candidate fish for selection.

5.3 Breeding for disease resistance in farmed salmon

Global growth of aquaculture is often constrained by progressive loss of quality of the breeding germplasm due to inappropriate fish husbandry as well as selection requisite in particular fish breeding schemes and the repetitive use of certain (good looking or higher yielding) brood stock, and incidences of diseases, especially as production is intensified in pursuit of food security, higher incomes and livelihood.

Disease resistant fish are those that limit infection by curtailing the replication of the pathogen in the body of the fish [60]. In itself, disease resistance is a precious trait in fish, animal or plant breeding programmes, for it limits wanton use of chemicals or drugs, whose effect is more-broad based, even to non-target organisms in the environment [61], yet their efficacy at limiting incidences and severity of diseases may not be sufficient. Similarly, resistance to drugs or antibiotics by microbes is a real and serious problem in agricultural production [62], exacerbated by global warming [62]. Therefore, alternative, more environment friendly, cost effective and sustainable approaches are desirable in controlling diseases in salmon aquaculture. One of these strategies is the breeding of superior strains, which exploits natural genetic variation for disease resistance to improve the quality, efficiency, profitability and sustainability of the aquaculture enterprise. Today, breeding for improved strains or varieties is a highly efficient process, because of the increasing tool kit of genomic resources, especially for the high throughput next generation sequencing technologies. Therefore, it has been possible to focus on growth, sex determination or disease resistance as breeding objectives [63]. In farmed salmon production, breeding for disease resistant strains is an active agenda since the 1990s [53], since it imparts cumulative and permanent resistance to diseases in the fish. Breeding for resistance nevertheless requires a population of sufficient genetic variation for the trait. High levels of additive genetic variation for disease resistance are reported in different salmonid species (**Table 3**), indicating possibility of deriving gains in selective breeding for disease resistance in salmonids.

Therefore, it is possible to improve resistance to diseases in salmonids through genetic improvement, as a tool in disease control in salmon aquaculture,

Species	Pathogen	Heritability ($h^2 \pm \text{S.E}$)	Reference
<i>Salmo salar</i>	<i>Renibacterium salmoninarum</i>	0.2 \pm 0.1	[64]
	<i>Aeromonas salmonicida</i>	0.48 \pm 0.17	[65]
	<i>A. salmonicida</i>	0.59 \pm 0.06	[66]
	<i>A. salmonicida</i>	0.62	[67]
	IPNV	0.55	[67]
	Infectious Salmon Anemia Virus (ISAV)	0.13 \pm 0.03	[68]
	ISAV	0.16 \pm 0.01	[69]
	ISAV	0.24 \pm 0.03	[66]
	ISAV	0.37	[67]
	<i>Vibrio anguillarum</i>	0.38 \pm 1.07	[68]
	<i>Vibrio salmonicida</i>	0.13 \pm 0.08	[64]
	<i>Caligus royercreseyi</i>	0.10 \pm 0.03	[58]
	<i>Piscirickettsia salmonis</i>	0.18 \pm 0.03	[58]
<i>Salvelinus fontinalis</i>	<i>A. salomnicida</i>	0.51 \pm 0.03	[70]
<i>O. mykiss</i>	<i>Yersinia ruckeri</i>	0.21 \pm 0.05	[71]
	<i>Flavobacterium psychrophilum</i>	0.35 \pm 0.09	[72]
	<i>F. psychrophilum</i>	0.07 \pm 0.02	[71]
	Viral heamorrhagic septicemia	0.11 \pm 0.1	[71]

Table 3.
Heritability for resistance to different infectious and parasitic diseases in salmonid species. Adopted from [58].

since heritability for disease resistance is high (**Table 3**) [64–72]. Typically, disease resistance in salmon has been determined through marker assisted selection or genomic selection based only on information from relatives, since it is very difficult to measure disease resistance in the actual fish. By this approach, it is difficult to determine the genetic gain per generation imparted to the fish individuals by the selection effort [58]. This slowed the rate at which selection of disease resistant fish individuals and the realization of highly resistant individuals progresses, since estimated breeding values from sib information is less accurate than would that from the selection candidates themselves [58]. Previous research efforts determined correlation between immune parameters and resistance to diseases in salmon [73]. However, while this may be a pointer to some of the fish individuals that may be resistant to diseases, the total variability in survival of salmon is too low to be attributed to immune variables [58]. Similarly, resistance of fish to diseases is a function of many more factors, and not just immune parameters. Although high genetic variability necessary for improvement of disease resistance exists in salmon, correlations between genetic variation and disease resistance report mixed results [58], with non-existent relationship [72], negative relationship [74], or low to moderately positive relationship [70].

Due to these complexities in studying disease resistance for breeding improved strains for commercial production of salmon, genomic resources have been developed over the last decade, to enable a more focused approach to breeding for disease resistance in salmon. These include: high quality reference sequence for trout, which is also applicable to salmon [52], high density SNP genotyping arrays for *S. salar* [75], and lower density SNP platform for QTL mapping [76]. These resources support the study and understanding of the genetic basis of disease resistance in salmon through identification of candidate genes for resistance to certain diseases, mapping QTL regions with genes of interest for resistance to certain diseases, and gene expression studies [58] in fish challenged with certain pathogens.

5.4 Studying candidate genes driving disease resistance in salmonids

This approach of understanding disease resistance in aquaculture species exploits the candidate gene theory, in which phenotypic variance for a trait in a population is a result of polymorphisms that exist in genes known to drive that trait [77], and utilizes annotated gene sequences of known function [58]. Due to limited availability of annotated gene sequences in most aquaculture species, studies of association between candidate genes and resistance to diseases has shifted to the Major Histocompatibility Complex (MHC) [58]. The MHC is a multigene family, or a gene-complex region, comprising several genes mediating diverse immune and phenotypic responses or characteristics [78], and interfaces the immune system and pathogens [78]. The MHC presents the class I and II genes, which encode polypeptides that recognize and bind self and foreign peptides and present them to T-cells for destruction [79]. The MHC class I genes bind peptides produced by intracellular degradation of pathogens (such as viruses), and present them to the immune system (cytotoxic T-cells), triggering cellular immune response that destroys the cells. On the other hand, class II genes bind peptides produced outside cells (e.g. bacteria) and present them to helper T-cells, which secrete cytokine mediators. Cytokines elicit humoral (antibody), cytotoxic and inflammatory responses that destroy the pathogens. A unique feature of MHC gene complex is its high levels of polymorphism, with different regions showing high allelic diversity [78]. For instance, *S. salar* from the Baltic Sea has a single MHC class IIB locus with up to 16 alleles within populations [80]. This diversity, thought to be maintained by balancing selection in different taxa, is what makes the MHC a hotbed of scientific interest

and research. Class I and class II genes are well characterized and highly polymorphic in *S. salar*, and rainbow trout. Association between MHC class IIB alleles and resistance against *A. salmonicida* is reported [81], while variant fish for MHC class I and II are susceptible to IHN [79], but have resistance to furunculosis and ISA [82]. Some salmon fish individuals that bear certain genes in the MHC are more susceptible to furunculosis [81]. These studies seem to suggest that a clear understanding of the MHC and its associated polymorphism can provide useful insights in selecting suitable phenotypes of salmon for breeding for disease resistance, to support intensive and commercial production of the fish. While the number of studies showing correlation of MHC genes to disease resistance and vice versa in salmonids is on the rise, these largely form anecdotal evidence rather than solid evidence for correlation between certain genes of the MHC and resistance to diseases in salmon. This is because resistance to diseases in salmon is a polygenic trait, driven by several genes rather than certain gene(s). Furthermore, the class I genes in the MHC are highly diverse, and this large number of alleles seems to mask the effect of certain alleles, making it difficult to study roles of such alleles in disease resistance or susceptibility. However, since disease resistance traits are typically polygenic, future efforts to understand the genetic basis of disease resistance in salmon should study genetic architecture of variants in the whole genome, as well as possible interactions between genes. Additionally, for populations of salmon where correlation between certain genes and disease resistance or susceptibility has been demonstrated, even where such correlation only seems anecdotal, research should concentrate on studying the suitability of such populations (genotypes) as brood stock for seeds used in selection to improve resistance to diseases. Additionally, loci already identified as having some association with disease resistance should be tested further using modern marker technology, such as next generation sequencing, to improve the confidence of inference.

5.5 Mapping QTL regions for resistance to diseases in salmon

Quantitative trait locus (loci) (QTL), is the variability of loci, leading to increased variation in the expression of a quantitative character [83]. A QTL is a locus that controls a quantitative phenotypic trait, identified by showing a statistical association between genetic markers surrounding the locus and phenotypic measurements [84]. The presence of QTL improves the understanding of the number of genes and their relative effects in determining expression of the trait. The identified QTL is then mapped through marker association (association mapping) in the whole genome, thereby identifying genomic regions involved in genetic variation of a trait. Fish individuals with the identified QTL or the genomic regions are used in the breeding programme if the QTL is of advantage, or left out if the QTL confers a disadvantage to the fish. SNP markers are especially important in the construction of high-density maps, which are used to fine map QTLs and facilitate identification of causative genes involved in genetic variation for specific characters. SNP markers are available for salmonids [85], and are used in high resolution mapping of disease resistance genes. Since QTL mapping relies on molecular markers, the technique is likely to be used in many breeding schemes, due to the presence of many modern marker technologies, most of which increase the throughput and subsequent output. In this regard, marker technologies like Genotyping by Sequencing (GBS) are already being used in salmon breeding [86]. Coupled with technologies like the Genome wide association studies, these next generation sequencing platforms are likely to accelerate breeding disease resistant salmon strains for use by farmers in commercial aquaculture. These highly versatile NGS platforms enabled the construction of genetic linkage maps, some

incorporating several different markers. GBS has especially opened up new opportunities for genotyping SNPs, which are used to construct dense linkage maps [87], from which genes driving commercially important traits like disease resistance can be deciphered, to aid choice of desirable genotypes for use in the breeding schemes by farmers. For instance, meiotic maps have been developed for sockeye salmon, *O. nerka* [87], suitable for salmonids as tetraploid fishes having duplicated genomes, and which enable comparative genomics and association mapping of important genes or genomic regions of importance in the fish breeding schemes. Analysis of genetic linkage maps aids the location of QTL or genes for important traits for aquaculture production.

In comparative genomics, genomic features in complete genome sequences of different organisms or species are compared. These genomic features vary from DNA sequences, genes, gene orders, regulatory sequences to other genomic structural landmarks, that distinguish fish individuals, and can therefore be used to identify suitable genotypes (by comparing regions of similarity and differences) for use in breeding schemes for profitable aquaculture. Autotetraploidization of the common salmonid ancestor 50–120 million years ago [49] made salmonids iconic in character, value and evolutionary potential. As a tetraploid resulting from a duplicated genome therefore, sex determination in salmonids is one of the most complex traits, and probably represents a classic example of diversification in this group of fishes. In itself, tetradiploidization provided evolutionary pressure to diversify species in the Salmonid family in to 11 genera [1]. In this regard, it is interesting to know if sex determination, a trait important for aquaculture, is influenced by the same mechanism for each of the genera within the family, or indeed different mechanisms underpin the process in different genera, or whether different species have different mechanisms, or whether the sex determining gene is the same in the different species, or has shifted to a different chromosome in different species, or whether sex has evolved differently in the different salmonid species that radiated following tetra ploidy. These are uncertainties that have been addressed by comparative mapping, where linkage maps developed for different species are compared, to study the presence or absence of genetic elements of interest, or if these genetic elements are located within different linkage groups or on different chromosomes. Through these comparisons, suitable genotypes are isolated for breeding for the trait of interest.

Through concerted efforts to generate linkage maps for species of salmon, many studies now report sex determining locus on the end of the long arm of chromosome 2. In other species like the brown trout, karyotypic studies report absence of sex determining chromosomes [88]. With this kind of information, gleaned from genetic linkage maps, suitable genotypes can be selected, which when crossed have very high chance of producing monosex seeds, either male or female, depending on which sex is preferred by the farmer. Due to enormous power of linkage mapping in identifying QTLs with important roles in tolerance or resistance of salmonids to diseases that limit intensive and profitable culture of salmon, several such maps have been developed for rainbow trout [89], *S. salar*, *Salmo trutta* [90], the Arctic trout, *Salvelinus alpinus* [91], and Sockeye salmon, *S. nerka* [87]. Apart from these linkage maps from which QTL for tolerance or resistance of salmon for diseases have been inferred, several other studies have also been carried out to improve breeding for disease resistance. For instance, QTL in a back cross of strains of rainbow trout resistant and susceptible to IPN has been detected [92], while QTL for resistance to whirling disease in rainbow trout has been detected [93]. Similarly, with these maps, much more information has been gleaned, such as on which chromosome sex determining genes are located, conservation of synteny, rates of recombination in certain species, loss of genes following autotetraploidization events among

salmonids and the rate at which such genes were lost, or indeed the emergence of new genetic or sequence features among different salmonid species that radiated following tetraploidization. These research efforts, among a majority of other and ongoing studies, are being incorporated in to breeding schemes by salmon farmers, and demonstrate the importance of salmonids both as high value fish food and sentinel species [94] for human consumption and conservation respectively, and partly explain why farmed salmon production is always on the increase.

On the other hand, association mapping or linkage disequilibrium mapping is the linking of observed phenotypes to the presence of the genotype which drives the observed phenotypic characters or variations [95]. The farmer is interested in seeing the best phenotype from the fish stocked in the ponds or cages or ranches that form his farm, as this translates to higher average tonnage of fish produced and therefore sufficient food for consumption, export and higher profitability of the enterprise. Therefore, to help farmers sustain profitability of their enterprises, researchers try to apply linkage disequilibrium mapping to choose the best genotypes of salmonid species which when used by farmers, give the highest produce, with respect to the trait that the farmer is interested in. As the very basis of Marker assisted breeding, association mapping has hastened identification of suitable genotypes for use in breeding schemes for salmon, addressing a specific breeding objective. In this regard, using RFLP markers, association is reported in backcross families resistant and susceptible to IHN [96]. This means backcross genotypes with RFLP markers show resistance to IHN, while those without RFLP markers are susceptible to IHN, and this easily guides which fish individuals to choose for use in the breeding scheme for resistance against IHN, and which rainbow trout fish individuals to discard, because they lack resistance to IHN. Similarly, AFLP markers associate with resistance to ISA in two full-sib families of *S. salar* [97], with the AFLP markers mapped on to linkage group 8 of the *S. salar* genome [98].

The efforts at comparative mapping and linkage disequilibrium mapping for salmon will be more relevant for precision or more efficient breeding of better performing salmon strains when a large number of markers are available on the map in a clear order, supported by testing of a large number of families (both half sib and full sib) for the presence or lack of important QTLs that associate with certain phenotypes. The studies enumerated above appear disjointed, but will fit better in the international collaboration to sequence the Atlantic salmon genome to be used as the reference sequence for many salmonid species [86] for improved breeding. Furthermore, as more efficient and cost-effective next generation sequencing platforms become available, both genetic high density SNPs marker panels and high-resolution genetic maps are generated, from which association between markers and QTLs for important traits are deciphered [94]. Mapping of these genetic resources on to the reference map generated for *S. salar* [94] facilitates the identification of mutations [58] that underpin disease resistance in many salmonid species and guide precision breeding for improved resistance to diseases for more profitable aquaculture enterprises.

5.6 A study of gene expression for disease resistance

One of the ways fish resist diseases and therefore some infections do not translate in to full scale sickness is through mounting an immune response to the infection or the pathogen. Related to this immune response are a series of mechanisms that synergize the protective apparatus of the fish. In a population of fish, there will be some individuals with a higher ability to resist pathogens and therefore full manifestation of sickness or symptoms (i.e. resistant fish), and fish that lack ability or do not have sufficient ability to resist pathogens, and therefore develop

the disease (i.e. susceptible fish). Therefore, functional genetic variation for disease resistance will exist in such population of fish [58]. Fish that are resistant to diseases usually show less infection, with fewer viral or bacterial pathogens getting in to the body or cells of the fish. This is because differential immune response in resistant fish inhibits attachment of the pathogen, as well as entry and subsequent replication of the pathogen in fish cells. This inhibition allows the immune system of the fish ample time to mount a sufficient response to completely combat the pathogens [91]. However, should the pathogen succeed to enter the body of the fish, several genes are released by the fish to help fight off foreign invasive agents, with a faster rate of and more intense release in susceptible than resistant fish [99].

For IPNV infection in salmon for instance, interferon induced genes are released to fight the virus. These include Mx, ISG 15, Vip-2, gig 2, and CCL 19 [100]. Additional genes activated to fight IPNV infection in salmon include: Interferon regulatory factor 3 and 8, interleukin 3 receptor, and the macrophage colony stimulating factor, transcription factor 3, and the transcription factor E2-alpha [99]. Similarly, infection with furunculosis stimulates gene expression in response, to help counter-attack the infection. In this regard, Mx1, ubiquitin-protein ligase HERC 4, HERC 5 and HERC 6, ISG 15, eukaryotic translation Initiation factor 4 gamma 1 are elicited during an invasion with ISAV [101]. On the other hand, furunculosis infection in salmon elicits several genes, including JunC, JunD, NFkB, NF-kappaB-105, NFkB1, CYP3A4 and fibronectin [102], which act in different ways and mechanisms to confer protection of the fish against the effects of furunculosis. Since these genes are expressed differently in resistant and susceptible fish, and the fact that in a population of salmon, there are disease resistant and susceptible individuals, resistance has a genetic basis [99, 101, 102]. Therefore, gene expression profiles for disease resistance and susceptibility can help identify suitable fish for use in the breeding programme to improve the resistance of the fish to diseases.

In conclusion, future efforts should focus more on saturating the genetic map for salmon, from which loci for commercially important traits can be inferred, to support breeding efforts for improved strains.

Conflict of interest


Authors declare no conflict of interest.

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