



A summary of 20 years (1998-2017) of scientific work on genetics and survival in anadromous brown trout (*Salmo trutta* L) and Atlantic salmon (*S. salar* L) in the river Guddalselva western Norway



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PROSJEKTRAPPORT



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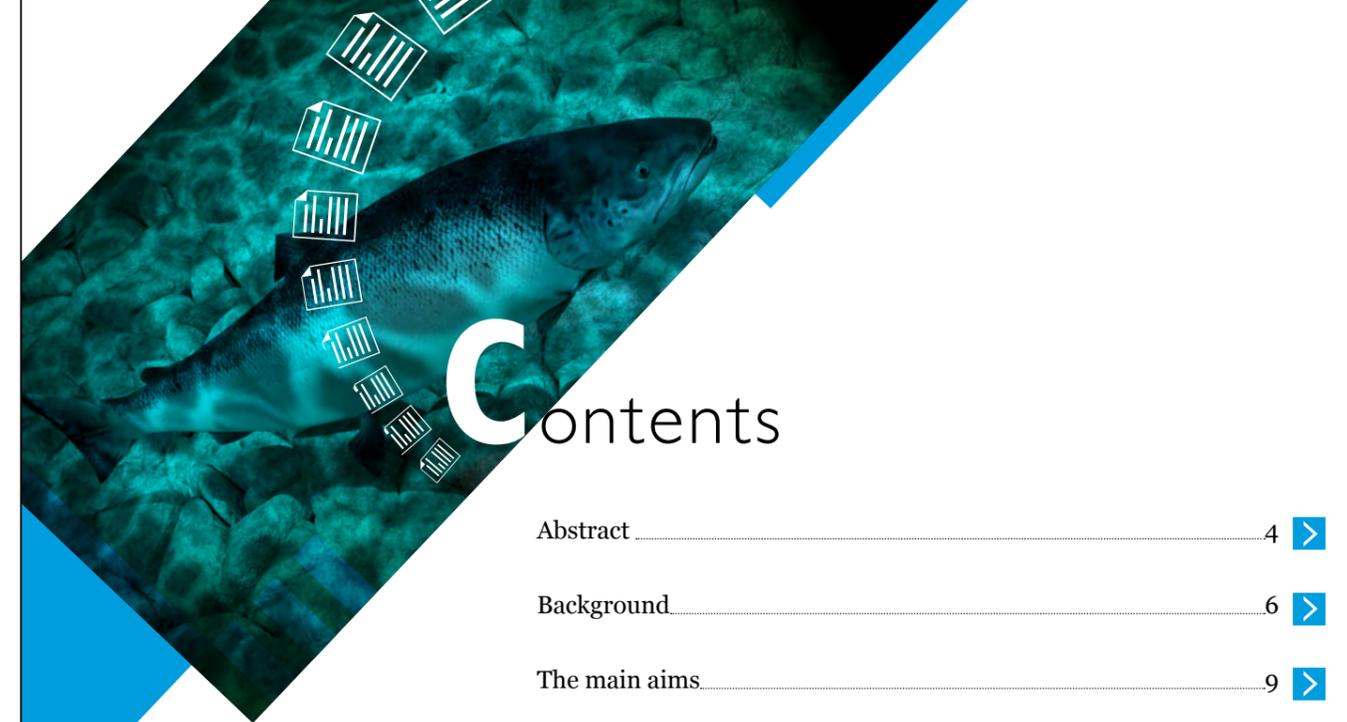
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A

bstract

During the 1990s, there was a rapid expansion of salmon farming in Norway, with observations of escaped farmed salmon in many rivers, and reports of high salmon louse infections in anadromous brown trout. National authorities became increasingly concerned about the potential detrimental impacts of salmon aquaculture on wild populations; there was a growing awareness of the need for greater genetic and ecological knowledge about wild populations and the interaction between aquaculture wild salmonids. A decision was made to use the river Guddalselva, located in the Hardangerfjord, as a “river laboratory” - i.e. as an experimental facility to study the interaction between aquaculture and wild salmonid populations in 2000 as a joint effort between several management authorities, river owners and research institutions.

The primary tasks were to a) Establish full control of fish migrations in a natural river system in order to assess the natural production of smolt, the timing of migration and the marine survival of anadromous brown trout, b) Investigate the occurrence of local adaptation in anadromous brown trout and to what extent populations may have different susceptibilities to marine parasites, c) Conduct experimental field research on impacts of genetic introgression on fitness and production in wild salmon populations.

Thus far, the results have been published in eight peer reviewed scientific papers. Another four manuscripts are also under preparation. These studies provide new insights into population dynamics, population differentiation, adaptation and marine survival in anadromous brown trout (sea trout). Moreover, survival of wild, hybrid and farmed salmon offspring has been studied in this river laboratory, providing unique insights into the potential consequences of escaped farmed salmon introgression into wild populations. Biological samples from Guddalselva has also contributed to a number of comparative studies on performance of Atlantic salmon families and



Photo: Elin Heland-Hansen

The river Guddalselva located in the Hardangerfjord.

populations under laboratory conditions, several of which have been conducted at the Institute of Marine Research’s facility at Matre. Data on salmon and trout smolt runs in the river in the period 2001-2016 have contributed to the national working group in modelling smolt migration for the so-called “Traffic Light System” for management of Norwegian aquaculture since 2016. The river, Guddalselva, represents one of only two rivers in Norway with permanent smolt traps where the whole river transect is covered. The data on smolt migration represents one of the longest and most complete time-series yielding unique empirical data on smolt migration in Europe.

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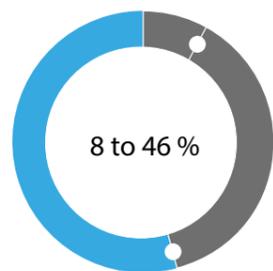
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The Hardangerfjord has a long aquaculture tradition dating back to the first attempts to produce Atlantic salmon *Salmo salar* in cages in Norway in the early 1970's. Following the pioneer period, the production of rainbow trout *Oncorhynchus mykiss* and salmon expanded in the Hardangerfjord rapidly from 17.000 tonnes in 1997 to 40.000 tonnes in 2002 (Otterå et al. 2004). A number of smaller and larger rivers that have populations of sea trout *Salmo trutta* and Atlantic salmon flow into the Hardangerfjord. Traditionally larger populations of wild salmonids are found in the Eidfjord and Granvin watercourses innermost in the fjord system, and the Etne watercourse towards the outer part of the fjord.

All in all, a total of 27 rivers with populations of sea trout and salmon flow into the Hardangerfjord. Historically there has been a significant angling activity in these rivers, as well as a bag net and gillnet fisheries in the fjord. Licenses to fish with bag nets and gillnets, as documented by the Hordaland County Governor, show that there were over 150 locations along the fjord where legal salmon fishery was regularly conducted up to around 1990.

The initial monitoring program of escaped farmed salmon (Lund 1998; Fiske et al. 2001) included the river Etneelva, where percentage escaped salmon varied from 8 to 46 % in summer catches and from 44 to 79 % in the spawning stock during the period 1989 - 2000. According to Fiske et al., (2001), in most of the years investigated Etneelva had the highest percentage of escaped farmed salmon in Norway. A test fishery conducted in the sea at Onarheim documented a very high fraction of escaped farmed salmon, ranging from 80 to 91 % in the period 1997 - 2000 (Fiske et al. 2001).

Registrations of salmon lice *Lepeophtheirus salmonis* on salmon and sea trout in the Hardangerfjord were conducted from the early 1990's



The initial monitoring program of escaped farmed salmon (Lund 1998; Fiske et al. 2001) included the river Etneelva, where percentage escaped salmon varied from 8 to 46 % in summer catches.

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The available information on high levels of escaped farmed salmon, and high infection levels of salmon lice triggered considerable national concern.

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(Grimnes et al. 1999). These surveys documented high infection pressure on returning salmon caught in bag nets at Onarheim, with lice larvae accounting for between 10 and 30 % of the total infection. According to Grimnes et al. (1999), Onarheim was one of two study sites showing particularly high infection levels in the caught salmon. Investigations of salmon louse infections conducted by Rådgivende biologer in 1995 found average infection intensities in prematurely returning sea trout in the range 49 to 124 lice, while in the Granvin area over 2000 lice per fish were registered (Birkeland 1998; Otterå et al 2004).

An investigation of regional differences in marine survival (Skurdal et al. 2001) on the Norwegian west coast indicated that while in most of the compared regions salmon populations recovered after a decline in the period 1993-2000, the populations in the Hardangerfjord failed to recover, and the estimated survival rates were only about 1 %, i.e., less than a quarter of the survival rate estimated for some of Norway's other regions. The catch statistics for sea trout are generally considered to be less reliable than those for salmon, and accordingly similar studies were not undertaken for sea trout.

The available information on high levels of escaped farmed salmon, and high infection levels of salmon lice triggered considerable national concern. In 1997 the government established Villaksutvalget, a scientific advisory committee on wild Atlantic salmon. This resulted in a comprehensive white paper, (NOU 1999:9 "Til laks åt alle kan ingen gjera; Om årsaker til nedgangen I de norske villaksbestandene og forslag til strategier og tiltak for å bedre situasjonen").

The continuing concern was later expressed in a joint letter from The Directorate of Fisheries Region West and the Hordaland County Governor, to The Fisheries Directorate and The Directorate for Nature Management. In this letter, the two directorates were encouraged to take an initiative towards the Ministry of Fisheries and Coastal Affairs and the Ministry of Environment in order to assess and get an overview of the environmental situation related to escapees, salmon lice, and various fish diseases in the Hardangerfjord, and to initiate appropriate measure.

During the 1990s, a number of international scientific conferences on environmental impacts of escapees and salmon lice expressed concern about the lack of hard data (see for example Anon 1991; Hutchinson 1997). As a consequence, an EU-funded project to study genetic impact of escapees on wild salmon was set up in Burrishoole, Ireland; the first results from this (McGinnity et al. 1997) caused

further concern in Norway. At this stage there were only two rivers in Norway with full control of upstream and downstream migration; Imsa in Rogaland and Talvik in Finnmark. The station in Talvik has now been terminated, so at the present Norway has two river systems which provide precise data on smolt production and returning spawners: Imsa and Guddalselva.

From the late 1980s, the need for a “river laboratory” to conduct studies on interactions between salmon farming and wild salmonid populations was discussed at the Institute of Marine Research (IMR). During a collaboration on brown trout genetics at the end of the 1990s, Statkraft requested research on genetic differentiation of wild brown trout populations and potential impacts of hatchery reared trout on wild populations. This is a question very similar to that raised about genetic impacts of escaped farmed salmon, and the planning of a river laboratory started to develop. The collaboration with Statkraft led to a user-controlled Norwegian Research Council (NRC) study on anadromous brown trout which included a Ph.D. scholarship in collaboration with the University of Stirling Scotland.

The need for a “river laboratory” was raised once more, and a set of physical and logistic criteria needed to fulfill the requirements of a river laboratory were drawn up. These include river size, size of fish populations, a natural water flow which is not subject to unnatural fluctuations caused by hydroelectric power production, stable and good water quality, easy access along the river, and a positive attitude among river owners. With additional funding from the Directorate of Fisheries, the Directorate for Water and Energy, the Directorate for Nature Management and the Hordaland County Governor in the winter 2000, a Wolf smolt trap, the most essential components of a river laboratory, was set up on Guddalselva, a river that is near the central part of the Hardangerfjord. This was done in close collaboration with the river owners association in Guddalselva. In 2006-2007 a second NRC project (*Survival, growth and disease resistance in offspring of domesticated and wild Atlantic salmon and their hybrids*) contributed to the studies of genetic introgression in the river laboratory, in 2008-2011 additional funding was obtained through a third NRC project (*EPIGRAPH*), and finally supplementary funding came from the NRC project *MENTOR* (2009-2011). Over the years, the field station has been systematically upgraded with IMR funding.

The station in Talvik has now been terminated, so at the present Norway has two river systems which provide precise data on smolt production and returning spawners: Imsa and Guddalselva.



The main aims

Norway is the leading nation in salmon farming, and a substantial part of remaining European populations of wild Atlantic salmon and sea trout to be found along the Norwegian coast. The concern about environmental impacts of salmon farming prompted questions about the lack of knowledge of genetics and ecology of wild populations of Atlantic salmon and anadromous brown trout in general and specifically of populations in the Hardangerfjord rivers. Key questions include:

- Will introgression from farmed salmon affect fitness and production of wild salmon?
- To what extent are salmon lice affecting marine survival of wild salmonids?
- To what extent are anadromous brown trout populations genetically differentiated and locally adapted?
- Is it likely that individual populations of anadromous brown trout populations may have different susceptibilities to salmon lice?

Local adaptation, driven by differential natural selection regimes in different habitats is considered a paradigm in studies of salmonid fish populations. Yet, little is known about the geographical scale of such adaptation. Is adaptive divergence evident primarily at the scale of regions or individual populations? The questions raised highlighted the lack of field facilities required to investigate these fundamental questions. Thus, the main aims of the Guddalselva laboratory were to address the following issues:

- To provide data on impacts of genetic introgression on fitness and smolt production in wild salmon populations
- Establish a river system with full control of fish migration to assess natural smolt production, timing of migration and marine survival in anadromous brown trout
- Investigate the occurrence of local adaptation in anadromous brown trout, and to what extent local populations may have different susceptibility to marine parasites such as salmon lice.

The main aims of the Guddalselva laboratory were to address the following issues:

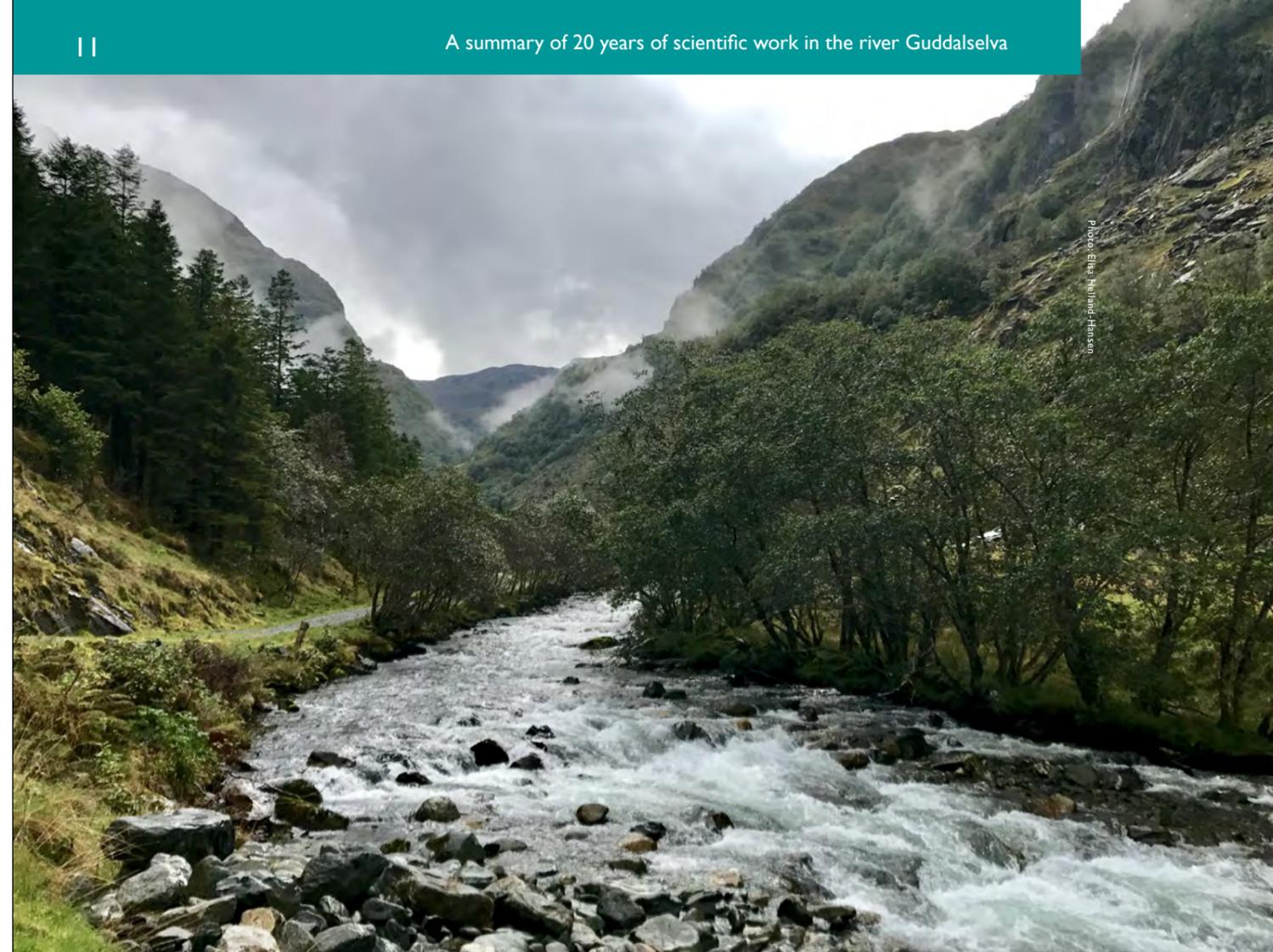
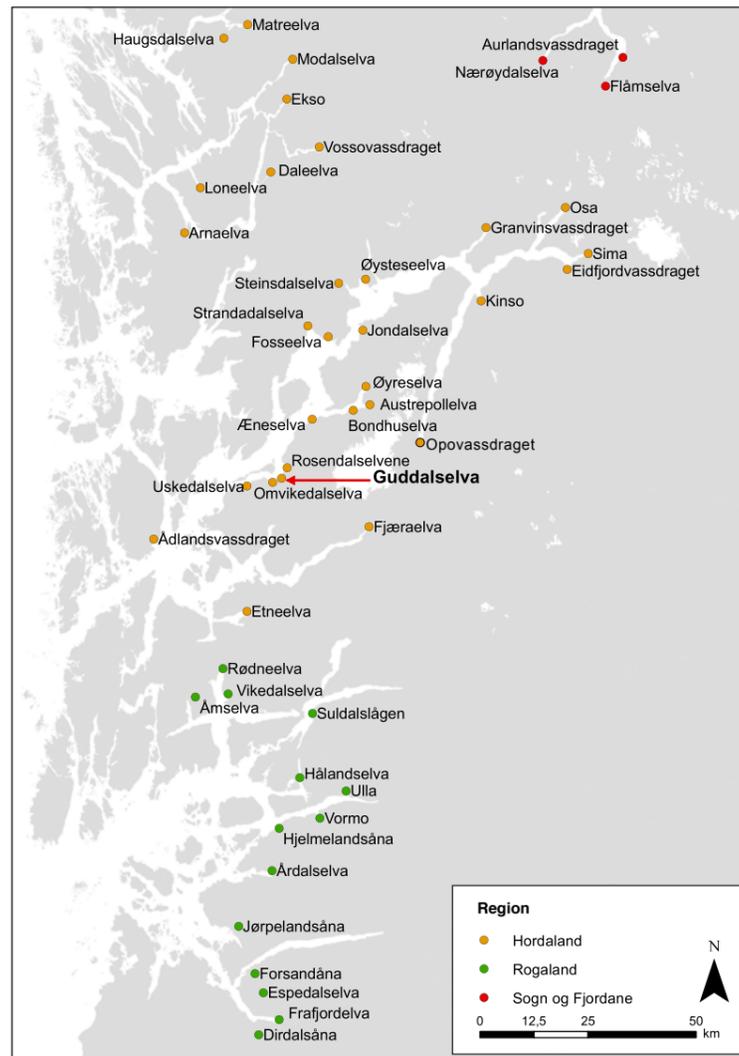
- genetic introgression
 - marine survival
 - local adaptation

Routine operation of the traps

THE RIVER LABORATORY

The river, Guddalselva, situated in the middle section of the Hardangerfjord, is one of a number of rivers in the area with anadromous brown trout and Atlantic salmon (Figure 1).

Figure 1. Map of the Hardangerfjord with the major rivers. Source: Uni-Research



Guddalselva

The river receives meltwater from the Folgefonna glacier, resulting in relatively low summer temperatures. The total length of the river is approximately 13.5 km, of which the lowermost 2 km, below the Liarefossen falls, is accessible to anadromous salmonids. The mean water discharge is $3.94 \text{ m}^3\text{sec}^{-1}$. There used to be a recreational fishery for Atlantic salmon as well as anadromous brown trout in the river. Since 2001, fishing has been strongly restricted due to the low number of ascending fish.

In collaboration with the Norwegian Water Resources and Energy Directorate, loggers for recording water discharge, water temperature and air temperature have been installed just above the smolt trap (NVE.sildre.no). Water quality of the river is monitored once a week or every second week as part of the national water quality program administered by the Environmental agency.



Figure 2. The smolt trap in Guddalselva.

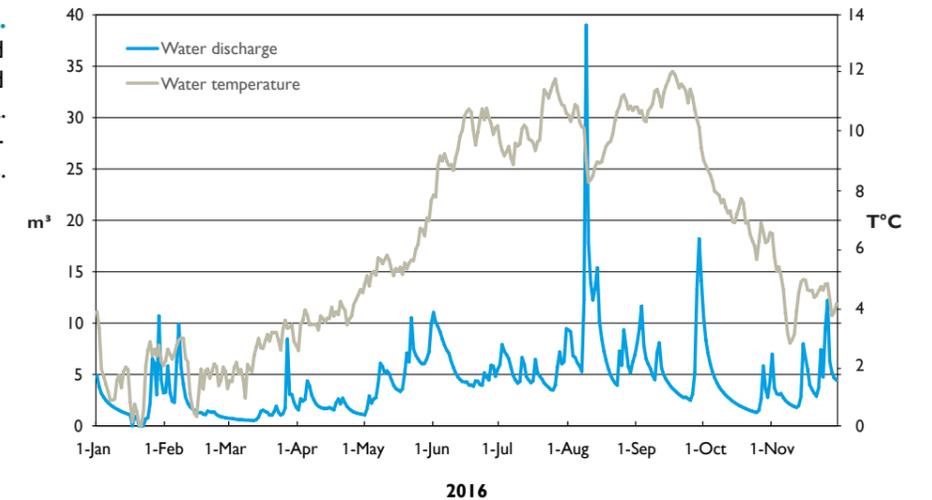
THE SMOLT TRAP

In order to capture descending smolts, a Wolf trap covering the whole river transect was constructed about 100 m from the tidal zone. Every year, the Wolf trap is installed in March or early April depending on water discharge, in advance of the smolt run. It is dismantled a few weeks after the smolt run is over. All captured smolts are anaesthetised with benzocaine, before length and weight measurements and tagging. After recovery, smolts are released through a pipeline down to a holding tank below the waterfall where they are held and observed for a few of hours before being released back into the river. From 2002, smolts were tagged by adipose fin clipping, and from 2007, all trout smolts were tagged with individual passive implant transponders (PIT tags 12 x 2 mm) in order to obtain individual data on growth and age during sea migration. The PIT tags are implanted in the posterior part of the body cavity by a single-shot injector (TRAC ID systems, Stavanger, Norway), and all returning adipose fin clipped individuals are checked for PIT tags. In order to secure continuity and scientific profile of the river laboratory, a reference group was set up with representatives from institutions that had played an

ASCENDING TRAPS

In 2000, a trap to capture ascending trout was installed in the old fish ladder below the smolt trap and Seimsfossen falls. The trap was designed to catch sea trout as there was very limited production of salmon smolt and no local salmon stock in the river. The size of the opening in the inlet is 80 x 400 mm. The upstream trap is operated from early June to the mid November after the spawning migration is over. All fish captured here are transported in a water tank up to the field station where they are anaesthetised with benzocaine before inspection, weighing and length measurement. From 2002 onwards, dorsal fin damage related to salmon louse infections was recorded systematically in ascending fish, using a scale from 0 (no damage) to 3 (massive damage). After recovery, ascending fish are released above the smolt trap. Most of the remaining fish not captured in the trap are captured by anglers in the pool below the waterfall. According to agreement with the river owner's association, scale samples and a full data set from killed fish are to be delivered to IMR. Fish that are not killed are put in a holding tank at the river bank where IMR personnel record data and then release the spawners upstream. During the spawning season, divers check the remaining salmon and anadromous trout in the pool below the trap for adipose fin clips.

Figure 3. The water discharge and temperature is monitored continuously in Guddalselva. The water quality is monitored at fixed intervals.



In 2015, the river owners built a new fish ladder in the river. This also included a trap chamber, and was located on the opposite side of Seimsfossen falls where ascending fish pass close to the field station. IMR personnel monitor this trap as well as the original upstream trap. Escaped farmed fish and individuals from experimental egg planting are killed and samples and data extracted. Wild salmon and trout are allowed to move upstream after data has been extracted and a tiny tissue sample from a pectoral fin is taken and preserved in a 2ml microtube with ethanol. The traps and the collaboration with the river owners secure almost total control of smolt production and ascending fish.

Studies 1–6

Population dynamics, differentiation and local adaptation in anadromous brown trout

STUDY 1

Glover, K.A., F. Nilsen, Ø. Skaala, J. B. Taggart and A. J. Teale. 2001. *Differences in susceptibility to sea lice infection between a sea run and a freshwater resident population of brown trout*. *J. Fish Biol.* 59: 1512-1519.

HYPOTHESES AND SCIENTIFIC APPROACH

H1: There is no significant difference in susceptibility to *Lepeophtheirus salmonis* between a freshwater resident trout and a sea trout population.

Differences in susceptibility of salmonid host species to sea louse infection have been observed in populations at sea and in fish in laboratory experiments. These differences are thought to reflect behavioural as well as nutritional and/or immunological differences between host species. Despite the fact that genetic differences in susceptibility have been demonstrated at the species level for *L. salmonis*, and at the family level for *C. elongatus*, there are no published data on susceptibilities of different populations within a species to *L. salmonis*. Such data may be of value in view of: (a) the threatened status of many salmon and trout populations; (b) the suggested link between infection levels on sea farms and local sea trout populations, (c) the need to control sea lice infection levels in salmonid aquaculture and (d) the lack of understanding of *L. salmonis* population dynamics. The freshwater resident and anadromous ecotypes, with clearly different histories of exposure to *L. salmonis*, constitute a valuable resource with which to study potential population level differences in susceptibility to *L. salmonis*.

In the autumn 1998, wild sea trout and resident brown trout adults, from Guddalselva, and the lake Bjornesfjord respectively, were

paired randomly within group. Seven sea trout families and seven resident trout families were reared for one year in a hatchery on the river Sima river on 15 May 2000, 170 sea trout were selected from the seven sea trout families. At the same time, 140 resident trout were selected on the same basis from a single tank where all families were represented. Both groups were divided equally between two 1500 l tanks with fresh water. The fish were fin clipped (left ventral fin for resident trout and anal fin for sea trout) 10 months before mixing. This permitted reliable identification of individuals to population. Starting on 16 May 2000, the groups were gradually acclimatized to 30‰ sea water over 3 weeks, after which they remained at this salinity until infection with *L. salmonis* 71 days later.

Comparison of mean abundance and louse development between the sea run and resident groups revealed highly significant differences in lice abundance. The resident trout had an average abundance of 6.3 ± 0.37 and 6.6 ± 0.43 lice whilst the sea trout had an average abundance of 3.5 ± 0.25 and 3.3 ± 0.28 lice 29 days post infection at 9 °C. No differences in development of lice, of either sex, were detected between the groups. As host groups were naïve to sea lice at the start of the experiment, this suggests that there was a significant difference in susceptibility to sea lice infection between them, which may be genetically determined. The variation observed may have been generated by selection (or lack thereof), and suggests that similar differences may also exist between other populations of brown trout.

STUDY 2

Glover, K.A., Ø. Skaala, F. Nilsen, R. Olsen, A. J. Teale, and J. B. Taggart. (2003). *Differing susceptibility to salmon lice infection in Atlantic salmon and anadromous brown trout populations*. *ICES Journal of Marine Science*, 60, 1-10.

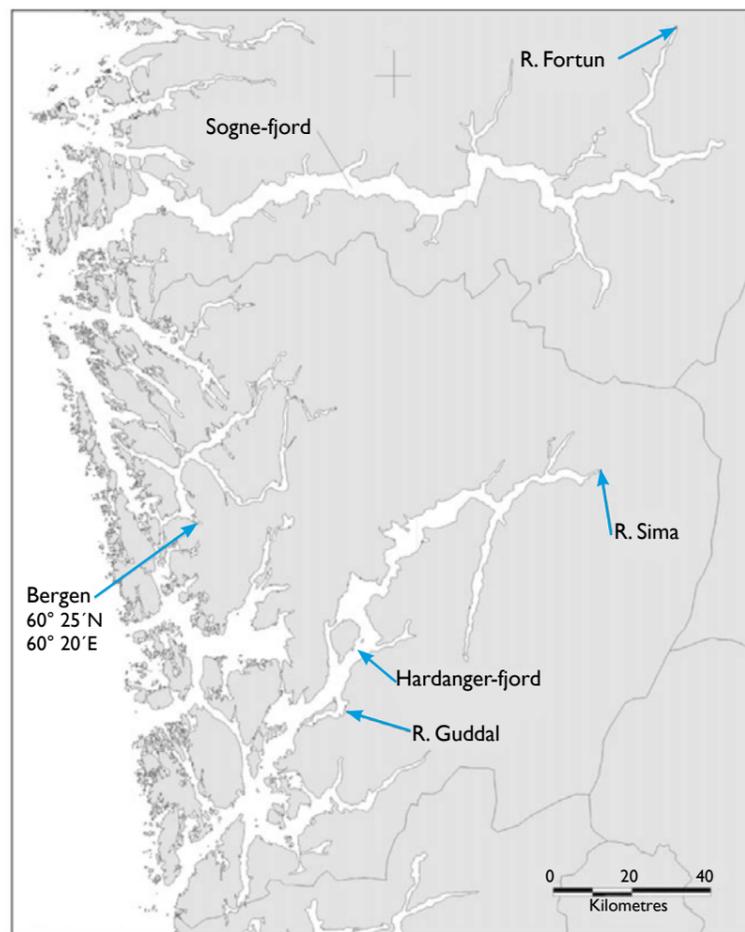
HYPOTHESES AND SCIENTIFIC APPROACH

H1: There is no population specific difference among anadromous populations of brown trout in susceptibility to the salmon louse.

Three Norwegian sea trout stocks and a farmed Atlantic salmon stock were challenged with salmon lice in a common garden experiment. Wild adult sea trout were collected from three rivers; Guddalselva and Sima on the Hardangerfjord, and Fortunselva on the Sognefjord. Fish were collected in the autumn of 1998, and crossed within stocks. Fish were hatched and reared in Statkraft's hatchery on the river Sima. In May 1999, all fish were fin-clipped to permit identification, then transferred to communal tanks, where stocks were mixed.

19 March 2000, all fish were graded into presumptive smolt and non-smolt according to size criteria.

Figure 4.
Map of the study area
and locations of the sam-
pling rivers within the fjords.



On 13 June 2001, a sample of 97–102 fish between 18 and 23 cm total length were sampled from each of the three stocks of sea trout. The selected trout were transported to the Institute of Marine Research in Bergen where they were divided between two identical outdoor 1500-litre tanks, each containing 150 sea trout. On 26 July, 65 farmed Atlantic salmon with length in the range 19–24 cm were added to each of the two replicate tanks containing sea trout. Copepodids were divided equally between the two tanks by alternately pouring 2 litre samples into each. On 17 September, 35 days post-infection, the experiment was terminated.

There were significant differences in infection level of salmon lice among fish representing three sea trout stocks and the farmed Atlantic salmon stock. Sea trout from Guddalselva displayed a significantly lower abundance and density of salmon lice than all other stocks. Salmon lice abundance and density were similar for the rivers Fortun and Sima stocks of sea trout, and abundance of lice, though not

density, was highest for farmed Atlantic salmon. Within stocks, there were no differences in infection levels of salmon lice between mature and immature fish, between sexes, or between analfin-clipped and non-clipped salmon.

In addition, both male and female salmon lice developed more slowly on the Guddalselva fish than on fish of the other stocks. All fish were reared and infected in communal tanks, and were naive to salmon louse infection prior to challenge. In addition, replicate tanks showed highly similar results and environmental variables were carefully controlled throughout the study. It is suggested that the observed differences in infection level of salmon lice among the three sea trout stocks reflect genetic differences, and may also be linked with adaptation.

STUDY 3

Glover, K.A., O. Skilbrei, and Ø. Skaala. 2003. *Stock specific growth and length frequency bimodality in brown trout (Salmo trutta L.)*. *Transactions of the American Fisheries Society* 132:307–315.

HYPOTHESES AND SCIENTIFIC APPROACH

H1: In sea trout there is no population specific differentiation in growth pattern.

The brown trout *Salmo trutta* exhibits a range of phenotypically variable traits, such as coloration, growth, the age and size of a smolt at first entry into seawater, and morphological characteristics. Furthermore, genetic variation within the brown trout as estimated from isoenzyme loci is extensive. Since brown trout exhibit a range of life history strategies and extensive phenotypic variation, it is suggested that growth potential and the patterns of growth may differ between populations. By comparing stocks under common domestic environmental conditions, it is possible to minimise environmental noise so that stock-specific genetic differences for these traits can be studied (albeit within the limitations of the domestic environment). The growth of three pure stocks and one hybrid stock of anadromous brown trout comprising 19 families and 15,000 individuals, was monitored under controlled conditions from hatching, and for a period of 16 months.

Significant differences in growth were detected among the three pure stocks, and the hybrid stock outgrew its two parental stocks. Significant differences in family growth were also detected. Two of the stocks developed clear bimodal length frequency distributions,

whereas the other two stocks displayed skewed or weakly bimodal length frequency distributions.

These data are the first to show clear evidence of length frequency bimodality development in hatchery-reared brown trout (a phenomenon very clearly described in the Atlantic salmon). The Sima stock grew significantly larger than both the stock from the river's Fortun and Guddalselva, both of which displayed similar lengths but different average weights. The Guddal-Sima hybrid stock significantly outgrew both the pure Sima and pure Guddalselva stocks and produced a higher percentage of upper-mode fish than either stock.

Because stocks were reared in mixed family tanks for the most of the duration of this study, and no significant maternal effects on offspring size or percentage of upper-mode fish were detected, we conclude that the results probably reflect genetic differences in growth potential between the stocks under the described experimental conditions.

STUDY 4

Hansen, M.M., Skaala, Ø., Jensen, L.F., Bekkevold, D., & Mensberg, K.L.D. 2007. *Gene flow, effective population size and selection at Major Histocompatibility Complex genes: brown trout in the Hardangerfjord, Norway. Molecular Ecology.* doi: 10.1111/j.1365-294X.2007.03255.x.

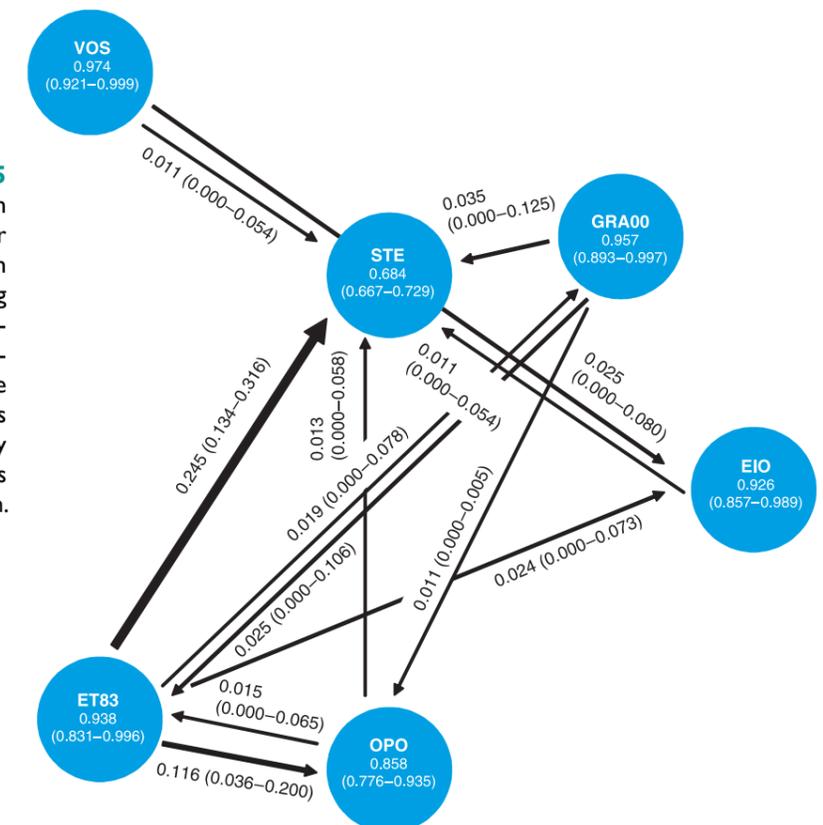
HYPOTHESES AND SCIENTIFIC APPROACH:

Ho: The anadromous brown trout in the Hardangerfjord basin is one panmictic population. Adaptive responses at immune related loci are independent of patterns and directions of gene flow.

In this study we analysed brown trout samples from the Granvinselva, Guddalselva, Eio, Etneelva, Opo and Steinsdalselva rivers, all of which flow into the Hardangerfjord, as well as the Vosso river flowing into a neighbouring fjord (Fig. 1). These populations represent nearly all major anadromous populations in the Hardangerfjord, with Etneelva and Granvinselva known to be historically two large populations. All samples consisted of archived scales, except for Guddalselva which consisted of fin clips. Most sampled individuals were adults on spawning run, but samples from Guddalselva, Etneelva (1997) and partly Steinsdal consisted of juveniles (age 1+ to 3+). From two populations, Granvinselva and Etneelva, we obtained temporally replicated samples, 1972 and 1999–2001 for Granvinselva, 1983 and 1997–1998 for Etneelva. For these samples, we used the mean sampling year to define the time of sampling for estimating

effective population size. We analysed 11 microsatellite loci, including one tightly linked to the UBA gene of the major histocompatibility class I complex (MHC) and another locus linked to the TAP2A gene, also associated with MHC.

Figure 5
Migration rate (m) between populations, along with their 95 % confidence intervals in parentheses, estimated using the program BayesAss (Wilson & Rannala 2003). Numbers within circles denote the proportion of non-immigrants within populations. For clarity of presentation m values less than 0.01 are not shown.



The results revealed an asymmetric gene flow from the two largest populations to the other smaller populations. This has important conservation implications, and we predict that possible future population recoveries will be mediated primarily by the remaining large population. Tests for selection suggested diversifying selection at UBA, whereas evidence was inconclusive for TAP2A. There was no evidence of temporally fluctuating selection. We assessed the distribution of adaptive divergence among populations. The results showed that the selection footprints were most pronounced in the two largest populations that were subject to the least immigration. We suggest that asymmetric gene flow has an important influence on adaptive divergence and constrains local adaptive responses in the smaller populations. Even though UBA alleles may not affect salmon louse resistance, the results bear evidence of adaptive divergence among populations at immune system genes. This suggests that similar genetic differences could exist at salmon louse resistance loci, thus rendering it a realistic scenario that differential population

declines could reflect differences in adaptive variation. In conclusion, adaptive divergence is present between the largest populations that are subject to the least immigration, whereas immigration constrains local adaptive divergence in the smaller populations.

STUDY 5

Meyer K, Hansen MM, Bekkevolk D, Skaala Ø, Mensberg K-LD.

2011. An assessment of the spatial scale of local adaptation in brown trout (*Salmo trutta* L.): footprints of selection at microsatellite DNA loci. *Heredity* 106: 488-499.

HYPOTHESES AND SCIENTIFIC APPROACH:

H1: Footprints of selection are more evident among regions separated by 522 ± 228 km (mean \pm s.d.) than between populations within regions separated by 117 ± 79 km (mean \pm s.d.).

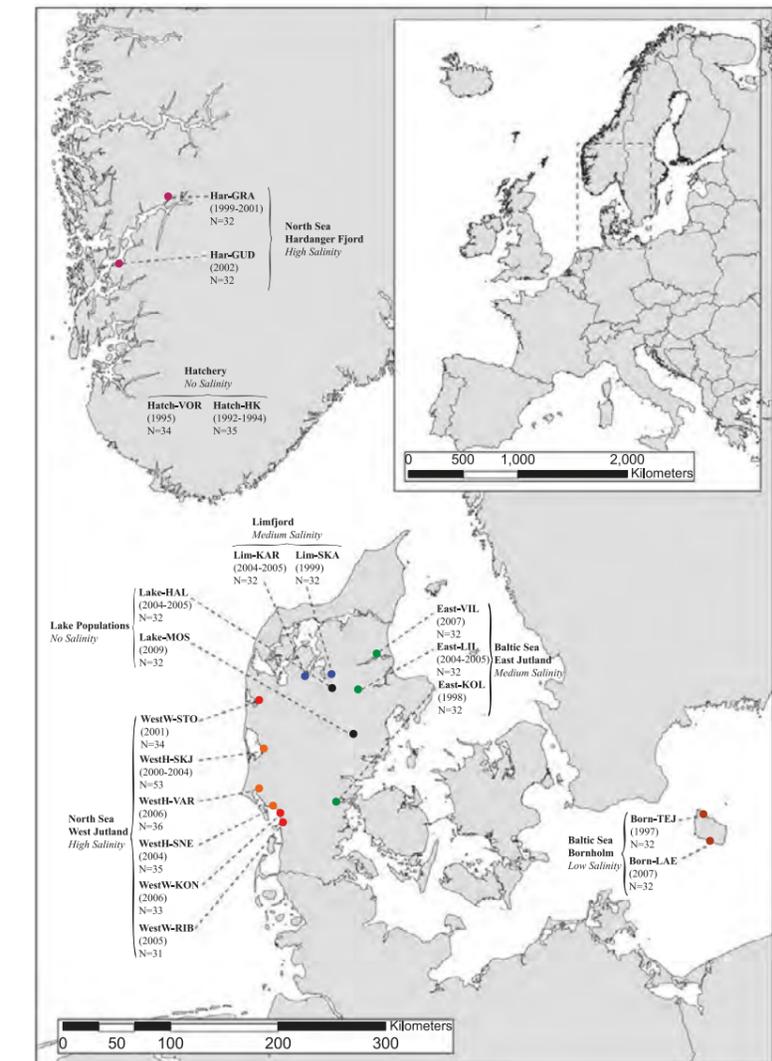
H2: Footprints of selection are more pronounced among hatchery versus wild populations than among wild populations.

In this study we addressed the questions: What is the geographic scale of local adaptation, and are adaptive differences between wild populations and hatchery strains more pronounced than between different wild populations? We addressed these issues by analyzing variation at 74 microsatellite loci (including anonymous and expressed sequence tag- and quantitative trait locus-linked markers) in 15 anadromous wild brown trout (*Salmo trutta* L.) populations, representing five geographical regions, along with two lake populations and two hatchery strains used for stocking some of the populations. The 19 populations covered seven geographical and/or environmental groupings, delimited by the North Sea coast in the west, the Baltic Sea in the east and the Hardangerfjord in Norway to the north. Specifically, this encompassed six populations from rivers on the North Sea Coast, western Jutland, two populations from the Limfjord region of Jutland, three populations from rivers on the east coast of Jutland, two populations from Bornholm Island in the Baltic Sea, two populations from the Hardangerfjord (Guddalselva and Granvinselva), two lake-dwelling populations from Jutland and, finally, two hatchery strains that had been used for stocking the trout populations in western Jutland.

The results showed that FST-based outlier tests revealed more outlier loci between different geographical regions separated by 522 ± 228 km (mean \pm s.d.) than between populations within regions separated by 117 ± 79 km (mean \pm s.d.). A significant association between geographical distance and number of outliers between regions was

evident. There was no evidence for more outliers in comparisons involving hatchery trout, but the loci under putative selection generally were not the same as those found to be outliers between wild populations.

Figure 6
Map showing the location of sampled populations, sampling year and sample size. The different colours represent the different sampled regions; Western Jutland (wild); Western Jutland (significantly admixed with hatchery trout); Hardangerfjord; Limfjord; East Jutland; Bornholm; Lake. Guddalselva, Granvinselva, Stora, Skjern, Varde, Sneum, Kongeaa, Ribe, Karup, Skals, Villestrup, Lilleaa, Kolding, Tejn, Laesaa, Lake Hald, Lake Mossoe, Vork hatchery strain, Haarkaer hatchery strain.



Our study supports the notion of local adaptation being increasingly important at the scale of regions as compared with individual populations, and suggests that loci involved in adaptation to captivity environments are not necessarily the same as those involved in adaptive divergence among wild populations.

This study provided one of the first empirical assessments of the spatial scale of local adaptation at the molecular genetic level in salmonid fishes. Along with other studies, the results illustrate that the dynamics of local adaptation cannot be understood solely at the level of individual populations, but must integrate geographical distance, and consider spatially varying environmental conditions and demo-

graphic parameters such as gene flow. Our findings also suggested that diversifying selection between hatchery and wild salmonids may involve different loci than those under selection between wild populations.

STUDY 6

Skaala Ø, Kålås S, Borgstrøm R. 2014. Evidence of salmon lice-induced mortality of anadromous brown trout (*Salmo trutta*) in the Hardangerfjord, Norway. *Marin Biology Research* 10: 279-288.

HYPOTHESES AND SCIENTIFIC APPROACH:

H1: There is a recruitment failure of anadromous brown trout in the river, Guddalselva.

H2: Marine survival rate of anadromous brown trout in the central Hardangerfjord lies within the range observed in other studies.

H3: Salmon lice contribute to the marine mortality of anadromous brown trout populations in the central part of the Hardangerfjord.

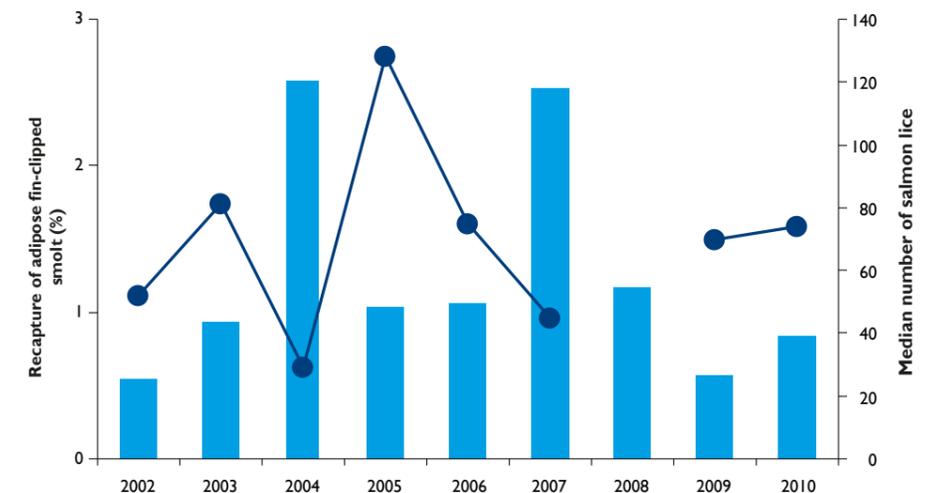
The Hardangerfjord in western Norway, has a high concentration of salmon farms, high levels of infection of salmon lice in anadromous brown trout, and declining trout populations. This study assessed the marine survival rate of anadromous trout from the Guddalselva, in the central part of the fjord, and tested the hypothesis that trout populations in this area are depressed by salmon louse infection. From 2001 to 2011, all descending smolt and trout returning from the fjord, were captured in the traps at the IMR field station. Angling activity in the pool below the trap and snorkelling surveys confirm that very few returning sea trout escape the upstream trap. The number of tagged, recaptured trout was used as a proxy for marine survival rate comparable to other studies, although it is known that some individuals stray and may overwinter in other rivers.

In 2004 and 2005, parts of the smolt cohorts were treated with the Substance EX to prevent sea louse infection. From 2007 to 2010, all smolt (n= 3557) were also individually tagged. Recordings of infection levels in prematurely returning sea trout from four rivers in the Hardangerfjord; Mundheimselva, Bondhuselva, Daleelva, Folkedalselva, and part of a national monitoring programme on salmon lice infection levels, were used as a proxy for infection levels of sea trout from rivers in the central part of the fjord.

The smolt production from Guddalselva corresponded well to the production area of smolt in the river, demonstrating that the low number of returning trout was not caused by recruitment failure in

the river. The marine survival rate from the smolt stage to return to the river was only 0.58-3.41 % for tagged smolts, which is extremely low compared with some other studies such as those in the river Burrishoole in Ireland, as well as the Norwegian rivers Imsa, and Vardnes.

Figure 7
The highest survival rates appeared in the years with the lowest recordings of salmon lice.



Finally, the highest survival rate appeared in years with lowest recordings of salmon lice in spring, and the survival rate of Substance EX-treated smolt and controls was 3.41 % and 1.76 % respectively. These findings suggest that salmon louse infection is a contributor to the high mortality of anadromous trout populations in the Hardangerfjord. A relatively high number of sea trout without tags ascended the river. This reflects the small production area for anadromous fish in Guddalselva compared with the much larger and productive neighbouring rivers which cause an asymmetrical migration pattern among these rivers.

Studies 7–14

Genetic and ecological impacts of escaped farmed salmon on wild populations: Performance of wild and genetically introgressed salmon in freshwater and in the marine environment.

STUDY 7

Skaala Ø, Glover KA, Barlaup BT, Svåsand T, Besnier F, Hansen MM, Borgstrøm R. 2012. Performance of farm, hybrid and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. *Can. J. Fish. Aquat. Sci.* 69: 1994–2006.

HYPOTHESES AND SCIENTIFIC APPROACH:

The following null-hypotheses were tested:

H1: Offspring of escaped farmed salmon survive as well as offspring from wild salmon in natural river systems.

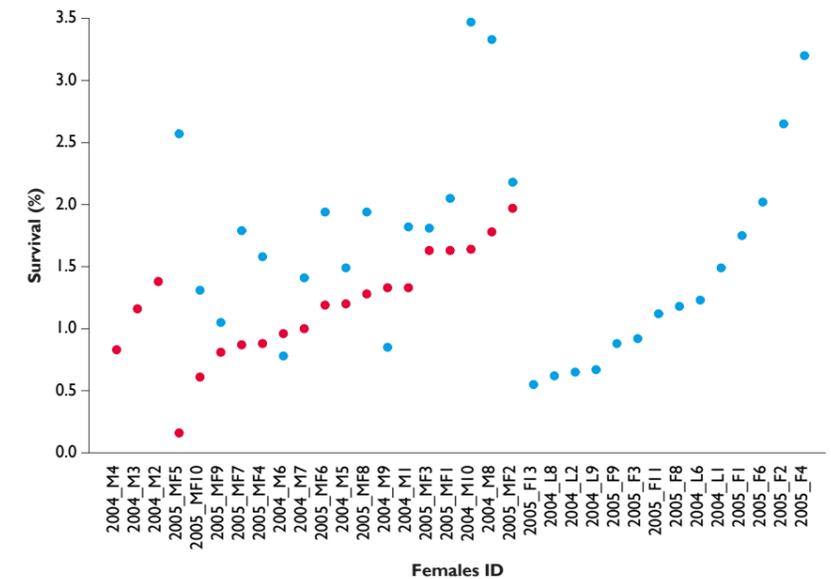
H2: In Nature, there is no difference in growth rate between offspring of escaped farmed salmon and wild salmon.

Survival, growth, and diet were compared for farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families from the eyed egg to the smolt stage in the river Guddalselva, Hardangerfjord, Norway. Cohorts of 69 farmed, hybrid, and wild Atlantic salmon families were established over three years, with hatching in spring 2003, 2004, and 2005. Eggs from the various families were thoroughly mixed through agitation in several containers to ensure that families and experimental groups were entirely randomised prior to being transported to Guddalselva. At the river, eggs were planted in artificial redds that consisted of perforated plastic trays prearranged with gravel. The number of eggs planted per square meter was increased from 2.4 in C2003 to 4.0 in C2004, and further to 6.8 in C2005, in order to study potential type-specific changes in growth rate and survival as a result of increasing juvenile competition. The annual smolt migration was sampled using the Wolf trap. To identify parentage and experimental

group, DNA was extracted from fin-clips from captured smolts. Microsatellite DNA analyses were conducted at the Institute of Marine Research in Bergen on an ABI 3730 Genetic Analyser. Genotypes across the four loci were used to unambiguously identify recaptured smolt to their source family using the family assignment program FAP (Taggart 2007).

Survival of farmed salmon progeny was significantly lower than that of hybrids and wild progeny. However, survival rates varied considerably, from 0.17 % to 6.4 %, among farmed families. Egg size had an important influence on survival.

Figure 8
Half-sib hybrid families with a farmed mother had higher survival when fathered by wild salmon than by farmed salmon.



The overall relative survival of farmed families compared with that of their hybrid half-sib families fell from 0.86 in the second cohort to 0.62 in the last cohort with increasing fish density. Smolt of farmed parents showed significantly higher growth rates than wild and hybrid smolt. The overlap in diet among types of crosses demonstrates competition, and farm and hybrid progeny will therefore reduce the river's capacity for production of genetically wild salmon.

STUDY 8

Besnier F, Glover KA, Lien S, Kent M, Hansen MM, Shen X and Skaala Ø. 2015. *Identification of quantitative genetic components of fitness variation in farmed, hybrid and native salmon in the wild.* *Heredity*, 115, 47–55.

HYPOTHESES AND SCIENTIFIC APPROACH:

The following questions were investigated:

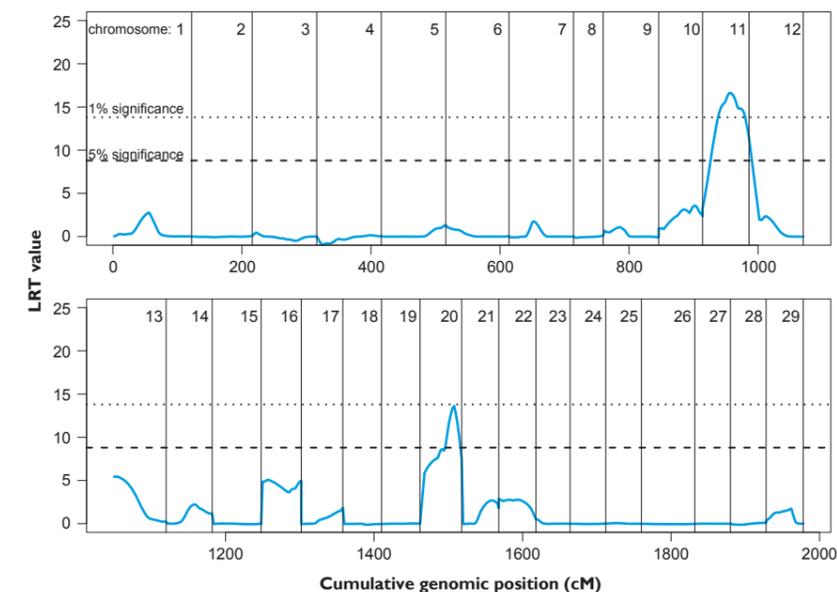
Can we identify QTL regions for fitness-related traits that diverge between wild and farmed Atlantic salmon, that is, length, weight and condition factor in a natural river system? b) Do the QTL regions identified in a natural environment correspond to QTL for the same traits previously identified in hatchery environments? c) Does strong selection at the traits in farmed salmon manifest itself at the genomic level, for example, as loss of variation around QTLs due to selective sweeps?

Studying the genetic factors underlying relative performance between wild and domesticated conspecific can help to provide a better understanding of how domestication modifies the genetic background of populations, and how it may alter their ability to adapt to the natural environment. In the present study, we used a variance component mapping approach to identify QTLs for mortality rate in the river, and three other important fitness-related morphological traits that diverge between wild and farmed Atlantic salmon, that is, length, weight and condition factor. These traits are related to growth and body conformation. They are expected to be differentially selected for in hatchery and river conditions, and thus, provide a suitable proxy for some component of fitness. We made use of an experiment where fertilised eggs from 50 full-sib families consisting of wild, farmed and wild x farmed crosses were transplanted into a wild environment as part of a large-scale common garden experiment.

Six QTLs were detected as significant contributors to the phenotypic variation of the first three traits, explaining collectively between 9.8 and 14.8 % of the phenotypic variation. The seventh QTL had a significant contribution to the variation in survival, and is regarded as a potentially key factor for the understanding of the fitness variability observed among salmon in the river. Interestingly, strong allelic correlation within one of the QTL regions in farmed salmon might reflect a recent selective sweep due to artificial selection.

The results provide evidence for the consistency of QTLs across contrasting captive and wild environments, and particularly for one of the QTLs where strong selection may have occurred in aquaculture. The environmental independence of the QTLs and thereby low geno-

Figure 9
Genome-wide scan every 1 cM of the female recombination map for QTL affecting CF. Horizontal dashed line and pointed line indicate the 5 and 1 % genome-wide significance threshold, respectively. Vertical lines separate chromosomes.



type × environment interaction further suggest that artificial selection in the aquaculture environment leading to phenotypic changes will have similar phenotypic effects in offspring of escaped farmed salmon in the wild. Therefore, selective changes in farmed salmon are expected to have direct influence not only on the genotypes but also on the phenotypes of wild salmon populations subject to spawning intrusion by farmed fish. This reinforces the general conception that interbreeding between farmed and wild salmon represents an important conservation problem, and that avoidance of escapes from aquaculture should be highly prioritised.

STUDY 9

Halttunen E, Gjelland K-Ø, Glover K, Johnsen IA, Serra-Llinares RM, Skaala Ø, Nilsen R, Bjørn PA, Karlsen Ø, Finstad B, Skillbrei OT. *Migration of Atlantic salmon post-smolts in a fjord with a high infestation pressure of salmon lice.* Submitted to *Marine Ecological Progress Series*.

HYPOTHESES AND SCIENTIFIC APPROACH

The primary aim of the study was to assess the consistency of migration behaviour throughout the fjord. In addition, we tested whether infestation of salmon lice alters post-smolt migratory behaviour by comparing progression rates, swimming speeds and migration routes of treated and untreated post-smolts in one of the three release experiments.

We found no significant difference in mean progression rates between the three releases (Opo, Guddalselva, Etneelva), genetic

groups (farmed vs wild) and treatments (range 11.5 – 16.9 km d⁻¹). However, individual variation in progression rate and migratory routes varied considerably, resulting in large differences in fjord residence times (range 2-39 days). Current directions during and after release affected swimming speed, progression rate and route choices. The predicted louse loads based on intensity growth rates from these fish, indicate that individuals taking more than 10 days to exit the fjord during periods with high infestation pressure, are likely to suffer a lethally high sea louse infestation. We conclude that, as migratory routes of post-smolts are hard to predict and migration times can stretch up to over a month, it is important to implement a salmon farming management regime which minimises salmon louse levels along all the potential migration routes and throughout the entire potential migratory period.

STUDY 10

Jørgensen KM, Solberg MF, Besnier F, Thorsen A, Fjellidal PG, Skaala Ø, Malde K, Glover KA. *Don't judge a salmon by its spots: environmental variation is the primary determinant of spotting patterns in Salmo salar*. Submitted to Scientific Reports.

HYPOTHESES AND SCIENTIFIC APPROACH

This study aims to investigate the relative roles of genetics and environment on the spotting patterns in Atlantic salmon. The results showed that regardless of their genetic background, fish reared up to smoltification in the hatchery were on average ten-fold spottier than fish reared up to smoltification in Guddalselva. Additionally, fish produced in the hatchery displayed scattered spot patterns, whereas fish produced in Guddalselva displayed clustered spot patterns. Spotting patterns that developed on the river-produced fish resembled those of wild salmon. This was despite the fact that the river-produced fish were reared in tanks for the marine part of their life-cycle. Heritability for spot density was 6 %, and a QTL for this was discovered on linkage group SSA014. These data clearly demonstrate that while genetics plays a role, environmental variation represents the primary determinant of spot pattern development in Atlantic salmon.

Summary of work in progress

STUDY 11

Survival, growth, production and timing of migration in offspring of farmed and wild salmon and their crosses in freshwater and marine phase (Skaala et al in prep).

HYPOTHESES AND SCIENTIFIC APPROACH:

Ho Genetic introgression from escaped farmed salmon will not affect smolt production and marine growth and survival of Atlantic salmon.

In this study, 75 groups consisting of pure farmed, F1 hybrid and wild families were planted above the smolt trap in the river, Guddalselva, in 2008, 2010 and 2011. In this study we used material from a large wild salmon population in the Etneelva as a wild control population. This is a refinement of the design compared with the first study where material from a wild population in the Norwegian gene bank was used (material from a wild local population was not available for the first study). Part of the egg materials from the same families used in the egg planting were used for production of smolt, released in the outlet of Guddalselva in 2011 and 2012. Extensive sampling of returning, tagged fish was conducted in Guddalselva and most other rivers of the Hardangerfjord. Genotyping and age analysis are completed and the data are about to be processed.

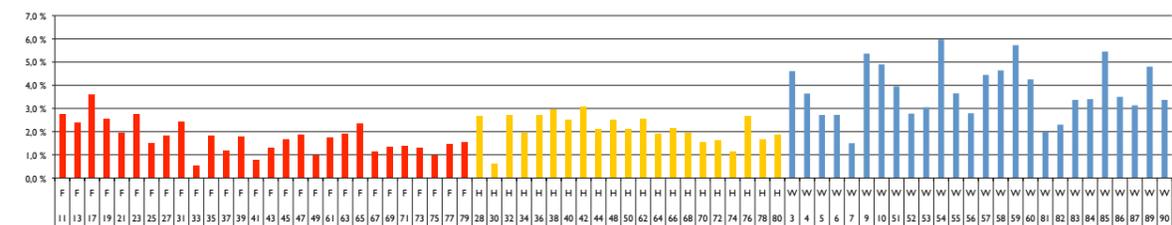


Figure 10

Survival from planted eyed egg to smolt shows significantly reduced output of smolt from farm (red bars) and hybrid (yellow bars) families compared with wild (blue bars) families. Please note the above figure is generated from preliminary and unpublished data.

STUDY 12

Skaala et al. in prep. *Spawning success, survival, growth and timing of smolt migration in introgressed and wild salmon.*

HYPOTHESES AND SCIENTIFIC APPROACH:

Ho = Atlantic salmon spawners introgressed with genetic materials from farmed salmon have similar spawning success as wild non-introgressed salmon.

Ho = Smolt production and timing of smolt migration from introgressed Atlantic salmon spawners are similar to that of wild non-introgressed salmon.

This study is based on phenotypic wild salmon spawners captured from 2011 on and released in Guddalselva to spawn freely. Genetic studies have demonstrated significant introgression in several salmon populations in the Hardangerfjord region. Tissue samples were collected from all individuals and F1 smolt captured on the smolt trap will be genotyped and levels of introgression determined, as will spawning success of individual fish with different degrees of introgression.

STUDY 13

Skaala et al. in prep. *Relative importance of anthropogenic and natural factors affecting marine survival in populations of Atlantic salmon and sea trout in the rivers Guddalselva and Etneelva*

HYPOTHESES AND SCIENTIFIC APPROACH:

Ho = There is no correlation between survival of smolt year classes and observed salmon louse infection levels in Atlantic salmon and anadromous brown trout.

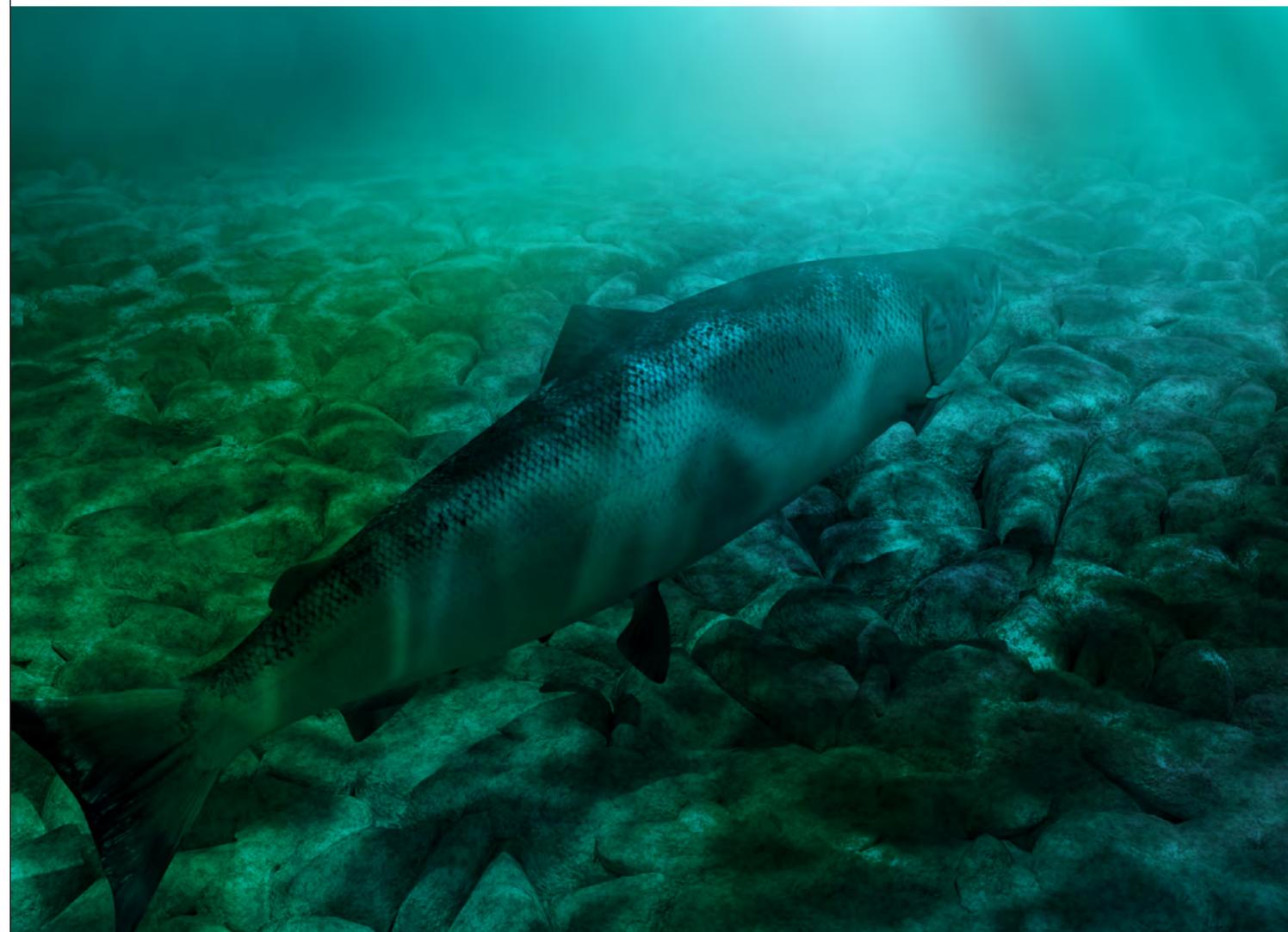
This study is using time-series of Atlantic salmon and anadromous brown trout spawners from traps in the rivers Guddalselva and Etneelva along with assessments conducted by divers in the rivers Etneelva and Eio, and data on salmon louse infection levels to analyse correlations between growth and survival of specific year classes of salmon and sea trout and observed infection levels.

STUDY 14

Harvey et al. in prep. *Relative importance of water discharge and temperature for timing of smolt migration in Atlantic salmon and sea trout.*

HYPOTHESES AND SCIENTIFIC APPROACH:

Based on the time-series of migration and density of Atlantic salmon and anadromous brown trout smolts in Guddalselva, and available data on temperature and water discharge, relative importance determining the timing of the smolt run will be analysed. This will provide insights into the triggers of smolt migration in both species based upon data from >15 years of smolt migration in the river, Guddalselva. While a low number of similar data sets do exist for a low number of rivers, as Guddalselva is partially glacier-fed, this data set will expand our understanding into the triggers of smolt migration, and potential for local adaptation.



Summary of materials and data delivered to other studies and projects

The monitoring of juvenile and adult salmon and sea trout migration and the experimental studies have contributed to a number of other studies on performance of families and populations under laboratory conditions, several of which were conducted at IMR Matre, either with egg and milt materials or ideas for research.

1. Guddalselva is one of the only two rivers in Norway with a permanent smolt trap covering the whole river transect. The data on smolt migration (2001-2017) from this “river-laboratory” represents one of the longest and most complete time-series on smolt migration in Europe.
2. The time-series on smolt migration contributed to the review: Otero J, L'Abée-Lund JH, Castro-Santos T, Leonardsson K, Storvik GO, Jonsson B, Dempson B, Russell IC, Jensen AJ, Baglinière JL, Dionne M, Armstrong JD, Romakkaniemi A, Letcher BH, Kocik JF, Erkinaro J, Poole R, Rogan G, Lundqvist H, Maclean JC, Jokikokko E, Arnekleiv JV, Kennedy RJ, Niemelä E, Caballero P, Music PA, Antonsson T, Gudjonsson S, Veselov AE, Lamberg A, Groom S, Taylor BH, Taberner M, Dillane M, Arnason F, Horton G, Hvidsten NA, Jonsson IR, Jonsson N, McKelvey S, Naesje TF, Skaala O, Smith GW, Saegrov H, Stenseth NC, Vøllestad LA. 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Glob Chang Biol.* 2014 Jan;20(1):61-75. doi: 10.1111/gcb.12363. Epub 2013 Nov 21.
3. The DNA profiles of planted salmon families were successfully used to identify family origin of salmon fry in stomach contents of brown trout predators (Skaala et al. 2014).
4. Data from the river Guddalselva is available as part of the scientific foundation for the IMR management advice on genetic and ecological impacts from aquaculture.
5. Data on individually tagged (PIT) Atlantic salmon and anadromous brown trout has been available for studies on marine survival and growth.
6. Data on individually tagged (PIT) salmon and anadromous brown trout provide an opportunity for calibration of age- and growth analyses based on growth patterns in fish scales. This has become increasingly important as various environmental factors cause artificial growth anomalies in scales.

7. The “river laboratory” has yielded time-series with a unique collection of physical materials (fin clips/DNA) from smolt and adult salmon and brown trout, available for additional research on reproductive success of individual fish.
8. The time-series has provided novel and important empirical data on smolt emigration of Atlantic salmon and anadromous brown trout to the working group on developing the so-called “Traffic Light System”. The time series also provides unique empirical data on the relation between spawners, egg deposition and smolt output for further modelling work in region no 3 under the “Traffic Light System”

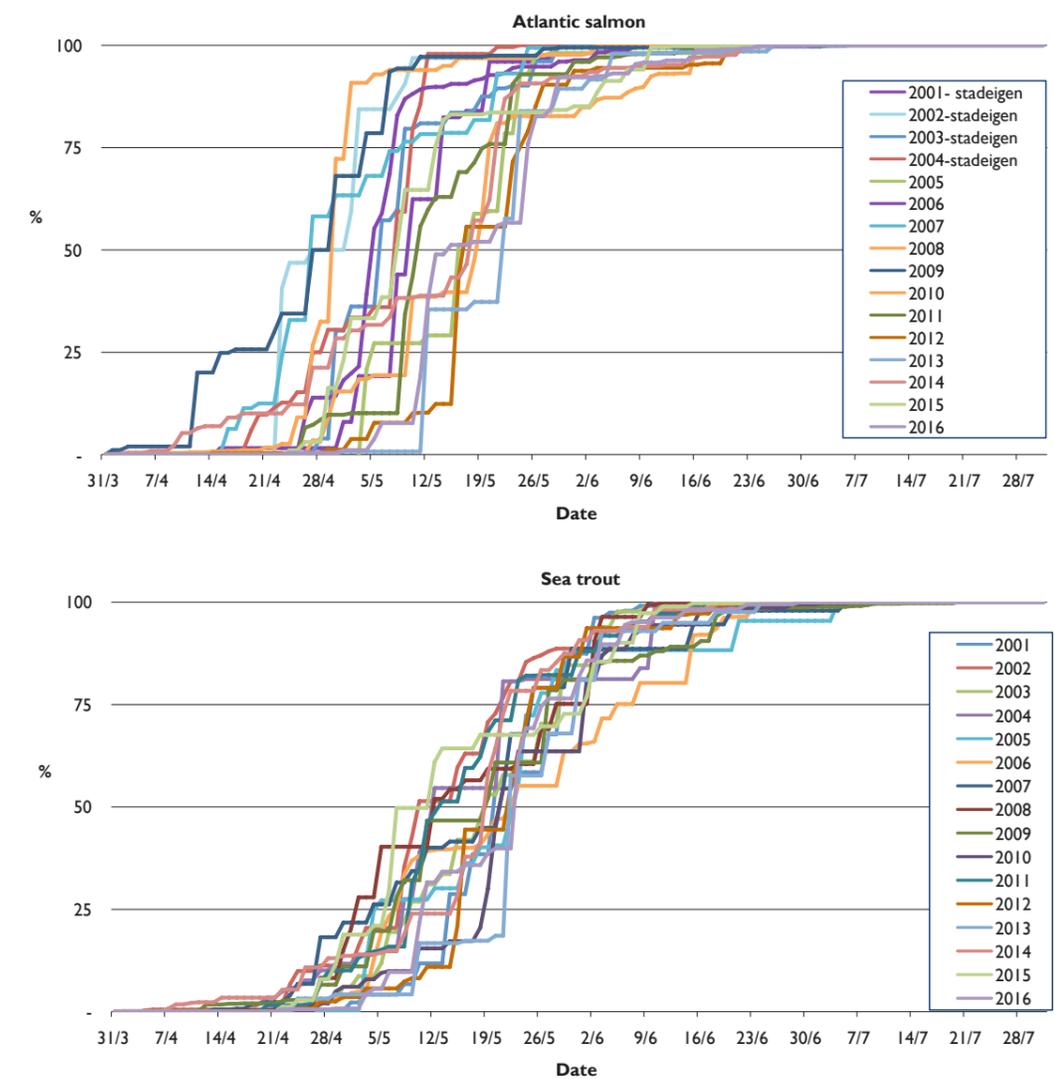


Figure 11

The 2001-2016 time-series from Guddalselva has provided essential knowledge and unique data on smolt run of Atlantic salmon (upper) and sea trout (lower). This has proved valuable to the national committee for developing the “Traffic Light System” for management of Norwegian aquaculture.

Overall conclusions

During the operation of the "river laboratory", studies have been conducted covering all the issues that we initially planned, and many of the results have been published in peer-reviewed journals. Several additional datasets have been harvested, and manuscripts analysing these are under preparation. Monitoring of fish migrations and PIT tagging of smolts continue to provide empirical and quite precise information on marine survival of Atlantic salmon and sea trout. Based on published information from the river laboratory we can draw the following conclusions:

1. Anadromous populations of brown trout are often genetically differentiated in qualitative genetic traits as well as in fitness-related traits. Examples are growth response and susceptibility to parasites such as salmon lice. Depending on geographic scale, such populations can be locally adapted to various environmental conditions.
2. The smolt production in Guddalselva reflects the available production area of the river and its spawning populations. There are no indications of recruitment failure due to poor water quality or pollution of the river.
3. The marine survival of sea trout from Guddalselva, estimated from tagged smolts, is very low compared with what similar studies have found for other rivers. The data confirms the observation from professional snorkelling surveys and the information from anglers in the central part of the fjord.
4. The low marine survival observed for sea trout smolt from Guddalselva is in agreement with observed infection levels of salmon lice on sea trout and mortality estimates in the central part of the Hardangerfjord, made by the national monitoring program conducted by IMR and it reflects the general situation for sea trout in this area. Salmon lice most likely contribute to the high mortality of sea trout in the central part of the fjord.
5. On average, offspring of farmed salmon grow faster than wild salmon, but have lower survival rates during the juvenile part of the life cycle. Their competitive ability is inversely related to juvenile density in the river. Half-sib families with farmed mothers sired with farmed males have on average significantly lower survival rates than those sired with wild males. There is full overlap in prey selection between offspring of juvenile farmed and wild salmon, suggesting that offspring of escaped farmed salmon compete with



wild juveniles for food. Due to competition for food and reduced survival rates, offspring from escaped salmon will reduce wild smolt output from a river.

6. Additional manuscripts on marine survival in sea trout and Atlantic salmon in general, and on comparative data on marine survival of offspring of wild and farmed salmon, are in preparation.
7. The river laboratory in the river Guddalselva, has provided unique time-series on smolt runs of Atlantic salmon and sea trout (2001-2016), which is used by the national working group in modelling smolt migration and the relation between spawners, egg deposition and smolt production for the "Traffic Light System" for management of Norwegian aquaculture, and for a continued scientifically-based management of wild salmonid species.

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Evaluation of the report:

A summary of 20 years (1998-2017) of scientific work on genetics and survival in anadromous brown trout (*Salmo trutta L*) and Atlantic salmon (*S. salar L*) in the river Guddalselva, western Norway, by Øystein Skaala et al.

Philip McGinnity & Michael M. Hansen

ASSIGNMENT OF TASKS

In April 2017 the evaluators (Drs Philip McGinnity and Michael M. Hansen) were asked by the Institute of Marine Research, Bergen, Norway to provide a critical evaluation of a report on scientific work conducted 1998-2017, centered on and around the River Guddal in the Hardangerfjord: A summary of 20 years (1998-2017) of scientific work on genetics and survival in anadromous brown trout (*Salmo trutta L*) and Atlantic salmon (*S. salar L*) in the river Guddalselva, western Norway, by Skaala et al. For simplicity, in the following we refer to this as the "Guddal report". At this point it should be made clear that one of the evaluators, Dr Michael M. Hansen, is affiliated with the Institute of Marine Research as an Adjunct Professor and is furthermore co-author of some of the papers. It was subsequently clarified that the intention was to have two persons with expertise in the research topics in the evaluation committee, with one also having more specific knowledge on the system (Michael M. Hansen).

The evaluators received and read the report itself and, furthermore, visited the Institute of Marine Research, Bergen, 24 May 2017. During the visit, Dr Øystein Skaala presented the report and subsequently we asked questions to Drs Øystein Skaala and Kevin Glover in order to further clarify specific issues and discuss critical points. This lasted in total from ca. 10 AM to 3 PM.

The Guddal Report is based primarily on results that have already been published in scientific journals with peer review. In contrast to "grey literature" such as reports, which may or may not

have been subject to quality control at the discretion of the responsible institution, papers in peer-reviewed scientific journals have been evaluated by typically 2-3 independent scientific experts (referees). They are in most cases anonymous to the authors. Based on the assessments by these referees, the editors of the journals can request varying degrees of revision of a paper pertaining to all aspects such as data and data quality, statistical methods, relevance of the science and soundness of conclusions. Ultimately, the editors decide if a paper is to be published or rejected in the journal. As the individual papers listed in the report have consequently been under independent quality control and have been accepted for publication, the tasks of the evaluation were defined as follows:

- In respect to the Guddal Research Station: what is the relevance of the facility, its capabilities, including its geographical location, and has it been put in proper use?
- Has the science been of a sufficient standard and appropriate for the questions being asked and addressed?
- Have the overall research aims been addressed (as stated in the Guddal Report p. 5, l. 15-21)?

Finally, it should be noted that the evaluators are aware that large-scale national monitoring programmes are operating on e.g. escapes of farmed salmon and salmon lice abundance that subsequently feed into management. However, it is beyond the scope of this evaluation to assess possible links between the scientific research reported in the Guddal

Report and the monitoring programmes that relate to management; this evaluation report focuses exclusively on the science reported in the Guddal Report.

THE GUDDAL REPORT

The Guddal Report itself consists of 24 pages, including references. It includes an abstract followed by sections describing the background of establishing the facility, the research aims and the specific trap facilities at the research station. The results of the individual studies are subsequently described. This is done on a paper-by-paper basis by first listing the hypotheses and overall methods/study designs followed by a summary of the results. The results of eight papers published in peer reviewed journals are reported, along with shorter accounts of four additional papers that are currently in preparation. The report then briefly describes materials and data from the Guddal studies that have fed into other projects. Finally, the overall conclusions of the studies are summarized.

The evaluators find that the report provides a logical and coherent account of the background for establishing the research station and for the research undertaken, with the possibility of looking up further details in the published research papers.

THE RELEVANCE OF THE FACILITY

Questions pertaining to impacts of escaped farm salmon on the fitness and productivity of recipient wild populations, marine survival and adaptation in brown trout and susceptibility of trout to marine parasites have proven difficult to address because they relate to animals living in unpredictable environments, which are difficult to replicate and parameterise. The most significant advances in our knowledge of how fish respond and perform in these environments have been achieved recently using a common garden experimental approach in studies

specifically undertaken in the wild. It is difficult if not impossible to tackle these questions under laboratory or captive breeding conditions and to accurately transpose the findings in to river populations. Nor can useful insights be ascertained indirectly from more broad-scale monitoring programmes as these programmes don't have the luxury of experimental control.

River based common-garden experiments are a relatively recent development and only made possible with the development of DNA profiling for accurate parentage assignment. A common garden experiment, also sometimes referred to as a transplant experiment, is an experiment to test the effect of environment by moving two populations from their native environments into a common environment. Common garden experiments are often used to test if there is a genetic component to differences in populations. Previously, salmon and trout had to be reared separately before they were large enough to tag physically. By taking experiments into the wild, experimental populations can be exposed to the variations arising in complex ecosystems, which are impossible to replicate in the laboratory.

The Guddal River and associated infrastructure has provided and provides a proven experimental framework to undertake a range of directed experimental studies (principally common garden experiments, such as comparing the relative performance - and ultimately their fitness - of populations of salmon and trout of differing provenances and histories in freshwater and marine environments. The Guddal experimental river enables studies to be conducted under natural rivers conditions and crucially those studies can commence at the earliest stage in the life cycle (from green or eyed egg onwards), thus minimizing experimental effects and errors.

Briefly, the experimental credentials of the Guddal are that it is an unregulated river (no hydro-power generation) with waters and in-river habitats of very high environmental quality allowing the introduction of experimental families at egg stage without concern for sedimentation, pollution or unnatural flow patterns. Importantly from the perspective of the statistical robustness of any experiment, the river is capable of naturally producing substantial numbers of experimental animals in the river right up to the smolt stage of development. In addition the large numbers of smolts produced are ideal candidates for provision of statistically robust tagging studies in the marine environment.

The key piece of infrastructure is the Guddalselva smolt trap, which is a wolf trap design deploying horizontal incline screens and is located approximated 100m upstream of the rivers tidal limit. The trap encompasses the whole cross-section of the river and is capable of capturing all downstream migrating smolts of salmon and trout. This complete sampling capability means that there is no equivocation in determining the output of any given experiment, which is a major limitation in the majority of study situations where partial trapping is the norm and doubt always persists as to the efficacy of sample recovery. The Guddal downstream trap and associated holding tanks provide access to entire run-time cohorts of fish for marine survival studies; facilitate a raft of new experimental capabilities in terms of ocean tracking; allow fish to be managed optimally from a fish welfare perspective. All these advantages have been exploited effectively in a number of the studies assessed below. A newly established upstream trapping capability enables the performance of those experimental groups released into the marine environment and returning to the river to be assessed. It is our opinion that the facilities in Guddal are equiva-

lent, and in certain respects superior, to those to be found elsewhere in the world and are appropriate for the studies being undertaken and are capable of addressing the questions that have been posed.

To the best of our knowledge the Guddal facility is one of only three rivers world-wide where such experiments, facilitating deliberate introduction of non-native material into the wild to address ecological and evolutionary questions associated with aquaculture, are allowed and undertaken and therefore the river should be considered to be of major national and international research importance; the Burrishoole River in Ireland and the Imsa River in Norway being the others.

Their uncommonness stems from the fact that such facilities and the studies carried out require considerable commitments in terms of permissions, people, investment, maintenance and time and as a consequence their operation and management are very much the preserve of government agencies such as IMR with sufficient wherewithal to successfully operate such installations, superior to either the universities or the private consulting sector, which would by definition have a much more limited capacity in terms of manpower, legal authority with much shorter timeframes and narrower perspectives in which to operate.

We would also suggest that the relevance of the Guddal facility should not be considered in isolation, but be assessed as an integral part of a broader IMR research capacity to address ecological and evolutionary questions arising, which includes two of the Institutes major research assets, namely the experimental station at Matre and the genetic and genomics laboratory in Bergen. It would also be important here to include among these the new research competences at the Etna River for the study of wild salmon and trout and their interactions with escaped farm salmon. Together these

represent an extraordinary powerful and complementary scientific resource.

One criticism that might be directed at the relevance of Guddalselva as a location for evolutionary and adaptive studies is that there was no substantive natural salmon population in the river prior to the establishment of the upstream passage in the river. It might be argued that such a population would be a better candidate (being locally adapted) by which to compare the relative performance of the progeny of farmed salmon than those wild populations sourced from neighbouring and more remote rivers. However, this we feel would be an unfair assessment of the systems capabilities and it would be unlikely that permissions would be granted to introduce an experimental population into a river which has an extant population. Rather not having a natural population might also be viewed as one of the Guddal systems principal advantages

The data and the scientific interpretation of the data emanating from the Guddal has had a substantial impact on international policy development in respect of parameterising the risk framework around salmon aquaculture (ICES http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2016/Special_Requests/NASCO_AquacultureEffectsAdvice.pdf). Moreover, countries such as Ireland, Iceland and Canada with nascent salmon farming industries are looking to data sourced from the Guddal to inform on risk to wild salmonid populations and to guide the formulation of their regulatory structures.

The Guddal and the studies that can be undertaken there will have considerable relevance into the future. We would consider it an ideal location for studies of the response of salmon and trout to climate change. In respect to technological developments associated with the sequencing of the salmon genome and opportunities for functional annotation and gene expression studies related to

important life history traits, we would see the Guddal as an ideal location to acquire and fulfil demands from the international genomics community for accurate phenotypes from the wild. Pedigree reconstruction using genetic analysis will provide a useful means to estimate fundamental population biology parameters relating to population demography, trait heritability and individual fitness when combined with other sources of data

In respect to the relevance of the facility's geographical location, the Guddal River is situated in one of Norway's most intensive salmon farming areas. This offers a distinct advantage to the facility in assessing the impact of aquaculture on co-occurring wild salmonids. And therefore its location within this area is highly relevant to the science being carried out. One indirect criticism in

respect to interpreting the data emanating from the facility specially in respect to marine experiments and marine survival studies might be the absence of a similar sister facility in a non-farming area. However we believe that this does not in any way denigrate the quality of the studies that have been undertaken or will be undertaken in the Guddal.

ASSESSMENT OF INDIVIDUAL STUDIES

STUDY I

Glover, K.A., F. Nilsen, Ø. Skaala, J. B. Taggart and A. J. Teale. 2001. *Differences in susceptibility to sea lice infection between a sea run and a freshwater resident population of brown trout*. *J. Fish Biol.* **59**: 1512-1519

This represents a hatchery-rearing experiment, where sea lice infection is compared between an anadromous (Guddal) and a resident brown trout population. It is a first study of population-specific differences in sea lice susceptibility and is as such important and relevant. It can be criticized for involving only two populations, and it is unclear to which extent the increased susceptibility of the fresh-

water resident population reflects stress related to the exposure to saltwater per se or more innate properties. However, the study was published 16 years ago and is probably best regarded as a pilot study which was highly important by then to assess effect sizes and test if population differences in susceptibility could at all be expected.

STUDY 2

Glover, K.A., Ø. Skaala, F. Nilsen, R. Olsen, A. J. Teale, and J. B. Taggart. (2003). *Differing susceptibility to salmon lice infection in Atlantic salmon and anadromous brown trout populations*. *ICES Journal of Marine Science*, 60, 1-10.

This study follows up on study 1 and tests for differences in salmon lice infection between different anadromous populations. It also includes one Atlantic salmon population. Significant differences in susceptibility are indeed found between different populations. This is a highly important result, indicating local adaptation for this trait. A criticism could be raised that e.g. the importance of non-genetic maternal effects cannot be ruled out. Hence, the points about local adaptation could have been strengthened by crossing designs allowing estimates of genetic and non-genetic components of variance. In order to be logistically feasible this would have required parentage assignment using genetic markers (as was done in study 3).

STUDY 3

Glover, K.A., O. Skilbrei, and Ø. Skaala. 2003. *Stock specific growth and length frequency bimodality in brown trout (Salmo trutta L.)*. *Transactions of the American Fisheries Society* 132:307-315

This also represents a hatchery-rearing experiment, this time making use of molecular parentage assignment to identify populations and families and allowing for rearing individuals in common tank environments. The study

revealed important differences in growth between families and populations, including length frequency bimodalities and is important in the context of local adaptation and genetic differences among populations in phenotypic traits.

STUDY 4

Hansen, M.M., Skaala, Ø., Jensen, L.F., Bekkevold, D., & Mensberg, K.L.D. 2007. *Gene flow, effective population size and selection at Major Histocompatibility Complex genes: brown trout in the Hardanger Fjord, Norway*. *Molecular Ecology*. doi: 10.1111/j.1365-294X.2007.03255.x.

It should be noted that one of the evaluators is first author of this paper.

The study analyzed both presumably neutral and some gene-linked microsatellite DNA markers (in total 11 loci) in anadromous brown trout populations in the Hardanger Fjord, including the Guddal population. The results suggested asymmetric gene flow from the larger to the smaller populations. Moreover, it was found that footprints of selection at markers linked to immune-related genes were strongest in the largest populations receiving the least gene flow. Hence, it provided empirical evidence for theoretical predictions. It also suggested general and possibly adaptive differences among populations in the Hardanger Fjord with respect to immune-related genes, although the analyzed markers themselves were unlikely to be related to salmon lice resistance.

In terms of methods, use of microsatellite markers in numbers of tens and in rare case a few hundreds were standard at the time (10 years ago). Keeping this in mind, the study was an important and valuable contribution at the time of publication. However, it should also be pointed out that the field has since experienced revolutionizing developments in an amazingly short time due to the advent of Next Generation Sequencing and platforms for SNP genotyping. Ana-

lyzing tens or hundreds of thousands (or even millions) of SNP (Single Nucleotide Polymorphism) markers is therefore now possible and feasible. Hence, more detailed and stronger inferences could be made using the methods available today. This should not be seen as a criticism but more an observation of the pace by which genomics methods have transformed the field.

STUDY 5

Meyer K, Hansen MM, Bekkevold D, Skaala Ø, Mensberg K-LD. 2011. *An assessment of the spatial scale of local adaptation in brown trout (Salmo trutta L): footprints of selection at microsatellite DNA loci*. *Heredity* 106: 488-499.

It should be noted that one of the evaluators is a co-author of this paper.

This study is related to study 4. It was based on analyzing 74 microsatellite markers in populations from Northern Europe, including Guddal and Granvin from the Hardanger Fjord. Using a hierarchical sampling design and landscape genetics methods it was analyzed over which spatial scales local adaptation was likely to occur, and among others the results suggested that the spatial scale of selection (that is at the level of single populations or across several neighbouring populations) is important to consider. Similar to study 4 more powerful genomic and statistical tools are now available, although the general conclusions must be considered sound.

STUDY 6

Skaala Ø, Kålås S, Borgstrøm R.2014. *Evidence of salmon lice-induced mortality of anadromous brown trout (Salmo trutta) in the Hardangerfjord, Norway*. *Marine Biology Research* 10: 279-288

This study made use of the Guddal River trap facility to assess whether or not salmon lice are likely to increase mortality in the sea in anadromous brown trout. The main results of the paper were based

on both correlative and manipulative experimental designs (readers unfamiliar with the principles of conducting biological scientific research should be aware that "manipulative" does not mean that the results have been manipulated, but that the system is "disturbed" in order to observe possible effects of this). The correlative approach consisted of tagging smolts from the Guddal River during their migration towards the sea and record the number of returning spawners from the same cohort. It turned out that return rates (assumed to reflect survival) were highest in years with lowest sea lice abundance. This could suggest a negative effect on mortality by salmon lice, but correlative designs are also sensitive towards confounding factors: perhaps an independent environmental factor would at the same time cause high survival of trout and low survival of salmon lice, without there being a causal relationship between trout mortality and abundance of salmon lice. Also, assignment of returning spawners to smolt cohorts was conducted by length-frequency distributions instead of age determinations by taking scale samples and reading these; this choice was made in order to minimize disturbance of the returning spawners. It is not clear how accurate this approach was. However, the effect of reduced accuracy would be to create more "noisy" data, thus diminishing the possibilities of seeing relationships between trout survival and salmon lice abundance. This is therefore unlikely to explain why a relationship was observed.

Given the possibility of confounding factors, it is important that the study also undertook a manipulative approach, where a proportion of smolts in two consecutive years were treated with Substance EX, which provides protection against salmon lice. Significantly higher return was indeed observed for treated versus untreated smolts, indicating that salmon lice played a role in marine survi-

val of trout. Given the low percentages of returning spawners as a whole, this inference is based on few individuals, making it indicative rather than conclusive. It would be preferable to conduct this experimental treatment with Substance EX over several more years. Moreover, combining survival of treated and untreated individuals with salmon lice abundance might allow for a stronger test supporting or refuting the hypothesis of salmon lice infection underlying high mortality. In fact, considering the importance of the topic it would be a recommendation for future activities to continue this line of research.

STUDY 7

Skaala Ø, Glover KA, Barlaup BT, Svåsand T, Besnier F, Hansen MM, Borgstrøm R. 2012. *Performance of farm, hybrid and wild Atlantic salmon (Salmo salar) families in a natural river environment*. *Can. J. Fish. Aquat. Sci.* 69: 1994–2006.

It should be noted that one of the evaluators is a co-author of this paper.

This is an important study, where eggs from families of farmed and wild salmon and farmed X wild crosses were planted into the River Guddal. Migrating smolts were sampled in the Wolf trap of the station and were assigned to families using microsatellite DNA markers. The results showed significantly lower survival of farmed salmon compared to wild salmon and hybrid crosses. However, there were also considerable differences in survival among families, and egg size was shown to have an important effect on survival.

Experiments conducted in natural settings comparing the performance of farmed, wild and admixed salmon are crucial for evaluating the fitness effects of wild salmon populations interbreeding with escaped farmed salmon. Only few such studies have been conducted, as it requires suitable experimental rivers like the River Guddal. This particular study suggests that survival differences among

families is an additional important factor to consider in farmed-wild salmon interactions. Moreover, it confirms, in a different setting, several conclusions obtained in the few related studies that have previously been conducted. A criticism could be raised that the study is not based on a local wild salmon population, which is not available in the River Guddal. However, conducting such an experiment in a river with a local, indigenous salmon population would be highly controversial and not likely to be permitted. Also, if the wild population used was less adapted to conditions in the Guddal River than a local, indigenous population would be, then this means that the differences between wild and farmed populations have in fact been underestimated.

STUDY 8

Besnier F, Glover KA, Lien S, Kent M, Hansen MM, Shen X and Skaala Ø. 2015. *Identification of quantitative genetic components of fitness variation in farmed, hybrid and native salmon in the wild*. *Heredity*, 115, 47–55.

It should be noted that one of the evaluators is a co-author of this paper.

This study made use of the same setup as study 7. It represents a rare and valuable example of a study attempting to identify quantitative trait loci (QTLs) in a natural setting. QTLs were identified for mortality rate and other phenotypic traits (length, weight, condition factor). Moreover, there was high concordance with QTLs observed in aquaculture settings. This has the important consequence that selection affecting these traits in aquaculture will have similar phenotypic effects when farmed and wild salmon interbreed.

It is difficult to come up with criticisms of this study, other than the fact that more phenotypic traits might have been scored. However, as the individuals were released for further use in studies 9 and 10, it has been important to minimize handling of fish.

The studies reported as in progress were not evaluated further, although it was noted that they were all interesting and relevant.

HAVE THE OVERALL RESEARCH AIMS BEEN ADDRESSED?

The report includes studies that either make direct use of the facilities at Guddal as an experimental river (studies 6-8), or analyze fish or material collected at the facility (studies 1-5).

In the report (p. 5) the research aims are stated as:

- 1) To provide data on impacts of genetic introgression on fitness and smolt production in wild salmon populations
- 2) Establish a river system with full control of fish migration to assess natural smolt production, timing of migration and marine survival in anadromous brown trout
- 3) Investigate the occurrence of local adaptation in anadromous brown trout, and to what extent local populations may have different susceptibility to marine parasites like salmon lice.

Concerning aim 1) this has clearly been addressed in studies 7-8 and studies 9-10 that are in progress. These studies have made excellent use of the experimental facilities and would likely not have been conducted without them.

Concerning aim 2) this has also been addressed. However, the evaluators note that interesting data and material covering a long time scale has been collected but not published. Such long-term data on smolt production and reproductive success are clearly of scientific interest, and it should be a priority to process the data and publish the results.

Concerning aim 3) this has also been addressed, although not directly making use of the Guddal experimental facilities, but more indirectly by analyzing fish or

material collected at the facility along with trout populations from elsewhere. This does not detract from the value of the research, and the Guddal research Station has played an important role in the studies.

In total, the stated research aims have been addressed, and more research is in progress. The evaluators furthermore note that the research activities of the Guddal facilities appear to have been continually evolving both in scope, ambition and methodology.

CONCLUSIONS

The evaluators find that the Guddal Research Station represents a valuable and well-considered research facility. There are very few of its kind, even though such stations are important for conducting long-term studies of population dynamics and long-term experiments in natural settings. The facility has been put into good use, both as a direct experimental facility (studies 6-8 and studies in progress) and for supplying material and information for other studies (studies 1-5). However, more papers could and should be published based on the data generated from the facility. For instance, there are unique long-term series of e.g. smolt runs, reproductive success and population dynamics that should be published. In this context, it is reassuring that several more papers are in the pipeline (studies 9-12).

Studies 1-8 have all been subject to peer review and have been published in scientific journals. For some studies, e.g. 1, 2, 4 and 5 technological developments would allow the studies to be conducted at higher resolution and with more elaborate designs with the methods now available. This is not a criticism but more an observation that illustrates the amazing progress in methodology that has occurred.

Papers 7 and 8, in particular, represent exceptional experiments with very

important results, illustrating the value of the facilities. Paper 6 focuses on an important issue, but continuing and expanding parts of the experiments is recommended to further strengthen the data and increase the conclusiveness of the study.

In total, the evaluators find that the research conducted in connection with the Guddal River facility meets scientific standards, and use of the facility has led to a number of scientifically interesting and relevant results.

Aarhus, 2 June 2017

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Photo: Elin Helland-Hansen



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