Use and exchange of salmonid genetic resources relevant for food and aquaculture

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Abstract

This review describes the global use and exchange of salmonid genetic resources for human food from fisheries and aquaculture. Trends in population abundance, variations in the harvest of wild stocks, historic transfers and worldwide translocations of stocks for fisheries and aquaculture are briefly described for seven species of Pacific salmon (*Oncorhynchus*), for Atlantic salmon (*Salmo salar*) and for Arctic charr (*Salvelinus alpinus*). Also considered are the tools currently used to assist in the conservation of endangered wild populations (e.g. captive breeding programmes and gene banks) and the major techniques developed to enhance the production of cultured stocks (selective breeding, hybridization, sex control, chromosome set manipulation and gene transfer). The review briefly discusses the significance of salmon production to the economy of selected countries and the complexity of allocating economic value to long-range migratory fisheries resources that also hold direct and indirect value for aboriginal/native communities and recreational users.

Key words: aquaculture, Arctic charr, Atlantic salmon, fisheries, genetic resources, Pacific salmon.

Introduction

This review deals with the Pacific salmon species that migrate and reproduce in North American and Asian continental watersheds: *Oncorhynchus gorbuscha* (Walbaum, 1792) (pink salmon); *Oncorhynchus keta* (Walbaum, 1792) (chum salmon); *Oncorhynchus kisutch* (Walbaum, 1792) (coho salmon); *Oncorhynchus nerka* (Walbaum, 1792) (sockeye salmon); *Oncorhynchus tshawytscha* (Walbaum, 1792) (chinook salmon); *Oncorhynchus masou* (Brevoort, 1856) (masu salmon; *O. masou* occurs only in Asia) and *Oncorhynchus mykiss* (Walbaum, 1792) (rainbow trout). Other species of the genus *Oncorhynchus*, such as *Oncorhynchus rhodurus* (Jordan & McGregor, 1925), *Oncorhynchus clarkii* (Richardson, 1836), *Oncorhynchus apache* (Miller, 1972), *Oncorhynchus gilae* (Miller, 1950), *Oncorhynchus aguabonita* (Jordan, 1892) and subspecies, although important from a biological diversity perspective, are excluded because of their lesser relevance as genetic resources for food and aquaculture.

Also covered in this review is the Atlantic salmon (*Salmo salar* (Linnaeus, 1758)), which is the most important cultured salmonid species. The brown trout (*Salmo trutta* (Linnaeus, 1758)) has a long history of culture and translocation, but its relevance in commercial aquaculture is minor, thus it has been excluded. The review also includes the Arctic charr (*Salvelinus alpinus* (Linnaeus, 1758)), a salmonid species of increasing importance as a farmed commodity.

Although most salmonid species are anadromous, that is, they spawn in streams and rivers or along lakeshores and generally migrate to the sea, some populations of certain species remain in coastal waters or in landlocked freshwater bodies. Following an early period in the life cycle, most leave freshwater as smolts to perform extensive feeding migrations at sea or they may remain in lakes for most of their life until maturity, migrating to streams to spawn.

Maturation, depending on the species, occurs after 1–7 years and triggers a reproductive or 'homing' migration that takes them back to their original breeding grounds. This strong tendency to migrate to the river and spawning tributaries of origin has resulted in genetically distinct, reproductively isolated, subpopulations or stocks.

Reproductive isolation facilitates genetic adaptation to local environments and improves survival (Taylor 1991). However, such local adaptation makes difficult the transplantation of stocks from one river to another

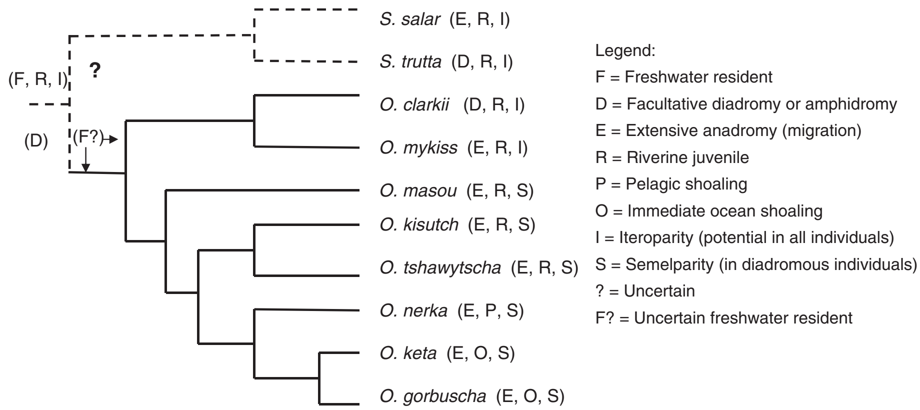

Figure 1 Phylogenetic relationships of *Salmoninae* species, genus *Salmo* and genus *Oncorhynchus*, indicating life-history similarities of related species (modified from Schaffer 2004).

(Withler 1982), or the restoration of threatened populations in modified habitats (Williams 1987). This is one reason why specific salmon populations cannot be recovered or replaced once extinct (Lichatowich *et al.* 1999).

The evolution and relationships of the genera in the *Salmonidae* is still unresolved (Crespi & Fulton 2004). Salmonids appear to have originated by adaptive radiation from a tetraploid common ancestor approximately 50–100 million years ago (Mya) (Allendorf & Thorgaard 1984). The hypothesis of the tetraploid origin is mostly based on the fact that cells of the *Salmonidae* have approximately twice the amount of DNA as other closely related families. In addition, most species in the family show several duplicate genes and allozyme loci (i.e. growth hormone Gh1 and Gh2) (Devlin 1993). Consequently, Pacific salmon species are considered to be monophyletic with an uncertain connection to Atlantic salmon and the European species of freshwater trout (i.e. *Salmo* and *Salvelinus*) (Fig. 1). The evolution of these genera (*Salmo*, *Salvelinus* and *Oncorhynchus*) probably came about ~20 Mya (Groot 1996). Fossil specimens of *Oncorhynchus* similar to present sockeye, chum and pink salmon, provide evidence that modern species of Pacific salmon and trout existed at least 6 Mya (Stearley & Smith 1993; Crespi & Fulton 2004). Parsimony analysis, based on life-history patterns, behavioural traits and molecular data of *Salmo* and *Oncorhynchus* species, suggests the phylogenetic development and relatedness shown in Figure 1 (Stearley & Smith 1993; Oakley & Phillips 1999; Osinov & Lebedev 2000; Crespi & Teo 2002).

Use and global exchange of salmon genetic resources

Pacific and Atlantic salmon are important biological and economic resources across their natural range of distribution in the North Pacific and North Atlantic rim. Because of their high food value and their value as sport fish they have been translocated far beyond their natural range of distribution within the northern hemisphere and into the southern hemisphere.

Native communities harvest some species as food fish during their reproductive migration into rivers in the USA, Canada and Russia. Several species, mainly coho, chinook and Atlantic salmon, are important to recreational fishers in the USA and Canada. Rainbow trout, coho, chinook and Atlantic salmon are intensively farmed with current production levels that largely exceed the capture fisheries of these species.

Pacific salmon are harvested commercially in the coastal waters of the USA, Canada, Russia, Japan, and North and South Korea. The average annual capture of the Pacific salmon species included in the present review for the period 2000–2006 was 827 000 t, with an estimated landed value of US$2.1 billion (FAO 2006). Some of the resources, however, are considered severely threatened in many areas and changes in the catches (Fig. 2) reflect trends in climate, the effects of fishing (Beamish & Bouillion 1993; Waples *et al.* 2008) and current severe fishing restrictions.

The capture fishery of Atlantic salmon has declined steadily over the past three decades. Catch statistics (FAO 2006) show that the average catch of 118 000 t during the 1980s decreased to 73 000 t in the 1990s and to 39 000 t during the period 2000–2006 (Fig. 3). In contrast, farmed Atlantic salmon production has increased from 53 000 t in 1980 to over 1 320 000 t in 2006 (Fig. 3). In 2007, 13 countries reported production of farmed salmon. The main producers are Norway, Chile, the UK and Canada.

The major *Oncorhynchus* species used in aquaculture are rainbow trout and coho salmon (Fig. 4). Chile is the main producer of both species. Canada and New Zealand

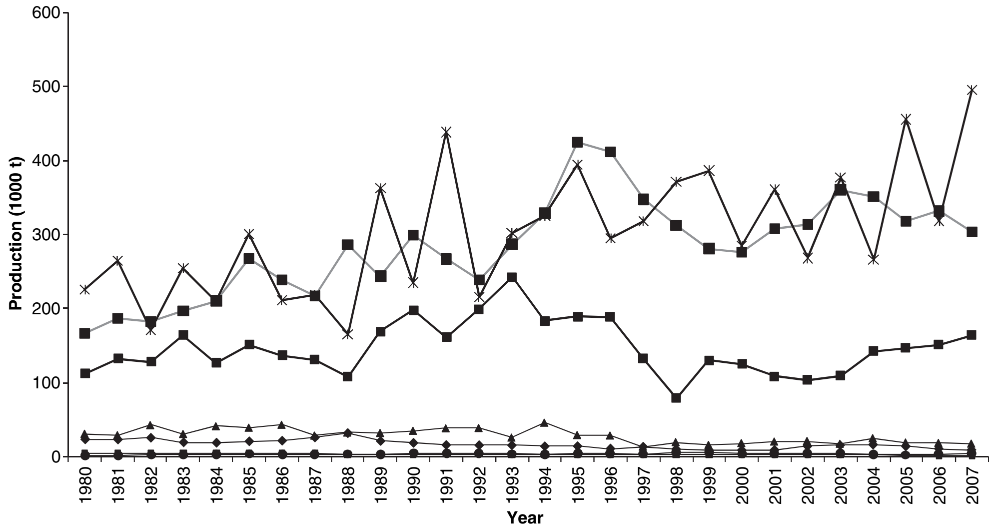

Figure 2 Capture fishery production of seven species of Pacific salmon from 1980 to 2007 (data from FAO 2007). –◆–, Chinook salmon; –✕–, Pink salmon; –■–, Chum salmon; –●–, Rainbow trout –▲–, Coho salmon; –■–, Sockeye salmon –■–, Masu salmon.

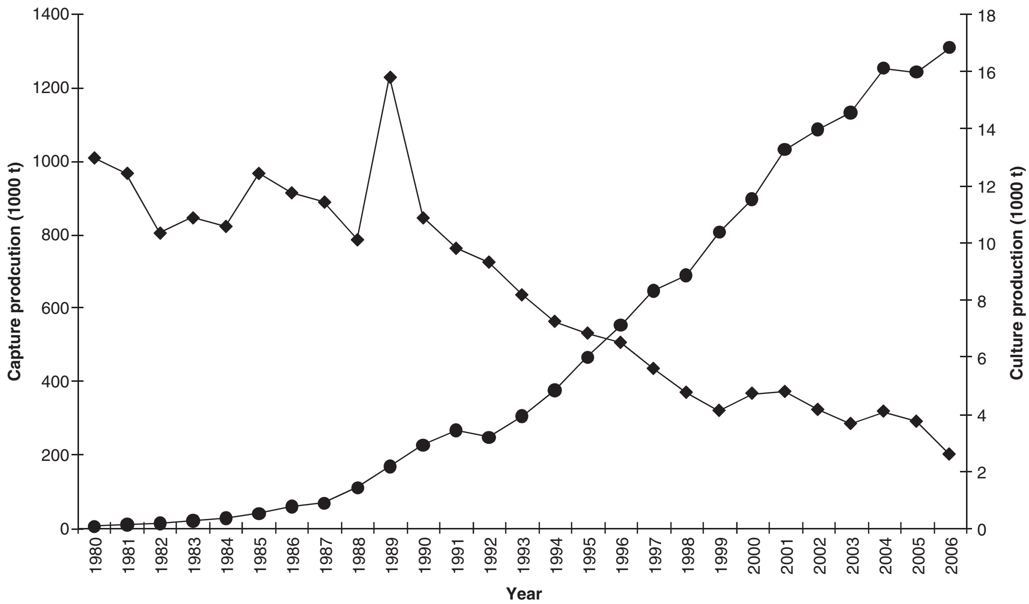

Figure 3 World capture fishery and aquaculture production of Atlantic salmon from 1980 to 2006 (data from FAO 2006). ●, Aquaculture; ◆, capture.

culture mostly chinook, and Norway is a major producer of rainbow trout. The average annual global aquaculture production of these three species for the period 2000–2006 was 643 000 t with an estimated value of US$2.08 billion (FAO 2006).

As with many other economically important genetic resources, salmonids have been extensively translocated both within and outside their natural range. As a result, in several countries, such as Chile, temperate Australia and New Zealand, aquaculture of salmonid species is based on species translocated from the northern hemisphere.

Many attempts to transplant salmonid species to other locations have failed (Withler 1982). This seems to support the notion of strong local adaptation of salmonids to specific environmental conditions. In contrast, numerous successful translocations of salmonid populations outside their native habitat challenge the strength of the local adaptation hypothesis. Examples are the introduction of

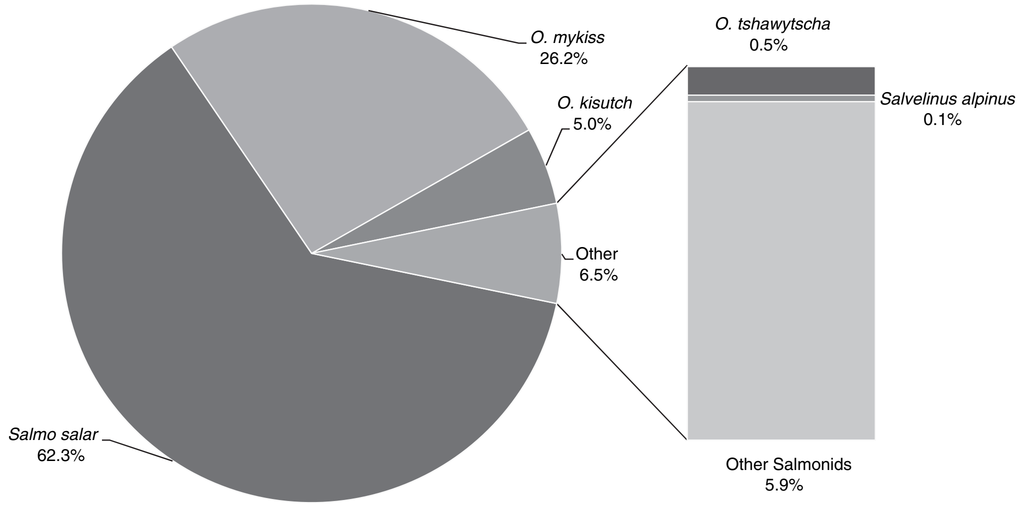

Figure 4 Main aquaculture salmonid species: 2007. 'Other salmonids' include species of several genera (*Salmo*, *Plecoglosus*, *Coregonus*, *Salvelinus* and *Oncorhynchus*) (data from FAO–Global Aquaculture Statistics 2007).

non-anadromous sockeye salmon to many lakes in Canada, the wide transplantation of rainbow trout all over the world, the establishment of chinook salmon in New Zealand and pink salmon in the Great Lakes. Other successful transplantations are those of brown trout for sport fisheries in New Zealand and to high-altitude streams and lakes in Africa and Asia (Tumi Tómasson, pers. comm., 2009). However, Taylor (1991) suggested that the apparent flexibility of such introduced populations may be the result of adaptation to highly variable environments through natural selection for phenotypic plasticity.

Salmonid genetic resources

Pacific salmon

Pacific salmon is one of the most important fish species in the North Pacific Ocean. *Oncorhynchus* species, along with those of the closely related genus *Salmo*, have occupied an important role in aquatic ecosystems in the northern hemisphere and, historically, a very significant place in human culture and economy.

Although several salmonid populations are currently threatened by overfishing, environmental changes and associated habitat degradation (Noakes *et al.* 2000), they represent a very valuable biological and economic resource for the countries in which they occur naturally. Hence, they are the subject of coordinated efforts in science and management aimed at preserving these valuable resources.

The natural range and spawning grounds of the Pacific salmon species extend from California (San Francisco Bay) along the north-west coasts of the USA (Oregon, Washington and Alaska) and Canada (British Columbia and Yukon) towards the Asian coasts of Russia, Japan and Korea. Their ocean range extends across the North Pacific Ocean, mostly north of latitude 40°N, the Bering Sea, the Sea of Okhotsk, Bristol Bay and the Gulf of Alaska. All species of North American salmon are known to intermingle with Asian salmon south of 45°N and between 175°E and 175°W (INPFC 1985).

Pink salmon (*Oncorhynchus gorbuscha*)

The pink salmon is the most abundant of all Pacific salmon (Fig. 2). The average catch of pink salmon from 1997 to 2006 was over 41% of all salmon caught commercially in the North Pacific. Because their life cycle is fixed and short, 2 years, they are relatively small (1–2.5 kg). Thus, by number, they represent approximately 60% of the total Pacific salmon harvest. Pink salmon are mostly canned, but are also used fresh, smoked and frozen; they are also valued as caviar, particularly in Japan.

Their natural range of distribution includes the north-west coast of the USA, from southern California (Sacramento River, 40°N) to coastal areas of the Beaufort Sea in the Arctic Ocean. In Asia, pink salmon spawn from 42°N (Tumen River, North Korea–Southern Russia), along the coast of Russia, Hokkaido in Japan, the Kamchatka Peninsula and the Bering Sea.

Some of the major runs and harvests of pink salmon are in Alaska, where the average for the period 1998–2007 was 173 million salmon, with a value of US$289 million. The largest captures (approximately 50% of the total catch) are in south-east Alaska, the coastal region along southern Yukon and northern British Columbia (NPAFC 2006).

Many attempts have been made to transplant pink salmon, but success has been extremely low (Withler 1982). Many of the transplants were aimed at establishing or improving even-year runs in locations where such runs did not exist or where the numbers of returning fish were too low. Most of the failures have been attributed to unfavourable environmental conditions in the new areas, including predation during freshwater and oceanic migration phases, unfavourable temperatures in rivers and insufficient numbers of eggs transplanted or fry released to produce viable populations under limiting environmental conditions. Heard (1991) gave a detailed account of pink salmon transplants both within and outside their natural range. Additional information on *O. gorbusha*'s translocations may be found in Welcomme (1988).

Chum salmon (*Oncorhynchus keta*)

Chum salmon are very tolerant of cold temperature and have the widest distribution of all *Oncorhynchus* species. In the USA, they range from the San Lorenzo River in California, the Aleutian Islands, to as far north and east as the Mackenzie River system in the Arctic Ocean. In Asia, their southern limit is the Naktong River in Korea, up north along the seas of Japan and Okhostk, the Kamtachka Peninsula and the rivers draining into the Arctic Ocean as far west as the Lena River (Salo 1991). In recent years, however, the southern limit of chum salmon distribution in the USA may not extend further south than the Columbia River because runs to rivers in California have been evaluated as extinct (Nehlsen *et al.* 1991).

Oncorhynchus keta is the second most abundant of the Pacific salmon species (Fig. 2). Chum salmon and its closely related species, pink salmon, are considered the least advanced of the Pacific salmon species from an evolutionary standpoint because of their short residence period in fresh water and more prolonged marine life stage (Salo 1991). The ability of chum and pink salmon to readily hybridize under experimental conditions (Table 2; Robert Devlin, DFO Canada) (reported in Alverson & Ruggerone 1997) and in nature (Abe *et al.* 2001) provides evidence of their genetic affinity.

The commercial fishery of *O. keta*, including coastal and high-seas fisheries (within the 200-mile exclusive economic zone), amounts to approximately 39% of all salmon caught by countries in the North Pacific Anadromous Fish Commission (NPAFC) (NPAFC 2006). Average annual capture of chum salmon from 1997 to 2006 was 324 000 t. Japan is the most important user of this species with over 58% of the total chum caught by all countries in the convention (NPAFC 2006).

As the main user of chum salmon, Japan has developed a complex ranching system that involves catch quotas in the high-seas mother-ship fishery and captures in coastal areas, and allows for sufficient river escapes to ensure production of the next year class and the supply of adult fish for the fishery in the following years. Close to 90% of the Japanese chum salmon fishery is based on hatchery output (Morita *et al.* 2006).

Most chum salmon caught are canned, some are smoked, dried-salted, frozen or their roe used as caviar. The flesh of chum salmon is rather pale and it has a lower fat content than other Pacific salmon. The quality deteriorates quickly with the onset of maturity and the market value is often lower. Chum are not considered a sport fish, however, they have traditionally been a valuable resource as subsistence fish for native people along coastal areas in Japan, the Arctic and in Alaska and British Columbia.

Transplant attempts of chum salmon to areas outside their normal range have been less numerous than other Pacific salmonids. Some attempts occurred around 1932, from Russia to Finland and Norway (Holcík 1991), in the 1960s, stocks from an unknown location were introduced to the Caspian Sea and Iran where unconfirmed reports claim that chum salmon are occasionally captured in the wild (Magomedov 1978; Coad 1996), and a large introduction programme lasting approximately 16 years (1972–1987) from Okkaido, Japan, to the Aysén Region in Chile (Méndez & Munita 1989).

Coho, silver salmon (*Oncorhynchus kisutch*)

The geographical distribution of coho salmon in the USA extends from the Sacramento River in California, along the coast of Oregon and Washington, through the coast of British Columbia, Alaska, the Aleutian Islands, to the Nome River and Kotzebue Sound in northern Alaska. On the Asian side of the Pacific, they range from Peter the Great Bay in south-eastern Russia, northern Hokkaido, the Sea of Okhostk, Sakhalin and Kuril Islands, along the Kamchatka Peninsula, to the Anadyr River (Sandercock 1991).

Coho salmon has a longer freshwater residence than most other Pacific salmon species, and as such its life cycle is similar to that of Atlantic salmon. From 1977 to 1985, coho salmon represented approximately 4.6% of the total catch of Pacific salmon (INPFC 1985). More recently, from 1997 to 2006, their average abundance, relative to other Pacific salmon species, has been approximately 2.2% (NPAFC 2006).

Historically, coho salmon has been a very important fish resource for indigenous people in coastal areas along their range of distribution. Many indigenous communities in the Pacific Northwest consider coho salmon to be a symbol of their identity, representing life and food. They also use its skin to make clothing, footwear and baggage, its oil for cooking purposes and the bones for making needles. Coho salmon is also important for sport fishermen in the USA Pacific Northwest.

Coho salmon culture in sea-net pens is an important economic activity in Chile where 118 900 t, close to 90% of all cultured coho salmon, was produced in 2006. From 1997 to 2006, Japan had an average annual production of 10 600 t. In 2007, farmed coho salmon accounted for 5% of all farmed salmon production worldwide (FAO 2007) (Fig. 4).

Coho salmon are, after *O. mykiss*, the most widely and successfully translocated species of the genus *Oncorhynchus*. Since the 1870s, attempts have been made to introduce coho salmon into the Great Lakes. In 1935, these efforts were discontinued after having failed to establish a self-sustaining population. Further efforts followed in the 1960s (Kwain & Lawrie 1981) and were very successful (Sandercock 1991).

In the 1970s, coho salmon from the state of Washington were introduced into rivers of South Korea and to several rivers in Hokkaido, Japan. These transplants have been considered a failure. Close to 1.3 million eyed eggs were transplanted from 1968 to 1971 from the state of Washington to Chile; however, no returning fish have been recorded (Basulto 2003). Since the 1990s, several additional transplants have taken place, initially with ranching objectives, and later for aquaculture in net pens. There is little evidence that the fish released for ranching have resulted in returning adults. However, escapees from net pens in freshwater and coastal locations apparently have become established both in Lake Llanquihue and in the inner sea of Chiloé Island (Soto *et al.* 2001).

Sockeye salmon (*Oncorhynchus nerka*)

Sockeye salmon have a wide geographical distribution in the sub-Arctic areas of the North Pacific Ocean. In Asia, they are most abundant around the Kamchatka Peninsula and coastal regions of the Bering Sea, and they are found less frequently in the Kuril Islands, the north coast of the Sea of Okhotsk, the Anadyr River, and the northern coast of the Bering Sea up to Cape Chaplina. In the USA, they occur along the coast of the Beaufort Sea, MacKenzie River, the west coast of Alaska and the Yukon River. Larger spawning populations are found in the Aleutian Islands, the Bristol Bay and Fraser River watersheds, lakes in British Columbia and in the Columbia River. Rarely, they migrate into rivers near the Oregon–California border (Burgner 1991).

Oncorhynchus nerka is the third most abundant of the Pacific salmon species (Fig. 2). In recent years (1997–2006) they have contributed to approximately 14% of salmonid fisheries in the Pacific Ocean (NPAFC 2006).

In many cases, villages of native communities had been located based on access to sockeye salmon runs and this species has been a major component of the aboriginal diet and the diet of their dogs. This species is also valued by sport fishers, often causing conflict between them and aboriginal fishers when stocks are limited.

Sockeye salmon have been transplanted to several lakes and other freshwater sites in the USA and Canada, but were unsuccessfully transplanted into Lake Tahoe and the Laurentian Great Lakes (Emery 1985; Moyle 1986). Attempts to introduce sockeye salmon from the USA to Europe, Finland (1930s and 1960s), Sweden (1950s) and Denmark (1960s) also failed. Other transplants have fared better, for example, to Lake Washington and to lakes in several Canadian provinces from Alberta to Quebec. In the early 1900s sockeye salmon were transplanted from Canada to several watersheds in New Zealand. Only one transplant, to the headwater lake of the Waitaki River, succeeded (McDowall 1984).

Chinook salmon (*Oncorhynchus tshawytscha*)

Chinook salmon are the largest of the Pacific salmon, frequently reaching a weight of up to 45 kg. Similar to other species of *Oncorhynchus*, they show genetic stock variations in life-cycle traits, including age at seaward migration, length of freshwater, estuarine and oceanic residence, ocean migratory routes, and age and season of upstream reproductive migration (Healey 1991). They also show differences in flesh colouration (Hard *et al.* 1989).

Chinook salmon are among the least abundant of the Pacific salmon species. Of the total commercial catch of Pacific salmon (round weight) from 2000 to 2006 only 1.5% were chinook salmon (FAO 2006). The USA (Alaska and California) accounts for approximately 82% of the total captures of chinook salmon.

Asian populations spawn from Northern Hokkaido, Amur River and Sakhalin Island, along the coast of the Sea of Okhotsk, the Kamchatka Peninsula, to the Anadyr River. The USA runs range from central California, Sacramento and San Joaquin Rivers, along the north-west coast of the USA and Canada, to Katzebue Sound in northern Alaska. The southernmost runs of chinook salmon (Sacramento–San Joaquin river system), however, have been severely reduced since 1942 after the construction of the Friant dam (Fisher 1994).

Chinook salmon have been translocated to several locations outside their normal distribution. Within North America they were transplanted (1870–1880) from the west coast to the east coast of the USA and Canada and to each of the Great Lakes. These translocations did not succeed and were discontinued. Another effort commenced in the 1960s, and by 1998 approximately

336 million chinook had been introduced into the Great Lakes (Crawford 2001). Currently, there is uncertainty about their establishment in the Great Lakes, however, some estimates suggest that approximately one-third of the chinook in the Great Lakes are the result of reproduction in the wild (Berends 2004). Beginning in 1876, chinook salmon from the USA were also introduced to New Zealand's South Island. Between 1901 and 1906, chinook eggs probably originating from Battle Creek or Mill Creek, tributaries of the Sacramento River, were sent to a hatchery on the Hakataramea River, a tributary of the Waitaki River (McDowall 1994). These transplants did succeed and since the 1920s several anadromous self-sustaining populations have been identified (Unwin & James 1998). This made it possible to transfer eggs from adults returning to hatcheries in New Zealand to other locations and to Tasmania.

The first transplants of chinook to South America, particularly to Chile, started in 1886. Efforts to introduce chinook to Chile started again in the late 1960s, but did not succeed (Basulto 2003). Further attempts to transplant chinook to Chile took place in the 1980s. Initial returns were encouraging; however, no self-sustaining population has been established. Nevertheless, in recent years, there have been reports of large numbers of adult chinook spawners in streams of the Puerto Montt area (Soto *et al.* 2001). The origin of these reproductive populations is, however, uncertain. Soto *et al.* (2001, 2006) assigned the presence of most salmonid species in Chilean lakes and streams draining into lakes to escapees from aquaculture facilities. Chinook spawning adults and young fish present in tributaries of the Puelo, Petrohué and Futaleufú Rivers, however, are found in watersheds that have direct connection to the sea.

Cherry salmon (*Oncorhynchus masou*)

Cherry or masu salmon are restricted to Asia. *Oncorhynchus masou* has the most southerly range of the *Oncorhynchus* species. It spawns in rivers along the coast of Japan, the Korean Peninsula and Russia (Kato 1991). Masu salmon spawning populations range in Japan from central Kyushu to the north of Hokkaido. Along the coast of Asia, they range from the south-eastern end of the Korean Peninsula, the coast of Russia, Primore region, to the Amur River. They are also found on the western coast of the Kamchatka Peninsula, Sakhalin Island and at the two southernmost Kuril Islands, Kunashir and Iturup. The easternmost record of cherry salmon has been in the central North Pacific Ocean (46°N, 180°E) (Ohkuma *et al.* 1999). An endemic, highly endangered, landlocked population (Formosan salmon, subspecies *Oncorhynchus masou formosanus* (Jordan & Oshima, 1919)) exists in Taiwan under strict protection and intense restoration efforts because the stock is near extinction.

Masu salmon are the smallest of the Pacific salmon species and adult size ranges from 0.3 to approximately 5 kg (Kato 1991). There are two forms or subspecies of masu salmon, the anadromous type *Oncorhynchus masou* (Brevoort, 1856) var. *masou* and the freshwater landlocked type *Oncorhynchus masou* var. *ishikawae*, known as yamame. The average commercial catch of masu salmon for the period 1997–2006 was 1200 t and represents only 0.14% of the total all-country catch of *Oncorhynchus* species (NPAFC 2006).

Masu salmon hatchery programmes have not shown the same success as chum and pink salmon programmes. Returns of hatchery-released masu have steadily declined in Japan since 1977, despite increases in the numbers released (Nagata & Kaeriyama 2003). Masu salmon are not reared commercially. The only records in FAO statistics with regard to farming of masu salmon are from Chile. From 1990 to 1992, a total of 202 t was produced (FAO 2006).

Masu salmon have been transplanted from Japan to several locations around the world: to Lake Michigan in 1929; to Lake Westward, Ontario, in 1965 (Christie 1970; Crossman 1984); to Hewitt Lake in Washington, USA, in 1970 (Courtenay *et al.* 1984); to Germany in 1976; to Nepal and Thailand during the decade 1975–1985; and to Claro River, Chile, in 1973 (references cited by Kato 1991 and Crawford & Muir 2008). All these attempts are deemed to have failed because no returning adults have been reported.

Rainbow (steelhead) trout (*Oncorhynchus mykiss*)

Formerly known as *Salmo gairdneri* (Richardson, 1836), this species was considered to be a closer relative of the Atlantic salmon (*S. salar*) and the brown trout (*S. trutta*) until the late 1980s. Based on fossil evidence and molecular genetic studies (Smith & Stearley 1989), its taxonomic status was changed to *O. mykiss*. Two forms of the species are recognized. One form is a permanent freshwater resident called 'rainbow trout' and the anadromous form is known as 'steelhead' or 'ocean trout'. However, *O. mykiss* farmed in coastal areas are often listed as rainbow trout. They are known to hybridize with other species of salmon and trout and several other varieties or subspecies are known to occur in the rivers and lakes of continental North America and Europe. Steelhead are reputed by recreational anglers to be excellent fighting fish. The steelhead fishery is small, from 1997 to 2006 they represented only 0.56 % of the total all-nation catch of Pacific salmonids (NPAFC 2006).

Steelhead range from the Baja Peninsula, Mexico, along the coast of the USA, to the Bering Sea in Alaska. The

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populations of steelhead in Asia, found along the Kamchatka Peninsula, the Kuril Islands and the Sea of Okhotsk, as far south as the mouth of the Amur River, are known as *mykizha* or *Parasalmo mykiss* (Kovalenko *et al.* 2005).

Rainbow trout is the main species of *Oncorhynchus* that is farmed (Fig. 4). At least 64 countries report farmed trout culture production. Commercial production of rainbow trout targets two markets: large fish over 3 kg, farmed mostly in Chile, Norway, Sweden and Finland, and 200–300 g (pan-size) cultured in freshwater in France, Italy and Denmark. These countries produced in 2006 close to 50% (89 300 t) of all freshwater rainbow trout cultured in Europe (FAO 2006). The main producers of cultured rainbow trout in freshwater in the Americas are the USA, Chile and Peru. In 2006 these countries produced 47.5, 17.6 and 10% of the total, respectively (total production in the Americas was 185 700 t).

The largest production of rainbow trout comes from mariculture facilities. Based on the average production over a 10-year period (1997–2006), Chile and Norway were the major producers with 100 000 (20.8%) and 59 000 t (12.2%), respectively. In 2006, Chile had a substantial increase in production, reaching 27.5% of the all-country production (151 000 t). In the same year, Iran also reported a significant increase, which placed this country in third place, after Chile and Norway, with 8.4% of the worldwide farmed trout production (FAO 2006).

Oncorhynchus mykiss is by far the most widely translocated species and the most successful in establishing self-sustaining populations outside of its native range and it is deemed as a major threat to biodiversity (Froese & Pauly 2009). The *O. mykiss* introductions page of FishBase lists 125 translocations, 81 of which qualify as 'established' or 'probably established'. Concerns about negative effects of introduced trout, mostly on native fish and invertebrates through predation and competition in many areas, have resulted in *O. mykiss* being included in the list of 'One Hundred of the World's Worst Invasive Alien Species' (Lowe *et al.* 2000).

The global success of this species can be attributed to a wide array of reasons, such as its ability to tolerate a range of environmental conditions including temperature, oxygen and culture density, its value as a recreational fish in western societies, its importance as a food fish in developing countries, the perseverance of transplant efforts, the development of hatchery and culture techniques in fresh and seawater and the use of selective breeding to alter life-history traits. All these factors have contributed to the high degree of domestication and adaptation of this fish to varied natural environments and culture conditions.

Atlantic salmon (*Salmo salar*)

Historically, wild populations of Atlantic salmon were abundant and their distribution was extensive. In Europe, they occupied several rivers draining into the Baltic Sea, some of the largest rivers of Central Europe (Elbe and Rhine), many rivers in England, and they extended their habitat to rivers in southern France and northern Spain (MacCrimmon & Gots 1979). In the USA, Atlantic salmon were an important subsistence and commercial resource for native North Americans and European settlers in colonial times and during the beginning of the industrial revolution. Over the past 150 years, however, they have become extinct in many rivers, and in some regions the remaining populations are severely depressed and frequently unable to maintain self-sustaining populations without supplemental hatchery-stocking programmes.

The decline in the wild populations of Atlantic salmon has been caused mostly by habitat loss and overfishing. Environmental degradation can be attributed to human settlement and subsequent activities, such as logging and dam and mill construction causing pollution, erosion and siltation of spawning grounds. Other factors causing a decrease in many stocks are capture fisheries and low rates of ocean survival. In addition, it has been suggested that the impact of Atlantic salmon farm escapes, directly and indirectly, impact wild salmon stocks through competitive, disease and parasite interactions. As a result, the former range of the species, both in Europe and in the USA, has gradually contracted and fragmented (Verspoor *et al.* 2007).

Although several reasons have been recognized for the decline in wild Atlantic salmon catches, other reasons, such as reduced fishing effort as a result of decreasing market value, also contribure to the lower volume of wild Atlantic salmon caught in commercial fisheries (Tumi Tómasson, pers. comm., 2009).

However, despite severe threats to the survival of this species in the wild, Atlantic salmon is now more abundant than ever because they have been translocated so widely. Currently, approximately 99.8% of all Atlantic salmon in the market originates from farming facilities (Fig. 3).

Despite being seen as a single valid species there are some important differences between European and North American Atlantic salmon. The variety present in the Western Atlantic (North American stocks) has 54 chromosomes, whereas the Atlantic salmon from the Eastern Atlantic has 58 chromosomes (Roberts 1970). In addition, several differences have been identified at allozyme loci (Verspoor *et al.* 2005) as well as variation in mitochondrial DNA (King *et al.* 2000) and divergence with respect to microsatellite loci (King *et al.* 2001).

On the basis of bone remains found in caves in Spain that were glacial refuges during the Pleistocene, it is believed that Atlantic salmon formed part of the diet of humans approximately 40 000 years ago (Consuegra *et al.* 2002). For thousands of years, men using spears caught this species, along with cod and eels. With advances in technological innovations, seine nets and other types of nets became more efficient fishing gear. Salmon in great numbers were netted or speared for food, for trade and even as agricultural fertilizer. Beginning in the 1600s, the effects of dam construction, overfishing and pollution during the Industrial Revolution resulted in declines and extinctions of salmon runs across much of its historic range.

In the late 1950s, intense high-seas fisheries using drift nets and long lines were operating off Greenland and the Faroe Islands. From 1964 to 1975 yearly catches of Atlantic salmon were in the range of 10 000–12 000 t. The capture of Atlantic salmon in Europe dropped from 8800 t in 1970 to 1100 t in 2006, whereas captures in the USA have fallen from 3600 t to 2 t over the same period of time (FAO 2007).

Conversely, farming of Atlantic salmon has steadily increased in the USA, Europe and in countries in the southern hemisphere, Chile and Australia, where it has been introduced for cultivation. Atlantic salmon accounts for more than 60% of all salmonid species cultured (Fig. 4). Production in 1986 was 59 000 t valued at US$306 million. In 2007, production was 1433 million t valued at close to US$6.7 billion (FAO 2007). Thus, in 2007, the production of farmed Atlantic salmon amounted to 99.8% of the total worldwide production of the species; the remaining 0.2% came from wild stocks. The three main producers of farmed *S. salar* are Norway, Chile and the UK, accounting for more than 87% of the total.

Aquaculture of Atlantic salmon, which was originally seen as providing relief to wild populations, has brought further risks and concerns to efforts to restore Atlantic salmon wild stocks. Although some argue that the evidence appears circumstantial, drawbacks to the recovery of wild stocks have been attributed, among other reasons, to problems related to competition, gene flow and disease transmission between farmed and wild fish (Ferguson *et al.* 2007). Nevertheless, documented evidence of behavioural and genetic interactions between farmed salmon escapees and wild salmon in the USA and Europe, predictions based on models for risk assessment and the potential for negative interactions with deleterious consequences for wild populations, warrant the application of the Precautionary Approach for the management of salmon stocks and the relevance of measures to prevent the interaction of escaped farmed salmon with wild stocks.

In Europe, wild Atlantic salmon populations are presently found in countries with rivers draining to the Atlantic Ocean or Baltic Sea, from the northern Portugal–Spain border (Minho/Miño River), through Europe and Scandinavia, to Russia's Pechora River. In the USA, wild populations are found in Maine, and north to Canada's Atlantic Provinces, Ungava Bay, Hudson and Davis straits. Wild populations of *S. salar* also occur in Iceland and southern Greenland (Verspoor 2007). Many translocations of *S. salar* have succeeded, particularly those intended for net-pen commercial culture.

Atlantic salmon have been transferred from the east coast of Canada and the USA to the USA and the Canadian Pacific coast. One of the first attempts to transfer *S. salar* to British Columbia for wild propagation occurred at the beginning of the twentieth century. Approximately 13 million eggs, alevins and fry were released between 1905 and 1935 in more than 50 water bodies in British Columbia (McKinnell *et al.* 1995). Transplants to New Zealand and Australia from the UK, the USA and Germany between 1864 and 1910 are reported to have been successful (Welcomme 1988). *Salmo salar* was translocated in the mid-1960s from the River Philip, Nova Scotia, Canada, for farming in Tasmania, Australia. Atlantic salmon originating from several (wild and domesticated) stocks in Norway (Namsen/AquaGen), Ireland (Fanad/Mowi, originally from Norway) and Scotland (Landcatch, Lochy) have also been transferred to Chile for culture through private commercial agreements.

Arctic charr (*Salvelinus alpinus*)

Arctic charr have the most northerly distribution of all anadromous salmonids. In addition, this species is the dominant, and in many locations the only fish, found in freshwater in Arctic coastal waters (DFO 2006). Its distribution extends in circumpolar marine areas and streams and lakes of the USA, Europe, Iceland, Greenland and Asia. This fish has been a traditional subsistence resource for the aboriginal Inuit of northern Canada, Alaska and Greenland.

The production of farmed Arctic charr has nearly doubled from 2000 to 2007 (estimate from FAO 2007). Still, because of the very large share of the farmed Atlantic salmon and rainbow trout (close to 94% combined), the volume of farmed Arctic charr production is just slightly over 0.1% of the major farmed salmonid species.

Compared with other salmonids, capture fisheries of Arctic charr have been traditionally low. The average catch of wild *S. alpinus* from 1970 to 2007 was 121.6 t (FAO 2007). In 1970 only two countries (Greenland and Sweden) reported catches of Arctic charr, whereas in 2007 seven countries (Greenland, Iceland, Switzerland, Norway, Germany, Sweden and Slovenia) reported catches ranging from 2 to 34 t (FAO 2007).

Production of farmed Arctic charr started in Iceland in 1987 with approximately 3 t cultured in brackish water. In 2006, five countries produced 1366 t in both fresh and brackish waters. Production for 2007 was approximately 2300 t (FAO 2007). The bulk of production (approximately 90%) came from Iceland. Other countries farming Arctic charr are the USA, Ireland, Austria, Norway and the UK.

Approximately 40 farms for Arctic charr were operating in Iceland in the early 1990s. Since then the industry has consolidated to approximately 20 farms, but production capacity has increased from 340 t in 1993 to 1664 t in 2003. Problems caused by bacterial kidney disease reduced production from 2004 to 2006. However, in 2007 production recovered to over 2000 t and projections of the industry estimate are close to 5000 t by 2010. An important factor in the increase of production of Arctic charr in Iceland has been the establishment of a government-sponsored genetic breeding programme. The use of better feeds, husbandry procedures and control of precocious maturation are also regarded as positive causes (Gunnarsson 2008).

Extent of use/addition of value: domestication and development of genetic resources for food

Selection and breeding programmes

An important factor in the potential for genetic improvement of salmonid species is the large genetic variability resulting from local adaptation and reproductive isolation of stocks. Natural populations of the same species show significant variation in traits that can be exploited, combined (hybridization) and improved to fit commercial production strategies and the development of 'domesticated' captive stocks.

Among the salmonids, the most domesticated species is the rainbow trout, *O. mykiss*, which has been held in captivity in Europe since the 1890s (Gjedrem 2005). It has been selectively bred, hybridized and submitted to various environmental conditions (e.g. light, temperature) to manipulate growth and reproductive traits for so many generations that captive stocks can be considered to be nearly tamed and very different to the wild varieties that they originated from. Other species of Pacific salmon, such as coho and chinook, have been selectively bred for improved performance for culture in the USA, Canada and Chile (Hershberger *et al.* 1990; Neira *et al.* 2006a,b). Several commercial breeding programmes for Pacific salmonids (coho, chinook and rainbow trout) are underway in Chile, Canada, Norway and Finland (Table 1).

The European Atlantic salmon aquaculture sector is mostly based on selectively bred strains of Norwegian origin. In Norway, selective breeding of Atlantic salmon started in the early 1970s with a mix of broodstock of approximately 600 fish, of 4 year classes, from 40 Norwegian rivers (Gjøen & Bentsen 1997). By the third generation, however, stock composition of the population was estimated to be dominated by one genetic stock, Namsen (Gjedrem *et al.* 1991). This prompted the addition of gene-flow from private hatcheries and the generation of up to eight lines or subpopulations (Gjøen & Bentsen 1997). Currently, there are four breeding programmes in Norway (Table 1). Trait selection started with growth and gradually expanded to include age at sexual maturation, disease resistance and carcass quality. Approximately 80% of Norwegian salmon farms grow fish originating from selective breeding programmes. In addition, eggs are exported to other countries within Europe, to Canada and to Chile. Similar breeding programmes are underway in Scotland, Ireland, Iceland and the Faroe Islands (Verspoor *et al.* 2007). Breeding programmes for Atlantic salmon are also ongoing in both coasts of Canada, in Tasmania and in Chile (Table 1).

A selective breeding programme for Arctic charr started in Iceland in 1992 with founders from seven stocks collected from the wild and obtained from farms (Table 1). The programme is owned by the state and funded by the Ministry of Agriculture and from proceeds from eggs sold to farmers. Currently, all Arctic charr farmers in Iceland use eggs originating from this selective breeding programme, with an annual production of approximately 3000 t (Einar Svavarsson, pers. comm., 2009).

In Canada, Icy Waters Arctic Charr maintains a breeding programme for Arctic charr and conducts research and development on the identification of genetic markers believed to be associated with growth rate and disease resistance (furunculosis) to be used in marker-assisted selection for this species (Woram *et al.* 2004).

One important area of research in salmonids, both for species conservation and for aquaculture, is the study of the major histocompatibility complex (MHC). This complex contains the genes that control the acquired immune response. The genes involved in the MHC of fish are highly polymorphic and can be used to study genetic variability, to define population structure, for species identification (Withler *et al.* 1997; Beacham *et al.* 2001) and to identify disease-resistant genotypes (Grimholt *et al.* 2003).

Genetic mapping of salmonids

Genetic maps for several salmonid species are currently under development. By 2008, three partial genetic maps had been published for Atlantic salmon. In addition,

Table 1 Active family-based selective breeding programmes of salmonids

Species	Country	Company	Start	Families tested[a]	Traits[b]
Atlantic salmon	Norway	Aquagen	1971	400	7
	Norway	SalmoBreed	1999	300	7
	Norway	Marine Harvest	n/a	n/a	n/a
	Norway	Rauma[c]	1985	400	2[b]
	Canada	ASBDP[d]	1984	90	2
	Canada	Heritage	2001	n/a	n/a
	Canada	Tri-Gen	n/a	93	n/a
	Iceland	Stofnfiskur	1995	400	n/a
	Scotland	LNS[e]	1996	200	6[b]
	Ireland	Marine Harvest	1998	n/a	n/a
	Chile	LNS[e]	1998	160	6[b]
	Chile	AquaChile	1997	200	4
	Chile	Camanchaca	2005	180	1[b]
	Australia	Saltas-SCIRO[f]	2004	144	4
Rainbow trout	Norway	AquaGen	1971	300	5
	Norway	SalmoBreed	2000	150	8
	Finland	MTT[g]	1992	190	2
	Chile	AquaChile	2000	120	3
Chinook Salmon	Canada	Marine Harvest/Creative Salmon	n/a	n/a	n/a
Arctic charr	Iceland	Public[h]	1992	150–170	2[b]
	Canada	Icy Waters[i]	1986	n/a	3[b]

[a]Number of families in some cases varies from year to year; an estimated average is given.
[b]Major traits considered; traits in addition to the number shown are monitored. n/a, nformation not available.
[c]Rauma Stamfisk AS (in cooperation with GenoMar ASA).
[d]ASBDP, Atlantic Salmon Broodstock Development Program. Managed by Huntsman Marine Science Centre.
[e]LNS, Landcatch Natural Selection (Scotland and Chile).
[f]Saltas (Salmon Enterprises of Tasmania) – CSIRO (Australian Commonwealth Scientific and Industrial Research Organisation).
[g]MTT, Agrifood Research Finland in collaboration with Finnish Game and Fisheries Research Institute (RKTL).
[h]Government of Iceland, Ministry of Agriculture – Hólar University College.
[i]Icy Waters Arctic Charr Limited, Whitehorse, Yukon – Simon Fraser University and funding from Canada's National Research Council Industrial Research Assistance Program (NRC-IRAP).

genetic maps have been reported for rainbow trout and Arctic charr. Partial maps have also been developed for specific linkage groups for particular traits in several salmonid species, primarily for rainbow trout. The genetic linkage maps developed to date and quantitative trait loci (QTLs) detected for traits of economic importance in salmonid species were reviewed by Araneda *et al.* (2008).

Hybridization

Intraspecific

River systems may harbour more than one distinct stock of the same species, but they rarely interbreed because of spatial and temporal separation. However, under culture conditions and using artificial breeding techniques (induced spawning, sperm cold storage or cryopreservation), intraspecific hybridization of stocks, even from geographically distant locations, is possible and is practiced with the objective of combining favourable traits (i.e. fast growth and late maturation) or to provide gene flow to avoid inbreeding depression inadvertently caused by a limited effective number of breeders or close relative crosses in mass selection.

Interspecific

Studies on interspecific hybridization of Pacific and Atlantic salmonids are limited. Some laboratory tests (Robert H. Devlin, unpubl. data; Table 2) on reciprocal crosses between Atlantic, coho, chinook, pink, chum, sockeye salmon and domestic rainbow trout have demonstrated that several interspecific crosses between *Oncorhynchus* species produce viable progenies, at least during the early stages of development. However, crosses of Atlantic and Pacific salmon are largely unviable, except for low survival to hatch in Atlantic–pink and Atlantic–steelhead crosses. Nevertheless, the surviving progeny had severe physical deformities and none of the hybrid fish showed signs of maturity up to 4 years post-hatch (Noakes *et al.* 2000).

These results are of particular interest because they provide evidence that the potential interaction of escaped farmed salmon pose a low risk of genetic impact on wild stocks, which may not be greater than the genetic impact

Table 2 Survival to hatch (%) from various Atlantic salmon × Pacific salmon crosses and interspecific Pacific salmon × Pacific salmon crosses

Female: Male:	Atlantic	Sockeye	Chum	Pink	Coho	Chinook	Rainbow trout
Atlantic	**64.1**	0.0	0.0	0.0	0.0	0.0	0.0
Sockeye	0.0	**88.4**	90.9	16.9	0.0	0.3	0.0
Chum	0.0	61.9	**94.9**	85.7	0.0	0.0	0.0
Pink	5.5	77.7	54.2	**83.9**	14.9	93.2	15.8
Coho	0.0	82.9	0.0	1.5	**73.3**	0.0	0.7
Chinook	0.0	43.2	35.3	64.3	52.3	**94.3**	10.6
Rainbow trout	0.0	0.0	0.0	0.0	0.0	0.0	**54.6**

Source: Robert Devlin, DFO Canada (unpubl. data reported in Alverson & Ruggerone 1997).
Number of eggs for each cross was approximately 500.
Intraspecific crosses are in bold.

of fish released from hatcheries in salmon enhancement programmes. Nevertheless, the unlikely hybridization of farmed Atlantic salmon with wild Pacific salmon has been mentioned as a major threat originating from farmed Atlantic salmon (Hansen *et al.* 1991). However, the extremely low probability of reproductive interaction and hybridization does not preclude potential ecological impacts and the eventual transmission of diseases that tend to be more prevalent in high-density farming situations.

Chromosome set manipulation

Induced polyploidy has been investigated in fish species, including salmonids, mostly as a means of reproductive control. The triploid (3n) condition is usually associated with sterility; therefore, the use of triploids in salmonid aquaculture is aimed at improving the quality of meat by preventing early maturation. Triploid fish are functionally sterile because the 3n condition interferes with meiosis, resulting in reduced gonadal development and aneuploid gametes (Benfey *et al.* 1986). Although the triploid condition in salmonids does not confer a growth advantage over diploid fish of the same age (Solar *et al.* 1984), certain triploid fish, such as the channel catfish *Ictalurus punctatus* (Rafinesque, 1818) (Wolters *et al.* 1981) and the blue tilapia *Oreochromis aureus* (Steindachner, 1864) (Valenti 1975), have shown better growth than diploids. The main effects of triploidy on the physiology and performance of cultured salmonids were reviewed by Benfey (1999) and Tiwary *et al.* (2004).

Another application of sterile triploids is as a mechanism for biological containment of cultured fish to prevent hybridization or genetic impact of escapees on native populations of conspecifics or genetically related species, and to promote long-term biodiversity conservation (Gausen & Moen 1991; Lura & Saegrov 1991). Researchers from several countries have proposed triploid induction of cultured fish as the most reliable alternative to ensure reproductive isolation between wild and cultured stocks (Triantafyllidis *et al.* 2007). Furthermore, the generation of triploids has been suggested as a measure of protection and a pre-requisite for the use of transgenics in aquaculture (Kapuscinski & Hallerman 1990; Donaldson *et al.* 1993).

The induction of tetraploids usually aims to produce broodstock capable of producing diploid gametes, which can be used for normal fertilization of gametes (haploid), thus generating triploid offspring (Guo *et al.* 1996).

Among salmonids, triploidy has been induced in Atlantic salmon (Benfey & Sutterlin 1984), chinook, coho and pink salmon (Utter *et al.* 1983), brown trout (Scheerer & Thorgaard 1983) and rainbow trout (Chourrout 1980; Thorgaard *et al.* 1981; Solar *et al.* 1984). The generation of triploid hybrids has also been tested in salmonids as a means of improving the survival of otherwise unviable hybrids (Scheerer & Thorgaard 1983), modifying life-history traits (Seeb *et al.* 1993), increasing disease resistance (Parsons *et al.* 1986) and preventing the establishment of domesticated fish stocks in natural environments or interbreeding with wild stocks (Galbreath & Thorgaard 1995).

Currently, no triploid salmonids are commercially produced in Europe or the USA, mostly because of concerns about the reduced growth rate of triploids and increased incidence of deformities.

Sex control: monosex populations

The use of techniques for the control of phenotypic sex in some species may be beneficial depending on the production strategies under culture conditions (Donaldson & Hunter 1982; Yamazaki 1983; Donaldson & Devlin 1996). This is because one gender may offer superior productive characteristics. Although the culture of males is economically advantageous in some species (e.g. tilapias), females are preferred by farmers working with salmonid species (Solar & Donaldson 1991). Males have the tendency to mature precociously before their full growth potential has been realized.

All-female stocks have been extensively used in the culture of rainbow trout in Europe and in the USA, and also for chinook salmon in British Columbia, Canada (Solar *et al.* 1987). Triploid Atlantic salmon have also been produced for culture on both the Pacific and Atlantic coasts of Canada and in Norway.

In addition to interest in monosex all-female stocks in salmonid culture, the technique can also be applied to prevent the establishment of feral populations of escaped farmed fish when conspecifics are not present in the wild. However, it may not prevent the hybridization of monosex fish with conspecifics or closely related species when these exist in the local environment. Therefore, the combined use of all-female and triploid induction techniques has been proposed for effective biological containment of farmed salmon species and for the prevention of genetic impact on wild populations (Mair *et al.* 2007).

Transgenics

Several species of salmonids have been genetically engineered for enhanced performance in commercial culture. The gene construct known as opAFPGHc, consisting of chinook salmon (*O. tshawytscha*) growth hormone cDNA (cloned complementary DNA) fused to an ocean pout (*Zoarces americanus* (Bloch & Schneider, 1801)) antifreeze protein (AFP) promoter (Hew *et al.* 1995) has been used to produce better growth in coho (*O. kisutch*), chinook (*O. tshawytscha*), rainbow trout (*O. mykiss*) and cutthroat trout (*O. clarki*) (Devlin *et al.* 1995). It is expected that the combination of the introduced DNA may allow reducing by half the time required to reach market size even in low-temperature culture conditions.

Aqua Bounty Technologies, a biotechnological company working on the development of genetically modified aquatic species, announced in December 2006 that major studies related to their application to the US Food and Drug Administration (FDA) for approval to market transgenic Atlantic salmon (AquAdvantage) were complete and they hope to have the product in the market by 2009 (Aqua Bounty 2006). If approved, Atlantic salmon may become the first transgenic fish species marketed for human consumption.

The regulatory process for the approval of the AquAdvantage transgenic salmon is mostly concerned with food safety. However, potential genetic or other ecological impacts of farmed transgenic salmonids on wild populations of salmonids or other indigenous species are a significant concern to regulators, scientists and the public. The application of sterilization techniques, such as triploidy, has been suggested to prevent interbreeding of transgenic escapees with wild salmon. Furthermore, it is anticipated that transgenic salmon production may only be allowed in escape-proof, land-based facilities to prevent other ecological impacts (Mair *et al.* 2007).

Conservation of genetic resources

Pacific salmon

Most species of Pacific salmon are the subject of subsistence, recreational and commercial fisheries in their natural range, with the exception of isolated reproductive populations migrating into rivers in nearly inaccessible regions. However, because commercial catches constitute the highest proportion of the combined fisheries, these catches have been considered surrogate for the abundance of the resource and for trends in abundance when exploitation and management have remained constant over time (Beamish & Bouillion 1993). Nevertheless, because the fishery is currently so heavily regulated, catch data may not reflect trends in effective abundance.

Based on statistics of commercial captures in the FAO–Global Capture Production Database, catches of the seven species of Pacific salmon included in the present review for the 28-year period from 1980 to 2007 (FAO 2007) have been above average relative to the period between the mid 1940s and the late 1970s (data from INPFC 1978). The overall catch of Pacific salmon in recent years has also exceeded the high levels observed in the 1930s (Eggers *et al.* 2003). Thus, in general terms, it can be said that the trend in abundance is increasing and the overall status of Pacific salmon appears favourable. However, there are important differences among species and areas. Over the past 28 years, captures of two species, pink and chum salmon, show significant increasing trends from slightly over 200 000 t in the early 1980s to approximately 400 000 t in the mid 2000s (Fig. 2). During the same interval, catches of sockeye salmon have remained steady with an average of approximately 150 000 t, whereas catches of coho and chinook salmon show a steady downward trend.

Many stocks of five species (chum, coho, chinook, sockeye salmon and steelhead trout) are listed as threatened or endangered under the US Endangered Species Act (FWS 2009). In Canada, four populations of three species have been designated as endangered and at serious risk of extinction: coho salmon from the interior Fraser River region, populations of sockeye salmon from Sakinaw and Cultus Lakes, and chinook salmon from the Okanagan (COSEWIC 2009).

Conservation concerns have prompted changes in fishing patterns in recent years by decreasing harvests of both abundant and less-abundant stocks, allowing increased spawning escapement of some stocks. Catches in the US Pacific Northwest and British Columbia are currently at approximately half of the long-term average. Variable marine survival has played a significant role in the variations in abundance for many salmon populations (Geiger *et al.* 2002), which in turn may be affected by global climate changes towards warming trends and the massive releases of salmon from large hatchery programmes in Japan, Canada and the USA, with subsequent impact on the ocean's carrying capacity (Beamish *et al.* 1997).

Atlantic salmon

Anthropogenic developments, including forestry, agriculture, urban expansion, and the impacts of freshwater and marine pollution, overfishing, artificial husbandry and propagation of genetically altered hatchery stocks coincide with the decline of wild populations of Atlantic salmon within most of its geographic range.

A study conducted by the World Wildlife Fund (2001) to categorize the status of wild Atlantic salmon populations in 2615 rivers in 19 countries concluded that there was insufficient information to categorize 610 of these rivers. In the remaining 2005 rivers, only 43% still hold wild salmon populations that may be considered to be healthy, 42% have populations that are either vulnerable, endangered or very close to extinction, and 15% have completely lost their salmon populations.

Wild Atlantic salmon are extinct in most rivers of Central and Northern Europe (Switzerland, Germany, Belgium, the Netherlands, Finland, Slovakia and the Czech Republic). They are also close to extinction or extinct in rivers of the USA and areas of southern Canada. In several other countries of the North Atlantic, anadromous populations remain abundant only in a few rivers. Only four countries (Norway, Ireland, Iceland and Scotland) still have jointly more than half (53%) of their historical wild Atlantic salmon populations considered as healthy and stable. The most favourable situation was identified in Iceland where 99% of the salmon-bearing rivers hold healthy populations. Conversely, Finland has lost 92% of their wild salmon populations (in 23 out of 25 rivers) (WWF 2001). The situation for salmon is also precarious in Poland, where seven out of eight rivers have lost their wild salmon populations and the status of the only remaining stock is listed as critical.

Wild salmon populations in Canada have declined over the past three decades. Canada banned commercial fishing of Atlantic salmon in Nova Scotia, New Brunswick and the Gaspé regions in 1972. Later, in 1992, salmon fishing was closed in Newfoundland and Labrador. By 1998, all fishing was banned, except for some food fisheries for residents in Labrador, which now constitute the only subsistence–commercial fishery remaining in Canada. Modest improvements in returns have been noted in recent years, prompting biologists to evaluate some stocks as approaching or exceeding conservation objectives (DFO 1999). Still, current runs in Canadian rivers (approximately 350 000 fish) are slim compared with records from the 1970s (1.5 million). Currently, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) considers the population of Atlantic salmon from Lake Ontario as 'extirpated' (the last Atlantic salmon was recorded in this lake in 1898) and the populations of the inner Bay of Fundy as 'endangered'. These fish have been identified as genetically distinct from the rest of the North American salmon complex. In 2003, <100 adults were recorded returning to the 32 rivers where the species used to be relatively abundant. Some causes for the near extinction of these stocks are attributed to historical habitat degradation and, more recently, to environmental changes (increased temperatures and pollution) and interbreeding with escaped farmed fish (COSEWIC 2009).

Several conservation efforts are under way in many countries that aim to protect salmon stocks in rivers where they are threatened or to restore already extinct populations. Two of these programmes are briefly described below.

In Poland, wild Atlantic salmon have been considered all but extinct in all rivers since the mid 1980s. In 1985, eyed eggs from the Daugava River in Latvia were imported to Poland and efforts continued in 1994. Since then, until 1999, approximately 1.64 million smolts have been released in several rivers and tributaries of the Pomerania region of Poland and in the Vistula River. Recovery rates of tagged fish have been low. However, several million eggs have been obtained and have been used for further releases (Bartel 2001).

Recent efforts have succeeded in the restoration of populations of Atlantic salmon in tributaries of the Connecticut River in the USA, where they have been extinct for over 200 years as result of dam building that blocked access to spawning grounds. Essential to the restoration efforts has been the building of fish ladders, the removal of dams, the construction of sewage treatment facilities, the control of invasive non-native aquatic vegetation and extensive environmental public education activities. The Connecticut River Programme has been in place for the past 25 years. The main source for restoration has been wild salmon from the Penobscot River in Maine, which is also under a restoration programme (US-FWS 2009).

Conservation and enhancement: hatcheries

Hatchery programmes using returning broodstock and the release of large numbers of juveniles to mitigate habitat destruction or degradation, to supplement wild populations and to enhance harvest fisheries have been implemented worldwide for many years. One of the major salmon hatchery and release programmes in the world commenced in Hokkaido, Japan, in 1878. The main species has been chum salmon, but pink and masu salmon are also released in large quantities. By 2006, 136 hatcheries were in operation in Japan releasing approximately 1.2 billion smolts annually (Morita *et al.* 2006). The main objective of the Japanese hatchery programme is to increase commercial fishery harvests. The fact that wild salmon populations in the 200 rivers where salmon spawners return may have been replaced by hatchery fish is acknowledged; however, very few studies have been conducted to evaluate the impact of the programmes on wild fish stocks.

Important enhancement programmes through the release of hatchery salmonids have been conducted since the 1950s in the USA Pacific Northwest and Alaska, and in British Columbia, Canada. In the state of Washington, native American bands have been granted access to fish stocks in many rivers and they manage most of the state hatcheries (Randall Brummett, pers. comm., 2009).

The Salmon Enhancement Program in British Columbia, Canada, was initiated in 1979 and includes a large-scale programme of hatcheries, spawning channels, river obstruction removal, lake enrichment and other enhancement techniques with the objective of increasing the freshwater production of selected wild stocks of coho, chinook and chum salmon, both to address conservation concerns and to support commercial fisheries. Following almost 30 years of operation, the balance is not positive (Hilborn 1992; PFRCC 2000).

The potential for hatchery salmon to impact on wild stocks has been identified and reported during the second half of the twentieth century (reviewed by Fleming & Petersson 2001). Negative effects of hatchery salmon on wild salmon populations include demographic, ecological and genetic impacts. Some specific concerns are a reduction of genetic diversity within and between salmon populations, decreased fitness from domestication, the creation of mixed-population fisheries leading to overfishing small, less productive stocks, altered behaviour of fish, the displacement of wild runs, and ecological changes as a result of the elimination of the nutritive contribution of carcasses of spawning salmon from streams (NRC 1996).

Recognizing the real and potential problems caused by hatchery releases, even those carefully planned and implemented, scientists and salmon advocates strongly recommend major changes in the traditional objectives of hatchery practices. These practices should shift from producing more fish to supplement commercial fisheries, towards the conservation and restoration of endangered wild salmon populations, particularly in cases where a genetic line would otherwise become extinct. The threats to wild stocks posed by hatchery-released fish, including genetic problems, behavioural problems, mixed fisheries of hatchery and wild fish and disease problems, have recently been reviewed by Harvey (2008).

Artificial spawning channels

Salmonid spawning channels are designed and used to reduce the impact of artificial hatchery practices by providing protected, specially constructed gravel spawning grounds for fish to breed under close to natural conditions. Normally, a serpentine channel is built adjacent to a salmon river. Water flow is controlled and directed over extensive gravel areas where salmon can spawn naturally. Because of the design the channels are not exposed to the seasonal floods that can wash away and kill salmon eggs in a natural river. It has been estimated that egg-to-fry survival may be up to 10-fold higher in spawning channels compared with that in the adjacent, natural stream. Fisheries and Oceans Canada operates several spawning channels in British Columbia mostly for the enhancement of sockeye and chum reproduction. One such facility is the Weaver Creek Spawning Channel located next to a tributary of the Harrison River, which drains into the Fraser River, one of the major salmon rivers in Canada's Pacific Northwest.

Captive breeding programmes

Two techniques are currently used to conserve and restore threatened wild salmon stocks. These are captive breeding, also known as live gene banks (LGB) and cryopreservation of sperm.

The concept of LGB is similar to the culture of fish in hatcheries, except that it focuses on captive rearing and breeding of critically endangered stocks in protected environments and requires the maintenance of multiple year classes, in family groups, to maturation. Normally, the LGB will take care of all of the remaining population, or a large proportion of it, for extended periods lasting several generations until the population effective breeding numbers become sufficiently large to ensure self-sustaining survival (Fleming 1994). This must be conducted in conjunction with the removal of the conditions that caused the decline of the wild stock.

The application of traditional hatchery techniques in long-term LGB programmes may lead to the problems identified in hatchery fish, such as a decrease in genetic variation, inbreeding resulting in an increased frequency of deleterious alleles and adaptation to captive rearing

Table 3 Captive breeding programmes for salmonids

Species	Stock	Location	Year started	Reference or source of additional information
Oncorhynchus tshawytscha	Winter-run Sacramento River	California, USA	1990	Arkush *et al.* (1997) Arkush and Siri (2001)
Oncorhynchus nerka	Cultus–Sakinaw Lakes	British Columbia, Canada	1998	COSEWIC (2003a,b)
Oncorhynchus mykiss	Keogh, Quinsam and Little Qualicum Rivers	British Columbia, Canada	1998	BCCF (2009)
Salmo salar	29 endangered stocks	Eidfjord, Haukvik and Bjerka, Norway	1988	Gausen (1993) O'Reilly and Doyle (2007)
	Inner Bay of Fundy	New Brunswick and Nova Scotia, Canada	1998	O'Reilly and Doyle (2007)
	Eight extirpated stocks†	Maine, USA	1991‡	NRC (2004)
	Connecticut River	New England, USA	1990§	Gephard and McMenemy (2004) Ward *et al.* (2008)

†Using Penobscot River stock as the donor.

‡Restoration efforts for Atlantic salmon in Maine started in 1966, but river-specific management through a captive breeding programme began in 1991.

§Restoration efforts for Atlantic salmon in the Connecticut River watershed started in 1976, but captive breeding using genetic data began in 1990.

conditions (Snyder *et al.* 1996). Hence, LGB programmes need to be conducted while keeping in mind the genetic constraints of working with small breeding populations and by applying the necessary measures to mitigate those limitations (O'Reilly & Doyle 2007).

Captive breeding programmes are complex, costly and labour intensive. As such, these efforts are seen as a 'last resort' and a proactive alternative between allowing a genetic resource to disappear and doing something to preserve it. However, because thus far there is insufficient information to evaluate their success, they are still considered to be an experiment in progress. Table 3 shows a summary of LGB for salmonids currently in operation. A detailed, critical analysis on the use and potential benefits and risks of captive breeding programmes in the restoration of endangered salmonid genetic resources was recently published by Fraser (2008).

Cryopreservation of gametes

Techniques for the long-term preservation of fish sperm have been developed and used in commercial aquaculture in various species and for gene banking of valued endangered resources (reviewed by Harvey 1993, 1996). Cryopreserved fish semen is used to store genetic material from salmonid stocks at risk of extinction, to introduce additional genetic variation into future populations of wild stocks and to minimize genetic limitations in captive breeding programmes. The Norwegian Atlantic salmon sperm bank contains samples from approximately 6500 individual fish belonging to 169 stocks and is stored at a livestock breeding and artificial insemination centre in Trondheim. In Canada, the Department of Fisheries and Oceans maintains a limited sperm cryopreservation programme for selected Pacific salmon stocks (Brian Harvey, pers. comm., 2009).

Because of the size and complexity of salmonid ova their long-term preservation is technically challenging. However, recent advances in the cryopreservation of mammalian embryos (reviewed by Moore & Bonilla 2006) suggest that these difficulties may be overcome.

Access and benefit sharing of salmonid genetic resources

Salmonid genetic resources are varied and widely distributed. Thus, the stakeholders concerned about the potential demise of salmon populations and the possible loss of access and benefit sharing of salmonid genetic resources are also varied. These stakeholders range from local aboriginal communities using salmon for food, through major industrial fishing and farming companies supplying international markets, to advanced biotechnological international corporations in search of the fastest growing fish.

Several examples or case studies referring to the access, use and conservation of salmon genetic resources have been described by Greer and Harvey (2004). Among these examples are the problems encountered by two aquaculture companies: Creative Salmon, to access genetically pure Yukon River chinook salmon broodstock, and Icy Waters, to access Arctic charr broodstock to expand the genetic basis of aquacultured charr by generating hybrids of Icy Water's Nauyuk Lake stock and Tree River stock owned by an Inuit aboriginal association.

Conflicting views on the access and protection of genetic resources of breeding companies and fish farmers, including access and legal rights to genetically improved genetic resources, have been reviewed and discussed by Rosendal *et al.* (2006) and Olesen *et al.* (2007). The issues addressed in these publications are mostly based on the access to, and legal protection of, wild and improved breeding genetic material of *Salmo salar* from a Norwegian perspective. The principles described, such as the rationale behind the access to wild and improved breeding material, patent legislation aimed to protect biotechnological innovations in genetics and breeding and tools for biological protection of costly research and development for genetically improved aquaculture breeds, are also applicable to existing and potential commercially important salmonid genetic resources.

Economic value of salmonid genetic resources

It is widely acknowledged that the greatest wealth of this planet is in the biological diversity of the living organisms and the complex ecosystems where they evolve. Occasionally, appropriate value is given to natural resources and incentives exist for the conservation of their genetic diversity and integrity. Unfortunately, many important and very valuable resources, such as long-range migratory fish stocks, have diffuse ownership and tend to be overexploited, mismanaged and depleted. Because of their reproductive behaviour, strong homing instinct and well-developed local adaptation leading to genetic isolation, salmonid populations are particularly vulnerable to the impact of intense mix-fisheries at sea and habitat destruction in freshwater. As a result, genetic resources of high direct and indirect value have become extinct.

The allocation of value to biological resources is a complex task. The major components of the total value of fish resources include their ecosystem relationships, subsistence use, commercial fisheries, sport fishing and the preservation values allocated to them by society. Subsistence, cultural and recreational values are particularly difficult to assess. Many aboriginal communities in Canada and the USA still use salmon as a major source of food, for barter agreements and for social and ceremonial purposes. They allocate to salmon such a high value that often they take governments to court in costly litigation to uphold aboriginal rights for the use of salmon for traditional purposes. For recreational fishers, the value of the experience of catching a 10-kg fighting salmon is much higher than the price of salmon in the fish market. Fish farming is an important component of the use of salmon as a genetic resource for food production and, as in all forms of farming, this activity has an inherent cost in environmental degradation and risk to wild stocks and species that is also hard to evaluate.

The economic value of fisheries resources involves harvest and farming revenues, processing, commercial and sport fishing expenditures, equipment, licenses, infrastructure, inputs for farming production and also the cost of conservation and restoration programmes. For salmon resources these costs are huge and often involve billions of dollars.

One of Alaska's main industries depends on the salmon returning to Alaskan rivers and streams. Fisheries products, particularly salmon, are the second highest source of export revenue for the state. In recent years, catches of Pacific salmon species in Alaska have represented approximately 95% (in round weight) of all salmon caught in the USA. The average annual value of the salmon harvest in the early 2000s was approximately US$230 million. Alaska also has very important sport and subsistence salmon fisheries. Many Alaskan aboriginal communities depend heavily on salmon for food and cultural purposes.

In 2007, the salmon farming industry in British Columbia produced 79 300 t and generated Cad$387.9 million in farm-gate value. The wild salmon harvest in the same year was approximately 20 000 t, with a landed value of Cad$40.7 million. Recreational fishing is a major tourist attraction in British Columbia, providing employment for almost 8000 people and generating revenues of approximately Cad$290 million per year. The salmon fishery also supports the traditional lifestyle and subsistence of numerous aboriginal communities along the British Columbia coast.

Norway and Chile have a large share of their economy associated with salmon genetic resources. The production of salmon in Norway in 2007 was close to 800 000 t (round weight) or approximately 44% of global salmon production and it is the third largest industry in the country after petroleum and mining. In Chile, salmon production in the same year was approximately 655 000 t (round weight) or close to 36% of global production. Exports from the salmon farming industry are approximately 65% of the total Chilean fisheries exports and have grown to become the third most important export commodity after copper and wood products.

Worldwide the trade of salmon and trout among fisheries commodities has increased to 11%. The demand for farmed salmon increases steadily with new markets opening up in developed as well as developing countries (FAO 2008). The availability of fish meal and fish oil for feed manufacturing and the incidence of pervasive viral salmon diseases (e.g. infectious salmon anaemia) are problems that affect and may curb continuous development of the industry in the main salmon farming countries.

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