## Mutual impact of wild and cultured Atlantic salmon in Norway

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The development and current status of the fish-farming industry, enhancement, and sea ranching of salmon in Norway are briefly described, and an account is given of the natural salmon river populations in different parts of the country. Records of cultured salmon in the open sea, coastal waters, and rivers are reviewed, as are migration studies on liberated farmed salmon. The recent development in farming and ocean ranching has led to an increased proportion of reared fish in nature. Survival and migration of such fish appear to be strongly dependent on season. Adults escaping in summer seem to behave like homeless fish, and enter rivers at random for spawning. Fish escaping at the smolt stage return to the area from which they escaped and enter rivers in the same area for spawning. Diseases common to wild and cultured populations are described and discussed in relation to possible intertransmission. The fluke Gyrodactylus salaris has been spread to 32 rivers, probably by stocking fish from infected hatcheries. The salmon lice, which normally are considered harmless to wild salmon, have been shown to affect salmon reared in net pens. Bacterial and fungal diseases are found among free-living as well as among cultured salmon; wild populations may act as reservoirs for the disease agents. The actual and potential effects of cultured salmon on natural gene pools are discussed. Escaped salmon may cause gene flow between cultured and wild populations, thus reducing the variation between natural populations. Hybridization, with possible hybrid vigour and short-term adaptation, is another potential consequence, which may reduce the capacity of the population to adapt to local environments. Initiatives to protect natural gene pools are described and briefly discussed. These include the technical improvement of farming facilities, the establishment of gene banks (now in operation), restrictions on the transfer of living material, and the use of indigenous fish for enhancement and establishment of areas protected from fish farming. Experiments to gain additional knowledge of the genetic resources are outlined.

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### Introduction

Farming of Atlantic salmon in Norway commenced around 1970, and since then production has increased steadily from 47 417 t in 1987 to about 114 000 t in 1989 (Fig. 1). Production takes place along much of the coast, but is low in the southeastern parts and in the northernmost county (Finnmark).

Wild Atlantic salmon are found in rivers throughout Norway, and despite damage to stocks in southern Norway due to acid rain and in mid- and northern Norway due to the parasitic monogean fluke *Gyrodactylus salaris*, the total reported catch of wild salmon has varied between 1050 and 1831 metric tonnes since 1971 (Fig. 1). The annual variation in the production of the different rivers is considerable. All rivers seem to have their own stock with specific life histories and production traits. Investigations of the population structure of Norwegian salmon using gene markers have been conducted by Ståhl and Hindar (1988).

Atlantic salmon have been released in Norwegian rivers for many years to enhance local stocks. They have been released mostly as unfed fry (10–15 million a year), but also as underyearlings or smolts. Smolts (400 000–

<sup>&</sup>lt;sup>1</sup> Dr Emmy Egidius died in February 1989, after a distinguished career of research in fish pathology and disease. This publication is a posthumous tribute to her achievements.

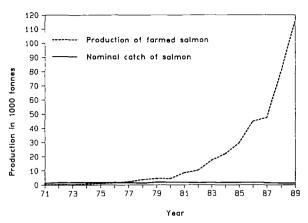


Figure 1. Production of Atlantic salmon in Norwegian fish farms and nominal catches of salmon in the Norwegian fishery from 1971 to 1989.

500 000 a year) are released primarily to compensate for the reduction in recruitment caused by river regulations (Hansen *et al.*, 1987a). Most fish released are from local stocks (Ståhl and Hindar, 1988). Ocean ranching has so far been carried out on an experimental basis only, although the results have been most encouraging (Hansen and Jonsson, 1989a).

It is a reasonable assumption that the fish farming industry in Norway will continue to increase, and we therefore need to take good care of our several hundred local populations of wild salmon. Moreover, the possibility of augmenting stock enhancement and developing ocean ranching of salmon need to be kept in mind.

Many questions have been raised about the effect of the growing fish farming industry on natural salmon populations. This concern has been focused mainly on two aspects (a) the transfer of disease from farmed to wild fish and (b) the dilution or elimination of distinctive gene pools by the breaking down of isolation mechanisms between wild stocks, with the possibility of decreased fitness of the wild salmon due to the introduction of non-indigenous gene or gene combinations. Transfer of diseases from wild to farmed fish is also a matter of concern, and for the fish farming industry strong and healthy wild populations with a high degree of genetic variation is a good insurance against disease outbreaks or unexpected genetic alterations in the cultured stocks.

The aim of the present case study is to give an overview of the interaction between wild and cultured salmon in Norway, including initiatives to protect the natural gene pools. The greater part of the study is based on published papers and reports.

## Description of the situation

Recent development in the farming and ocean ranching of Atlantic salmon has led to an increased proportion

of reared fish in nature. Based on fin morphology and scale analysis the proportion of reared fish (ranched and farm escapees) has increased from about 10% in 1986 to about 30% in 1989 in commercial fisheries in Norwegian home waters (Hansen et al., 1987a; Lund et al., 1989; Lund et al., 1991; Moen and Gausen, 1989). If not caught in the fisheries, the adult salmon enter rivers to spawn (Hansen et al., 1987b). Direct observations of body morphology and brood stock surveys in rivers in southern Norway in 1987 revealed that 23 (43%) out of the 54 rivers examined contained reared salmon (Gausen, 1988). Of the total of 615 salmon examined, 83 (13%) were determined to be of reared origin. Results from surveys carried out in 1988 showed a further increase in the proportion of reared fish (Moen and Gausen, 1989). In 1989, out of a total of 1791 salmon sampled from collected brood stock, 698 were of reared origin (Lund et al., 1991).

These escaped fish spawn in the streams. For example, in the small river Imsa in southwestern Norway there is an annual run of between 100 and 200 mature rainbow trout which have escaped from fish farms. They spawn and the offspring leave the river system as kelts (Jonsson and Hansen, unpublished data). The number of viable offspring is extremely low.

The reproductive success of escaped Atlantic salmon in nature is unknown (Ståhl and Hindar, 1988). Observations of sea-ranched Atlantic salmon, however, indicate that reproduction is lower than among wild fish. Hatchery-reared smolts of the river Imsa stock released at the mouth of the river Imsa migrate to sea and return as adults one or more years later, when they enter the river in the autumn about one month after the wild fish. A large part of the sea-ranched but not the wild fish descend unspawned later in the autumn. During the spawning period, sea-ranched fish also move more upand downstream than wild fish, and are more frequently bitten by the spawners (Jonsson *et al.*, 1990).

Experimental releases of farmed Atlantic salmon into the sea have shown that there is a seasonal variation in survival. Survival during their first sea year is much higher for salmon escaping in spring than for those escaping during the rest of the year (Hansen and Jonsson, 1986, 1989b). Adults escaping during summer seem to enter rivers at random and behave like homeless fish (Hansen *et al.*, 1987b). When escaping from sea cages at the smolt stage the fish return to the same area from which they escaped and enter rivers in this area to spawn (Hansen *et al.*, 1989).

Reared salmon might affect natural populations in several ways. For example, the fluke *Gyrodactylus salaris* has been spread to 32 rivers through fish being stocked from infected hatcheries. This parasite attacks salmon parr and causes heavy mortality. In 1984 the estimated loss of salmon to Norway from *G. salaris* was around 250–500 t (Johnsen and Jensen, 1986); the damage is now greater as the parasite spreads. Salmon smolts were still being imported to Norwegian fish farms in 1988 from other countries; this means a continuous risk of importing disease and parasites to which Norwegian salmon stocks are not adapted.

Extinction of local, indigenous fish stocks and erosion of genetic resources are subjects of growing concern to salmon management and biologists in Norway. For these reasons the Directorate of Nature Management has established a gene bank for salmon based on deep frozen sperm. In 1986 and 1987 sperm collected from a number of salmon rivers throughout the whole country were stored (Gausen 1986 and pers. comm.). In total, sperm from 69 stocks are now stored in the sperm bank.

#### Diseases

Of the interaction problems between wild and farmed salmonids, disease is possibly the largest and most serious one. Disease in fish farmed in fresh water has been known for a considerable time, and it was believed that conditions in sea water would be much better, with cleaner water and fewer disease problems. However, very little was known about diseases and parasites in free-living marine fishes when fish farming started, and there are still immense gaps in our knowledge. It has also become apparent that diseases expected to occur only in fresh water propagate very well in sea water.

The case of salmon lice, Lepeophtheirus salmonis, is probably the best illustration of an interaction between wild and farmed fish. This parasite is well known, being described by Krøver as early as 1838. It is a copepod with a life cycle of 10 stages, 3 pelagic stages and 7 attached to or living on the host. It is found circumpolarly in the northern hemisphere and is host specific to salmonids. The lice disappear from the fish in fresh water within a short time. When and where the free-living fish is infected is unknown, the opportunity for a pelagic larva to encounter its specific host in the open sea being apparently very small. When wild salmon were still abundant in the rivers, experienced fishermen would say that a high density of lice on the upward migrating fish was indicative of a good salmon run. Only once, in Canada in 1940, has the death of salmon due to salmon lice been reported (White, 1940), but it should have been foreseen that salmon lice would become a potential problem in salmon farming. Under the intensive conditions found in farms, it is easier for the larvae to find their specific host, complete their life cycle, and find new hosts. It soon became evident that numbers of lice were harmful to salmon. They live on mucus, skin, and blood and in the most advanced cases fish are seen with large open lesions, especially in the head region. Wild salmonids around fish farms have been observed carrying large numbers of lice (Djupvik, pers. comm.), but lesions or mortality in such fish have not been reported.

The largest problems in farmed fish arise in connection with bacterial infections. Vibriosis, due to the bacterium Vibrio anguillarum, is probably the best known of such diseases. Vibriosis was initially one of the economically most serious diseases in marine fish farming, but it can now be controlled effectively through vaccination. Vibriosis is also known from many freeliving marine fish, but epizootics are rarely seen. Along the Norwegian west coast local outbreaks of vibriosis in young saithe occur annually, reaching epizootic proportions in certain years (Egidius et al., 1983). Experiments have shown (Egidius and Andersen, 1978) that there is some host specificity amongst V. anguillarum strains isolated from, for example, rainbow trout and saithe, and more recent investigations have shown that at least at the DNA level there is a slight difference between strains from different hosts (Wiik et al., 1989). Mass mortality due to vibriosis is occasionally reported in homeward migrating salmonids when entering the rivers. Coldwater vibriosis due to V. salmonicida has not yet been reported in wild salmon.

Furunculosis due to the bacterium Aeromonas salmonicida var. salmonicida is another of the important bacterial diseases that must be considered. Furunculosis is endemic in the wild salmonid populations in Scotland, Ireland, and Canada, but rare in free-living fish. In fish farms, on the other hand, the disease can be disastrous. It seems that the free-living fish is the reservoir of furunculosis in farmed fish, where the disease outbreaks seem associated with fish density in tanks and cages and with other stress-inducing factors.

The bacterium Yersinia ruckeri is a newcomer in European fish farms. Even if the disease was believed to be a freshwater one, it has spread to salmon farms all along the Norwegian coast. Possible effects on freeliving salmonids are not known. Although the bacterium has been isolated from marine scavenger fish like saithe around affected sea cages, it is not known if the saithe just harbours the bacterium for a short time or if it can be pathogenic also for this and other marine species.

Bacterial kidney disease (BKD) due to *Renibacterium* salmoninarum is probably the most dreaded of all the salmonid diseases, mainly because its development is slow and diagnosis difficult and time-consuming. BKD was first thought to be purely a disease of farmed fish, but with improved diagnostic methods the bacterium was also found in wild stocks, though its impact there is unknown. As with furunculosis, the reservoir of infection is probably in the wild stocks, but the disease causes trouble under farming conditions. The existence of the disease in farms can lead to higher infection rates in wild stocks in the vicinity.

Of fungal disease agents *Ichthyophonus hoferi* is common and often harmful in several species of marine fish. It has been found in farmed salmon, but until now without showing much effect.

The fluke Gyrodactylus salaris (see p. 405) has done

great harm in Norwegian salmon rivers, but in the fishfarming industry it is no problem. Infected fish are easily treated and the parasite disappears when the smolts are put into sea water. This is the only disease mentioned here where wild stocks are the losers.

Examples have been given of disease interactions between free-living and farmed salmonids mostly, so far as we know, to the disadvantage of the farmed fish. It is clear that the utmost care must be taken in moving fish from different regions.

# Genetic variation and genetic structure of salmon in Norway

#### Population structure of salmon in Norway

Ståhl and Hindar (1988) have published a comprehensive monograph of the Norwegian salmon stocks with reference to the population structure, number of spawners (population size) and differences within and between wild and farmed salmon stocks. They concluded from their biochemical genetics studies that the natural salmon stock is divided into genetically distinct populations; sometimes more than one within the same river system. Farmed salmon (commercial stocks for intensive farming and culture aimed stocks) are not a homogeneous group and it is impossible to distinguish between individual wild and cultured salmon by the use of biochemical gene markers.

#### Potential genetic impact

Skjervold (1988) gave an overview of the types of genetic effects that fish farming could have on natural salmon stocks. In spite of the difficulties in estimating the numbers of escapees from fish farms, and of the magnitude of their contribution to the recruitment of salmon, a great potential evidently exists for significant gene transfer from farmed salmon in some rivers.

Farmed salmon have been subjected to intensive selection for improvement of productive traits, especially improved growth rate and late maturation. Genetic selection is performed systematically through a large-scale programme on improvements for fish farming conducted by the Fish Farmers' Association and the Fish Farmers' Sales Organization in Norway. In addition, most producers of salmon eggs exert phenotypic selection on broodstock, and probably also seminatural selection, as adaptation to life under farming conditions (domestication) has now occurred for 4-5 generations. The genotypes of the farmed fish may differ in several respects from the genotypes of the population from which they originated several generations previously. It is difficult to predict how this change will affect their adaptation with respect to survival in the natural environment, but escapees which reproduce in rivers chosen at random will always tend to reduce the genetic differentiations between the wild salmon populations.

The origin of the salmon used for fish farming is important. Ståhl (1987) has shown that Baltic salmon in particular differ in genetic composition from the salmon in the Northeast Atlantic, and Eastern Atlantic salmon differ in several respects from the Western Atlantic stocks. As far as we know there has been no importation of Western Atlantic live salmon to Norway (except for scientific purposes), but for several years smolts from Iceland, Scotland, and especially from Sweden and Finland (Baltic salmon) have been imported.

Gjedrem and Aulstad (1974) observed that a strain of Baltic salmon showed much lower resistance to vibrio disease than the Norwegian strains, indicating that genetic differences in resistance to certain diseases exist between geographically distant groups. Thus fish transferred from distant areas for intensive fish farming may carry disease agents or parasites to which they are well adapted or resistant. Escapement of such fish may be fatal to endemic populations.

## Hybridization, hybrid vigour, and short-term adaptation

Cross-breedings of natural and escaped salmon in the rivers are expected to cause increased heterozygosity, which may lead to hybrid vigour for some traits. Hybrid vigour is usually found for traits with low heritability (Skjervold, 1988), and survival traits have low heritabilities as far as they have been studied (Gjerde, 1986). Thus, farmed salmon/natural salmon hybrids in a river may give the impression of very well adapted fish which may oust non-hybrid natural salmon, but last only for the first generation. Altukhov (1981) described a similar case with chum salmon where liberation of non-indigenous fish resulted in very low production of both the introduced fish and the indigenous fish in the same river.

## Genetic drift, reduced genetic variability, and low numbers of spawners

Low numbers of spawners (effective population size) will always increase genetic drift, decrease heterozygosity, and consequently increase the risk of loss of genes. A minimum number of 100 individuals of each sex in one spawning unit is recommended by Allendorf and Ryman (1987); but in several cases of artificial reproduction for enhancement work and intensive fish farming, the spawning populations are considerably smaller than would be advisable on theoretical grounds. However, judging from the results of Ståhl and Hindar (1988), heterozygosity is higher in artificial populations than in most natural populations, and the genetic variability within populations is not reduced by culture activities. This may be due to the fact that cultured populations usually derive from several different natural populations and contain more genetic variation than any single one of them. Therefore the risk of reducing the fitness of salmon through reduced genetic variability within populations does not seem to be serious at the moment, although it should be kept in mind by monitoring both cultured and natural populations through several generations.

In conclusion, the escapement of farmed salmon and the liberation of non-indigenous salmon for enhancement work represents a risk of the genetic variability between natural populations being decreased, and possibly also the reduction of the long-term fitness by first generation hybrid vigour in adaptive traits through hybridization between indigenous and non-indigenous fish. For the moment, however, loss of genetic variability through low numbers of broodstock for culture purposes does not seem to represent a risk.

## Initiatives

The following series of initiatives have been taken or are being planned in Norway to minimize the influence of cultured salmon on wild stocks.

### Technical improvement

In addition to constituting a risk to wild stocks, salmon escaping from fish farms are a loss for the fish farmer. Improvement of technical facilities to prevent escapement are therefore worth while on both counts. Usually, the security of a fish farming facility is a compromise between the possibility of loss and the cost of investment. Land-based facilities are safer than ordinary net pens, and closed or semi-closed pens are also an alternative. For the moment, land-based facilities for marine culture are little used in Norway, but closed or semiclosed systems are under development. No specific technical demands are required for fish farming devices, but protective areas for wild salmon are established (see below). In such areas no farming activities will be allowed unless they are absolutely secure.

#### Gene banks (sperm banks)

Salmon strains from streams infected with *Gyrodactylus* are isolated by artificial breeding and liberation, and by intensive culture (Ståhl and Hindar, 1988). A programme for deep-freezing sperm has been undertaken (see p. 405). By using such sperm, populations which have been eradicated may at least partly be reconstructed. More complete natural populations may be reconstructed from sperm banks by using androgenetic techniques (Scheerer *et al.*, 1986).

#### Restriction on transfers of living material

For many years there has been a shortage of smolts for the fish farming industry in Norway, as smolt production did not keep pace with the market demand for salmon. For this reason, some imports have been permitted, in some cases with disastrous results for cultured salmon (i.e. import of furunculosis from Scotland) and natural populations (possible import of Gyrodactylus salaris from Baltic countries). In 1988-1990 there was a surplus of smolts in Norway. This situation is expected to persist, and there is no longer any reason for importing live salmon, although even in 1988 there was an importation of salmon eggs from Iceland. Transport of live material within the country has probably also contributed to the spread of Gyrodactylus. This appears to be a problem especially in cases where salmon farms are situated in freshwater systems which also support anadromous salmonids, or in brackish water with a salinity lower than 14 to 18%. For this reason, transfers within Norway are restricted.

#### Use of indigenous fish for enhancement work

Enhancement has been conducted for several years by releasing offspring from salmon of unknown origin, and also from farmed fish. To protect the between-strain variation, only endemic fish are now allowed, in principle, to be used for enhancement of natural stocks, unless such fish are unavailable.

#### Areas protected from fish farming

Hatcheries for commercial production of smolts for intensive fish farming are usually not located in or close to rivers with anadromous salmonid populations. However, this is sometimes the case, and inland plants for rainbow trout production (mostly small) are sometimes located in lakes draining to salmon rivers. Such fish farms have probably spread *Gyrodactylus salaris*. Henceforward, no new installation for intensive production or for enhancement work for other than indigenous populations will be allowed in rivers supporting anadromous populations.

Protected areas for wild salmonids have been created on a large scale. The aim is to protect larger areas and establish reference populations for monitoring gene introgression and spread of disease. To prevent further spread of *Gyrodactylus salaris* no new culture activities will be allowed where this parasite has been found. This includes river drainage and a defined area usually within about 20 km of river mouths. Usually, rivers having a mean annual catch of more than 500 kg anadromous salmonids will be protected. A few larger fjord areas (Sognefjorden, Trondheimsfjorden) are also proposed to be kept free from new aquaculture installations. Such protective areas are proposed for a duration of five years so that experience about the effect of such restraints can be gained before permanent decisions are made. Where escapement-free facilities are constructed, limited farming activities may be allowed and existing farms within the areas will be allowed to continue.

### Monitoring and research

The establishment and increase of the intensive fish farming industry represent a new and possibly serious threat to the natural populations of Atlantic salmon in Norway as well as in several other countries. From a management point of view action is being taken or will be taken to conserve the natural population in coexistence with the developing fish farming industry and possible commercial sea-ranching activities.

A first step is to monitor the changes that take place, and then to develop new methods for studying interaction. Further studies on the number of escaped reared salmon in coastal areas and in the rivers, on sources of infection sources for disease agents, occurrence of disease agents in the natural populations, and development of methods for defence against parasites (i.e. *Gyrodactylus*) in the natural environment are required. Reconstruction of eradicated (or severely reduced) natural populations from live gene banks or sperm banks by androgenesis is another area for research and development.

Concerning genetic impact, the discussion is often unstructured and is concentrated more on potential impact than on actual facts. To remedy this, field and experimental data will be needed, and this will be a mass scientific challenge for the near future. Further studies on genetic differentiation of natural populations will also be important. To study hybridization and gene introgression, the use of gene markers is a promising method. For other species (cod, brown trout) broodstocks homozygous for specific gene markers (biochemical or morphological) have been developed (Skaala et al., 1988). No suitable markers have yet been found for salmon, but the search will be continued for application in field studies on interaction between populations. If such studies prove difficult or impossible to carry out with salmon, brown trout can be used as a model species.

#### References

- Allendorf, F. W., and Ryman, N. 1987. Genetic management of hatchery stocks. *In* Population genetics and fisheries management. Ed. by N. Ryman and F. Utter. Washington Sea Grant Program. University of Washington Press, Seattle, Washington.
- Altukhov, Yn. P. 1981. The stock concept from the viewpoint of population genetics. Can. J. Fish. aquat. Sci., 38: 1523– 1538.

- Anon. 1986. Salmon and sea trout fisheries 1985. Norwegian Official Statistics B645. Central Bureau of Statistics, Oslo-Kongsvinger. 106 pp.
- Anon. 1987. Report of the Working Group on North Atlantic Salmon. ICES CM 1987/Assess: 12, 129 pp.
- Egidius, E., Braaten, B., Andersen, K., and Lohne Gokstad, S. 1983. Vibriosis in saithe (*Pollachius virens*) populations off the Norwegian coast. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 182: 103–105.
- Egidius, E., and Andersen, K. 1978. Host-specific pathogenicity of strains of Vibrio anguillarum isolated from rainbow trout, Salmo gairdneri Richardson and saithe, Pollachius virens L. J. Fish. Disease, 1: 45-50.
- Gausen, D. 1986. Bevaring av naturlige genressurser hos laksefisk. Direktoratet for naturforvaltning, Fiskekontoret, Trondheim, Norway.
- Gausen, D. 1988. Registreringer av oppdrettslaks i vassdrag. In Fagmøte om sikringssoner for laksefisk, pp. 58–69. Ed. by B. Lindgren. Stjørdal, Norway.
- Gjedrem, T., and Aulstad, D. 1974. Selection experiments with salmon. I. Differences in resistance to vibrio disease of salmon parr (*Salmo salar*). Aquaculture, 3: 51–59.
- Gjerde, B. 1986. Growth and reproduction in fish and shellfish. Aquaculture, 57: 37–55.
- Hansen, L. P., and Jonsson, B. 1986. Salmon ranching experiments in the River Imsa: effects of day and night release and of sea-water adaptation on recapture-rate of adults. Rep. Inst. Freshwat. Res. Drottningholm, 63: 47–51.
- Hansen, L. P., and Jonsson, B. 1989a. Salmon ranching experiments in the River Imsa: returns of different stocks to the fishery and to River Imsa. *In* Aquaculture a biotechnology in progress. Ed. by N. De Pauw, E. Jaspers, H. Ackefors, and N. Wilkins. European Aquaculture Society, Bredene, Belgium.
- Hansen, L. P., and Jonsson, B. 1989b. Salmon ranching experiments in the River Imsa: effect of timing on Atlantic salmon (*Salmo salar*) smolt migration on survival to adults. Aquaculture, 82: 367–373.
- Hansen, L. P., Lund, R. A., and Hindar, K. 1987a. Possible interaction between wild and reared Atlantic salmon in Norway. ICES CM 1987/M: 14, 18 pp.
- Hansen, L. P., Døving, K. B., and Jonsson, B. 1987b. Migration of farmed adult Atlantic salmon with and without olfactory sense, released on the Norwegian coast. J. Fish Biol., 30: 713–721.
- Hansen, L. P., Jonsson, B., and Andersen, R. 1989. Salmon ranching experiments in the River Imsa: is homing dependent on sequential imprinting of the smolts? *In* Proc. Salmon Migration and Distribution. Symposium, Trondheim, June 1987, pp. 19–29. Ed. by E. Brannon and B. Jonsson. School of Fisheries, Univ. of Washington, USA and NINA, Trondheim, Norway.
- Johnsen, B. O., and Jensen, A. J. 1986. Infestations of Atlantic salmon, *Salmo salar*, by *Gyrodactylus salaris* in Norwegian rivers. J. Fish Biol., 29: 233-241.
- Jonsson, B., Jonsson, N., and Hansen, L. P. 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon? Behav. Ecol. Sociobiol., 26: 225–230.
- Lund, R. A., Hansen, L. P., and Järvi, T. 1989. Identifisering av oppdrettslaks og vill-laks ved ytre morfologi, finnestørrelse og skjellkarakterer. NINA Forskningsrapport 1: 1-54.
- Lund, R. A., Økland, F., and Hansen, L. P. 1991. Reared Atlantic salmon (*Salmo salar*) in fisheries and rivers in Norway. Aquaculture (in press).
- Moen, V., and Gausen, B. 1989. Rømt oppdrettsfisk i vassdrag 1988. Report, Directorate for Nature Management no. 3, 26 pp.
- Scheerer, P. D., Thorgaard, G. H., Allendorf, F. W., and

Knudsen, K. L. 1986. Androgenic rainbow trout produced from inhed and outhed sperm sources show similar survival. Aquaculture, 57: 289–298.

- Skaala, Ø., Dahle, G., Jørstad, K. E., and Nævdal, G. 1988. Interactions between wild and farmed populations: Information from genetic markers. Genetics in Aquaculture. 3rd Int. Symposium. Abstracts. Trondheim, Norway. 47 pp.
- Skjervold, H. 1988. Kan enkelte kulturtiltak true våre laksestammer? In Fagmøte om sikringssoner for laksefisk, pp. 14–21. Ed. by B. Lindgren. Stjørdal, Norway.
- 14-21. Ed. by B. Lindgren. Stjørdal, Norway. Ståhl, G. 1987. Genetic population structure of Atlantic salmon. In Population genetics and fisheries management,

pp. 121-140. Ed. by N. Ryman and F. Utter. Washington Sea Grant, University of Washington Press, Seattle.

- Ståhl, G., and Hindar, K. 1988. Genetisk struktur hos norsk laks: Status og perspektiver. Rapp. fra Fiskeforskningen, Direktoratet for naturforvaltning, 1988 (I): 1-57.
  White, H. C. 1940. "Sea-lice" and death of salmon. J. Fish.
- White, H. C. 1940. "Sea-lice" and death of salmon. J. Fish. Res. Bd Can. 5: 172–175.
- Wiik, R., Hoff, K. A., Andersen, K., and Daae, F. L. 1989. Relationships between plasmids and phenotypes of presumptive strains of *Vibrio anguillarum* isolated from different fish species. Applied and Envir. Microbiol., 55: 826– 831.