ICES WKCULEF REPORT 2016

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Report of the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF)

1–3 March 2016

Charlottenlund, Denmark

ICES
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Executive summary

Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic [WKCULEF], Copenhagen, Denmark, 1–3 March 2016.

Chairs: Ian Russell (UK) and Ole Torrissen (Norway).

Number of meeting participants: 25 representing six countries: Norway (ten), Ireland (four), UK (Scotland) (four), Canada (three), UK (England & Wales) (two) and USA (one). Additional participants also attended from the ICES Secretariat.

WKCULEF met to consider a question posed to ICES by the North Atlantic Salmon Conservation Organisation (NASCO): *Advise on possible effects of salmonid aquaculture on wild Atlantic salmon populations focusing on the effects of sea lice, genetic interactions and the impact on wild salmon production.*

This question was originally included among a suite of questions developed by NASCO, and due to be addressed by the annual meeting of the Working Group on North Atlantic Salmon (WGNAS). However, given that the question was pertinent to other Expert Groups at ICES, particularly the Working Group on Aquaculture (WGAQUA), the Working Group on Pathology and Diseases of Marine Organisms (WGPDMO) and the Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM), it was recommended that the question would be best addressed by means of a Workshop, independent of the Working Groups. WKCULEF enabled experts in aquaculture effects, wild Atlantic salmon, disease transmission and genetic interaction to share and discuss relevant information and recent findings, in order to meet the objectives and timeline of the request.

The terms of reference were addressed though a comprehensive review of the recent peer-reviewed literature. This was facilitated by a range of presentations from participants, by reviewing working documents prepared ahead of the meeting as well as the development of documents and text for the report during the meeting. The report is structured in two main sections, one focusing on the effects of sea lice and the other on genetic interactions. The third issue specified in the question from NASCO, namely the impact of salmon farming on wild salmon production, has been relatively poorly researched and most information derives from attempts to evaluate population level effects related to sea lice infestation and genetic introgression. This information has therefore been reported in the sea lice and genetics sections of the report, respectively.

WKCULEF briefly discussed microbial diseases in aquaculture and the potential impact on wild salmon. However, it was not possible to review this issue in detail and it has not been included in this report.

The key findings of the Workshop were:

Sea lice

- The sea louse (*Lepeophtheirus salmonis*) has widespread geographic distribution, is an important parasite of salmonids and has been a serious problem for the Atlantic salmon farming industry since the 1970s. Sea lice have a greater economic impact on the industry than any other parasite and control of lice levels on farms is of key importance.

- Salmon farming has been shown to increase the abundance of lice in the marine environment and the risk of infection among wild salmonid populations. However, there is considerable uncertainty, and spatial and temporal variability, about the extent of the zones of elevated risk.
- It has been shown in laboratory studies that 0.04–0.15 lice per gramme fish weight can increase stress levels. Laboratory studies have also demonstrated that infections of 0.75 lice per gramme fish weight, or approximately eleven sea lice per fish, can kill a recently emigrated wild salmon smolt of about 15 g if all the sea lice develop into pre-adult and adult stages.
- A number of studies in Norway and Ireland have estimated the relative marine survival of smolts treated to provide lice resistance and control groups. All studies have reported an overall improved return rate for treated salmon, but all showed significant spatial and temporal variability in the magnitude of the treatment effect.
- The survival of Atlantic salmon during their marine phase has fallen in recent decades. This downturn in survival is evident over a broad geographical area and is associated with large-scale oceanographic changes. Viewed against current marine mortality rates commonly at or above 95%, the 'additional' mortality attributable to sea lice has been estimated at around 1%.
- In some studies, the impact of sea lice has also been estimated as losses of returning adult salmon to rivers. These estimates indicate marked variability, with losses in individual experiments ranging from 0.6% to 39%. These results suggest that sea lice induced mortality has an impact on Atlantic salmon returns, which may influence the achievement of conservation requirements for affected stocks.
- Much of the heterogeneity among trials comparing the survival to adulthood of juvenile salmon administered sea lice medicines and control groups could be explained by the release location, time period and baseline (i.e. marine) survival. In a recent meta-analysis of Norwegian data, baseline survival was reported to be the most important predictor variable. When this was low, the effect of treatment was high. In contrast, when baseline survival was high, the effect of treatment was undetectable. However, it is unclear whether baseline survival is affected by sea lice exposure.

Genetic effects

- Each year, large numbers of domesticated salmon escape from commercial fish farms. While many of these are reported, the true number of escapees is likely to be significantly higher. Escapees are observed in rivers in all regions where farming occurs, although the numbers of escapees vary both spatially and temporally. It has been noted that in some rivers in some years, the numbers of escapees have approached 50% or more of the spawning population.
- The spawning success of escaped farmed salmon is much lower than wild salmon. Despite this, genetic studies have demonstrated that farmed salmon have displayed widespread introgression in a large number of Norwegian populations where this has been investigated. Introgression has also been shown in other countries, but the full extent of introgression remains to be investigated.

- Farmed salmon are domesticated and display significant genetic differences to wild salmon in a wide range of fitness-related traits. Whole-river experimental studies have demonstrated that the offspring of farmed and cultured salmon in general, display lower fitness than their wild counterparts in the wild.
- Juvenile escapees and the offspring of farmed salmon compete with wild salmon for territory and food. Therefore, their presence in the natural habitat will reduce the total production of wild fish. Studies have also shown this can result in a decreased overall productivity of the population.
- Where farmed salmon have successfully interbred with natural populations, it is likely that recipient populations will display changes in life-history traits. These changes are likely to be maladaptive for the wild population.
- The long-term consequences of introgression across river stocks can be expected to lead to reduced productivity and decreased resilience to future impacts such as climate change (i.e. less fish and more fragile stocks).
- The evidence from studies in the wild, and the extensive literature relating to salmonids in general, demonstrates that the offspring of farmed salmon display reduced fitness in the wild. However, the results of these studies suggest that the relative success of farmed salmon and, likewise, the relative potential negative effect on a native population, is likely to vary in time and space. Wild populations that are already under evolutionary strain from other challenges such as disease pressure, sea lice infection, over exploitation, habitat destruction and poor water quality are more likely to be sensitive to the potential negative effects of genetic introgression and loss of fitness. Therefore, such effects have to be seen in the context of other challenges.
- While recognising that there were still uncertainties, WKCULEF considered that the evidence relating to the impacts of escapees / genetic introgression provided a clear indication of impacts on wild salmon populations. A substantial reduction of escaped farmed salmon in the wild, or sterilization of farmed salmon, would be required in order to minimize effects on native populations.

In reviewing the latest evidence pertaining to sea lice and genetic interactions, WKCULEF considered where there were gaps in current knowledge and identified areas for further investigation.

1 Introduction

1.1 Workshop rationale and objectives

At its 2015 Statutory Meeting, ICES resolved (C. Res. 2015/2/ACOM10) that the Working Group on North Atlantic Salmon [WGNAS] (chaired by: Jonathan White, Ireland) would meet at ICES, Copenhagen, 30 March–8 April 2016 to consider various questions posed to ICES by the North Atlantic Salmon Conservation Organisation (NASCO). However, one of these questions, relating to the possible effects of salmonid aquaculture on wild Atlantic salmon, has a particularly broad remit and cuts across the work of a number of ICES Groups. In subsequent discussions between the ICES Secretariat and WGNAS participants, it was agreed that responding to this question required the input of experts from a range of disciplines and different Expert Groups within ICES. Given the timing of the annual meetings of these different Expert Groups and the requirement for the advice to be drafted, reviewed and made available by early May 2016, it was decided that an independent workshop needed to be convened to address this question.

ICES subsequently resolved (C. Res. 2015/2/ACOM:42) that the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF), chaired by Ole Torrissen (Norway) and Ian Russell (UK), will meet at ICES, Copenhagen 01–03 March 2016.

WKCULEF was publicised on the ICES website and members of the following relevant ICES Expert Groups were encouraged to send appropriate representation: the Working Group on Aquaculture (WGAQUA), the Working Group on North Atlantic Salmon (WGNAS), the Working Group on Pathology and Diseases of Marine Organisms (WGPDMO) and the Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM). ICES Workshops are open to all interested parties and participants from academic and stakeholder organisations also registered to attend WKCULEF. The level of interest in the Workshop was such that numbers of participants exceeded the space originally set aside for the meeting at ICES. The workshop was therefore relocated to DTU-Aqua, located at Charlottenlund just to the north of Copenhagen.

The terms of reference for WKCULEF are to:

a) Identify the possible effects of salmonid aquaculture on wild Atlantic salmon populations, focusing on the effects of sea lice, genetic interactions and the impact on wild salmon production.

b) Based on the issues identified in (a):

  i) Update the findings of the 2005 ICES/NASCO symposium on the impacts of aquaculture.

  ii) Update the ICES advice provided to OSPAR in 2010 and 2014 (ICES, 2010; 2014).

  iii) Prepare the first draft of the advice to address the NASCO request.

WKCULEF will report by 11 March, 2016 for the attention of the ICES Advisory Committee.

WKCULEF were advised that NASCO plan to hold a Theme-based Special Session on the topic of developments in relation to minimizing the impacts of farmed salmon on wild salmon stocks at their annual meeting in June 2016, and the advice will provide a very useful input to that process. ICES are expected to provide the opening presentation at this event.

The terms of reference for WKCULEF focus on interactions between salmon farming and Atlantic salmon and supporting evidence utilised in this report primarily draws upon the scientific literature pertaining specifically to this species. Salmon farming activities can impact on other salmonid species, in particular sea trout and Arctic char, and there is an extensive literature related to these species. However, the majority of such work has not been incorporated into this report.

In addressing the terms of reference, WKCULEF felt that it was particularly difficult to disentangle the issue of the possible impact of salmon aquaculture on wild salmon production from the sea lice and genetic interaction questions. As a result, information pertaining to population level effects was integrated into both these sections and has not been included as a separate section of the report. WKCULEF sought to highlight where there were gaps in current knowledge and identified areas where further investigation was required.

WKCULEF briefly discussed microbial diseases in aquaculture and the potential impact on wild salmon. However, it was not possible to review this issue in detail and such information has not been included in the report.

In response to the Terms of Reference, the Workshop considered 14 Working Documents / presentations submitted by participants (Annex 1); other references cited in the Report are given in Annex 2. A full address list for the meeting participants is provided in Annex 3.

1.2 Participants

Member	**Country**
Jonathan Carr	Canada
Catherine Collins	UK (Scotland)
Anne Cooper	ICES Secretariat, Denmark
Mark Coulson	UK (Scotland)
Bengt Finstad	Norway
Kevin Glover	Norway
Paddy Gargan	Ireland
Kjetil Hindar	Norway
Dave Jackson	Ireland
Martin Jaffa	UK (England & Wales)
Simon Jones	Canada
Bjørn Olav Kvamme	Norway
Marie Lillehammer	Norway
John Martell	Canada

Philip McGinnity	Ireland
Olav Moberg	Norway
David Morris	UK (Scotland)
Kjell Emil Naas	Norway
Hans Petter Næs	Norway
Michael Pietrak (by Skype)	USA
Ian Russell (chair)	UK (England & Wales)
Terje Svåsand	Norway
Ole Torrissen (chair)	Norway
Eric Verspoor	UK (Scotland)
Jonathan White	Ireland

1.3 Background

The farming of Atlantic salmon has expanded rapidly since the early 1980s. Production of farmed salmon in the North Atlantic is now approximately 1.5 million tonnes (over 2 million tonnes worldwide) and vastly exceeds the nominal catch of wild Atlantic salmon (FishstatJ, FAO, 2013). In 2014, it was estimated that farmed Atlantic salmon production exceeded the nominal wild catch in the North Atlantic by over 1900 times (ICES, 2015).

Interactions between salmon farming and wild stocks have raised concerns, in particular related to disease, parasite, genetic and ecological interactions. Such issues have been subject to extensive research and dialogue as efforts have been made to balance the needs of industry with the requirement to safeguard wild stocks. The topic remains an area of continued intensive research interest. In seeking fresh advice from ICES on the possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic, NASCO have highlighted that this should update previous findings and advice, citing in particular the ICES/NASCO symposium on the impacts of aquaculture held in 2005 and previous ICES advice to OSPAR on aquaculture impacts. The following paragraphs provide a brief overview of these earlier information sources.

ICES/NASCO Symposium, 2005

The ICES/NASCO Symposium (*Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: Science and management, challenges and solutions*) was held in Bergen, Norway in October 2005. This, in turn, aimed to build on two earlier international symposia on the subject. In 1991, an initial symposium was convened by the Norwegian Directorate For Nature Management and NASCO in Loen, Norway (Hansen *et al.*, 1991), and this was followed by an ICES/NASCO symposium in Bath, UK in 1997 (Hutchinson, 1997). This latter symposium helped to inform development of a NASCO resolution aimed at minimising impacts from aquaculture, introductions and transfers, and transgenics on wild salmon stocks (Williamsburg Resolution; NASCO, 2006).

The objectives of the 2005 ICES/NASCO symposium were:

i) to summarise available knowledge of the interactions between aquaculture and wild salmon stocks and other diadromous fish species;

ii) to identify gaps in current understanding of these interactions and to develop recommendations for future research priorities;

iii) to review progress in managing interactions, the remaining challenges, and possible solutions; and

iv) to make recommendations for additional measures to ensure that aquaculture practices are sustainable and consistent with the Precautionary Approach.

A convener's report was prepared (Hansen and Windsor, 2006) with many of the papers included in a special edition of the ICES Journal of Marine Science (Hutchinson, 2006).

The issues covered by the symposium in relation to sea lice included:

- *Gaining a better understanding of the behaviour and ecology of sea lice*. Topics covered: the impact of temperature and salinity on development, behaviour and dispersal of lice; population structure and genetic diversity of sea lice; dispersal patterns / models; evaluation of changes in lice levels relative to the farm production cycle; and the refinement of pest management strategies, including assessing risks to wild populations and possible vaccine development.
- *Evaluation of interactions / impacts*. Topics covered: the effects of lice on the physiology and osmoregulation of fish; infection pressure relative to farm proximity, site and year; the possible development of 'threshold' levels and predictors of mortality to aid management. A particular gap was the lack of information on the effects of lice on wild populations, with the hope that 'new' studies would provide such assessments.
- *Sea lice management*. Topics covered: monitoring programmes; the heavy reliance on a few key medicines and treatments; development of resistance to treatments; alternative controls measures (e.g. wrasse); and the importance of effective integrated pest management strategies.

The issues covered by the symposium in relation to genetic and ecological interactions included:

- *Escapees*. Topics covered: improvements in reporting (both successes and failures) and in understanding the causes of escapes and in management responses; dispersal investigations and variable survival / behaviour with timing of release (and other factors); indications that levels of farmed salmon in cages were a better predictor of escapees rather than reported losses (suggesting possible failure to account for 'trickle' losses / concerns about the reliability of reporting); cage design developments; escape of juveniles from freshwater hatcheries and risks posed by hatchery releases and stocking.
- *Genetic developments and interactions*. Topics covered: genetic selection in farms and 'domestication' of strains; potential for the genetic tracing of the source of escapees; clear evidence of farmed fish contributing to spawning

> in rivers and of changes in genetic composition of wild stocks over time (reduced population differentiation can occur quite quickly); impacts on wild stocks related to numbers of farm-origin spawners; application of models to predict cumulative effects over generations; and meta analysis suggesting reduced productivity of wild populations in proximity of farms.

In an overview, the conveners concluded that the symposium had provided significant advances in understanding in the management of both sea lice and escapees. However, significant challenges remained and risks were not fully understood. They welcomed the recognition from industry representatives that farming can have damaging impacts on wild stocks. This was seen as a clear prerequisite to cooperative action, but needed to to be continued and enhanced if solutions to remaining challenges were to be found. Ongoing data sharing, trust and cooperation between industry, regulators and wild fish interests was seen as essential to developing effective management control strategies.

The conveners noted that numbers of escapees remained large relative to wild stocks, with risk of irreversible damage to the stock structure and diversity of wild salmon and potential consequences for the fitness and productivity of stocks and their ability to adapt to environmental change. As a result, they proposed that interactions needed to be virtually eliminated, not just reduced, and that containment measues needed to be much improved, or production shifted to the use of sterile salmon.

Priorities for further work were seen as improving understanding in:

- The dispersal and spawning success of escapees;
- Impacts on wild populations;
- Genetic techniques for tracing the origin of escapees;
- The potential for using sterile fish / triploids;
- Sea lice treatments and other emerging disease challenges;
- Cage designs and the possible increased risk from storms related to climate change.

ICES advice to OSPAR

In recent years, ICES has been asked to provide advice to OSPAR on interactions between wild and farmed fish (ICES, 2010; 2014). These requests have extended to all finfish mariculture activities, although such activities are dominated by Atlantic salmon production.

In 2010, ICES was asked to provide advice on the current state of knowledge of the interaction of finfish mariculture on the condition of wild fish populations at a local and regional scale, including from parasites, escaped fish and the use of fish feed in mariculture. Advice was also requested on how the interactions will change as a result of an expansion of mariculture activities. ICES collated available information and completed a risk analysis of interactions between mariculture and wild fish populations. The summary of the advice generated noted that the degree of interactions may be ‘moderate’ between finfish mariculture and wild fish populations at the scale of a river local to a salmon farm, but are lower at a broader scale.

In 2014, the request from OSPAR identified a number of potential pressures arising from mariculture on which advice was required:

i) introduction of antibiotics and other pharmaceuticals;

ii) transfer of disease and parasite interactions;

iii) release of nutrients and organic matter;

iv) introgression of foreign genes, from both hatchery-reared fish and genetically modified fish and invertebrates, in wild populations;

v) effects on small cetaceans, such as the bottlenose dolphin, due to their interaction with aquaculture cages;

vi) non-indigenous species.

ICES provided a brief update on the knowledge in each of these areas, commented on potential management solutions to mitigate pressures and outlined monitoring needs. The advice summary was similar to that in 2010 in concluding that most interactions examined in the request are expected to be localized to the vicinity of the mariculture sites. However, the advice noted that although there is reasonable evidence that interactions occur, scientific support for the significance of identified interactions is generally weak. ICES advised that formal risk assessments prior to establishing new mariculture developments may help identify issues and prevent the development of negative interactions. ICES further advised that the inclusion of genetic risks in such assessments is critical and often over-looked.

2 The effects of sea lice on Atlantic salmon

2.1 Introduction

All fish are susceptible to parasitic infections. The sea louse (*Lepeophtheirus salmonis*), also commonly called the salmon louse, has widespread geographic distribution, is an important parasite of salmonids and has been a serious problem for the Atlantic salmon farming industry since the 1970s (Thorstad *et al.*, 2015). Sea lice have a greater economic impact on the industry than any other parasite (ICES, 2010) and control of lice levels on farms is of key importance. The high density of salmon in cages has provided a large number of potential hosts and promoted the transmission and population growth of the parasite (Torrissen *et al.*, 2013). As a result, salmon farming has been shown to increase the abundance of lice in the marine environment. However, knowledge of parasite infection rates and resulting effects in wild populations of fish is relatively poor.

Historically, naturally occurring lice levels on wild salmonids have typically been low - a few (0–10) adult lice per returning salmon and sea trout (Torrissen *et al.*, 2013; Serra-Llinares *et al.*, 2014). Elevated levels of sea lice on wild salmonids collected from coastal areas in the vicinity of salmon farms has been regarded as evidence that mariculture is a main source of the infections and studies have demonstrated a link between fish-farming activity and sea lice infestations on wild salmonids (Helland *et al.*, 2012; 2015; Middlemas *et al.*, 2010; 2013; Serra-Llinares *et al.*, 2014). Thus, the risk of infection among wild salmon populations can be elevated in areas that support salmon mariculture, although louse management activities can reduce the prevalence and intensity of infection on wild fish (Penston and Davies, 2009; Serra-Llinares *et al.*, 2014). There is considerable uncertainty about the extent of the zones of elevated risk of infection and this will be subject to both spatial and temporal variability, for example as a result of changes in local hydrological processes (Amundrud and Murray, 2009; Salama *et al.*, 2013; 2015; Jones *et al.*, 2015; Johnsen *et al.*, 2016).

The extent to which elevated infections of sea lice pose a risk to the health of wild salmon populations has been the subject of extensive research. However, there are many difficulties in quantifying effects at the population level, particularly for fish stocks that are characterised by highly variable survival linked to environmental variables, such as Atlantic salmon (Vollset *et al.*, 2015; Helland *et al.*, 2015). The following sections aim to summarise the current state of knowledge in relation to the impact of sea lice on Atlantic salmon.

2.2 Physiological effects

Several laboratory studies have presented the effect of sea lice on host physiology of Atlantic salmon, sea trout and Arctic charr smolts (reviewed in Finstad and Bjørn, 2011; Thorstad *et al.*, 2015). Major primary (nervous, hormonal), secondary (blood parameters) and tertiary (whole body response) physiological effects, including high levels of plasma cortisol and glucose, reduced osmoregulatory ability and reduced non-specific immunity in the host occur when the lice develop from the sessile chalimus 2 stage to the mobile first pre-adult stage. Sublethal tertiary effects, such as reduced growth, reduced reproduction; reduced swimming performance and impaired immune defence have also been reported (see Finstad and Bjørn, 2011 for references). In addition, differences in genetic susceptibility to sea lice are recognised among host stocks and species.

It has been shown in laboratory studies that 0.04–0.15 lice per gramme fish weight can increase stress levels, reduce swimming ability and create disturbances in water and salt balance in Atlantic salmon. In sea trout, around 50 mobile lice are likely to give direct mortality, and 13 mobile lice, or approximately 0.35 lice per gramme fish weight might cause physiological stress in sea trout (weight range of 19–70 g). Moreover, around 0.05–0.15 lice per gramme fish weight were found to affect growth, condition and reproductive output in sexually maturing Arctic charr (Tveiten *et al.*, 2010).

Laboratory studies have also indicated that infections of 0.75 lice per gramme fish weight, or approximately eleven sea lice per fish, can kill a recently emigrated wild salmon smolt of about 15 g if all the sea lice develop into pre-adult and adult stages (Finstad *et al.*, 2000). Studies of naturally infested wild salmon post-smolts indicate that only those with less than ten lice survived the infection. This is consistent with field studies on sea lice infections in salmon post-smolts in the Norwegian Sea where more than 3000 post-smolts have been examined for lice, but none observed carrying more than ten adult lice. Fish with up to ten mobile lice were observed to be in poor condition with a low haematocrit level and poor growth (Holst *et al.*, 2003). Further support for this threshold comes from an experimental study of naturally infected migrating salmon smolts collected during a monitoring cruise. Half of the fish were deloused as a control, and the health of the two fish groups were monitored in the laboratory. Only fish carrying eleven mobile lice or less survived (Holst *et al.*, 2003). The results have been further verified in the laboratory on wild-caught Atlantic salmon post-smolts infected with sea lice and showing the same level of tolerance for sea lice infections (Karlsen *et al.*, in prep.)

These results have been used in Norway to provide estimates of death rates according to lice densities on migrating salmon smolts as a management tool and have been adopted in the Norwegian risk assessment for fish farming (Taranger *et al.*, 2015). The categories are: 100% mortality in the group >0.3 lice per gramme fish weight, 50% mortality in the group 0.2–0.3 lice per gramme fish weight, 20% mortality in the group 0.1–0.2 lice per gramme fish weight and 0% mortality in the group <0.1 lice per gramme fish weight. Wagner *et al.* (2008) discuss the wider factors that should be taken into account when estimating sea louse threshold levels detrimental to a host.

2.3 Evidence from monitoring programmes

Monitoring programmes have been implemented in a number of countries to assess lice levels to inform management decisions. Given the difficulties of sampling outmigrating wild salmon smolts, sea trout are commonly sampled and in some cases may be used as a proxy for potential levels on salmon (Thorstad *et al.*, 2014).

In Norway, the lice infection on wild salmonid populations is estimated through a national monitoring programme (Serra-Llinares *et al.*, 2014; Taranger *et al.*, 2015). The aim of the sea lice monitoring programme is to evaluate the effectiveness and consequences of zone regulations in national salmon fjords (areas where salmon farming is prohibited), as well as the Norwegian strategy for an environmentally sustainable growth of aquaculture.

Monitoring is carried out during the salmon smolt migration and in summer to estimate lice levels on sea trout and Arctic charr. The fish are collected using traps, fishing nets and surface trawling (Holm *et al.*, 2000; Holst *et al.*, 2003; Heuch *et al.*, 2005; Bjørn *et al.*, 2007). Also, sentinel cages have been used to investigate infestation rates (Bjørn *et al.*, 2011).

The results indicate considerable variation between years and sampling locations in the risk of lice related mortality, based on the Norwegian risk assessment criteria for detrimental lice threshold levels (low: <10%, moderate 10–30% and high: >30%). The risk for sea trout (and also Arctic charr in the Northern regions) is higher compared with Atlantic salmon post-smolts and the results show moderate-to-high risk of lice related mortality on sea trout in most counties with high salmon farming activity.

The estimated risk of lice-related mortality for Atlantic salmon varies between years and sites, and was low at most sites in 2010 and 2013, but moderate and high at several sites in 2011, 2012 and 2014.

In Scotland, analysis of wild sea trout monitored over five successive farm cycles found that lice burdens above critical levels (based on laboratory studies of sea trout) were significantly higher in the second year of the production cycle (Middlemas *et al.*, 2010). In Norway, preliminary analysis of data from fallowing zones indicate that lice levels in farming areas are also correlated with farmed biomass. In years with high biomass lice epidemics are present in some zones, but such epidemics are not seen in years with low biomass (Serra-Llinares *et al.*, submitted).

2.4 Population effects

Population level impacts of sea lice infestation have been estimated in Atlantic salmon post-smolts from a series of long-term studies and analyses in Ireland and Norway involving the paired release of treated and control groups of smolts (Jackson *et al.*, 2011 a and b; Jackson *et al.*, 2013; Gargan *et al.*, 2012; Skilbrei *et al.*, 2013; Krkošek *et al.*, 2013; Vollset *et al.*, 2014; 2015). These studies assumed that the sea louse treatments were efficacious, and that released smolts were exposed to sea lice during the period of the outmigration in which the treatment was effective. Furthermore, the studies were not designed to discriminate between lice from farm and non-farm sources.

Survival estimates have been based on a statistical analysis of differential survival to adults among release groups (Gargan *et al.*, 2012; Jackson *et al.*, 2011 a, b; 2013) including odds ratios (Jackson *et al.*, 2013; Skilbrei *et al.*, 2013; Krkošek *et al.*, 2013; Torrissen *et al.*, 2013; Vollset *et al.*, 2015). An odds ratio is a measure of association between an exposure and an outcome and represents the odds that an outcome will occur given a particular exposure, compared to the odds of the outcome occurring in the absence of that exposure. Thus, in these studies, the odds ratio represented the probability of being recaptured in the treated group divided by the probability of being recaptured in the control group. All studies reported an overall improved return rate for treated vs. control salmon, but all showed significant spatial and temporal variability in the magnitude of the treatment effect.

Gargan *et al.* (2012) reported that the ratio of return rates of treated:control fish in individual trials ranged from 1:1 to 21.6:1, with a median ratio of 1.8:1. Similarly, odds ratios of 1.1:1 to 1.2:1 in favour of treated smolts were reported in Ireland and Norway, respectively (Torrissen *et al.*, 2013). Krkošek *et al.* (2013) reported that treatment had a significant positive effect with an overall odds ratio of 1.29:1 (95% CI: 1.18–1.42). A recent meta-analysis of Norwegian data (Vollset *et al.*, 2015) based on 118 release groups (3989 recaptured out of 657 624 released), reported an overall odds ratio of 1.18:1 (95% CI: 1.07–1.30) in favour of treated fish. Further analysis found that the age of returning salmon was on average higher and weight lower in untreated fish compared with treated fish (Vollset *et al.*, 2014; Skilbrei *et al.*, 2013).

The survival of Atlantic salmon during their marine phase has fallen in recent decades (Chaput, 2012; ICES, 2015). This downturn in survival is evident over a broad geographical area and is associated with large-scale oceanographic changes (Beaugrand and Reid, 2003; Friedland *et al*., 2000; 2005; 2009; 2014). For monitored stocks around the North Atlantic, current estimates of marine survival are at historically low levels with typically fewer than 5% of out-migrating smolts returning to their home rivers for the majority of wild stocks, with lower levels for hatchery-origin fish (ICES 2015). Viewed against marine mortality rates at or above 95%, the 'additional' mortality attributable to sea lice has been estimated at around 1% (Jackson *et al*., 2013).

In some studies, the impacts of sea lice have also been estimated as losses of returning adult fish to rivers. Such estimates indicate marked variability, ranging from 0.6% to 39% in individual trials (Gargan *et al*., 2012; Krkošek *et al*., 2013; Skilbrei *et al*., 2013). These results suggest that sea lice induced mortality has an impact on Atlantic salmon returns which may influence the achievement of conservation requirements for affected stocks (Gargan *et al*., 2012).

Vollset *et al.* (2015) concluded that much of the heterogeneity among trials could be explained by the release location, time period and baseline (i.e. marine) survival. Baseline survival was reported to be the most important predictor variable. When this was low (few recaptures from the control group), the effect of treatment was relatively high (odds ratio of 1.7:1). However, when baseline survival was high, the effect of treatment was undetectable (odds ratio of ~1:1). One explanation for this finding is that the detrimental effect of lice is exacerbated when the fish are subject to other stressors; the findings of other studies support this hypothesis (Finstad *et al*., 2007; Connors *et al*., 2012; Jackson *et al*., 2013; Godwin *et al*., 2015). Vollset *et al.* (2015) concluded that their study supported the hypothesis that sea lice contribute to the mortality of salmon. However, they cautioned that the effect was not consistently present, was strongly modulated by other risk factors and suggested that population-level effects of sea lice on wild salmon stocks cannot be estimated independently of the other factors that affect marine survival.

2.5 Summary

- The sea louse (*Lepeophtheirus salmonis*) has widespread geographic distribution, is an important parasite of salmonids and has been a serious problem for the Atlantic salmon farming industry since the 1970s. Sea lice have a greater economic impact on the industry than any other parasite and control of lice levels on farms is of key importance.
- Salmon farming has been shown to increase the abundance of lice in the marine environment and the risk of infection among wild salmonid populations. However, there is considerable uncertainty, and spatial and temporal variability, about the extent of the zones of elevated risk.
- It has been shown in laboratory studies that 0.04–0.15 lice per gramme fish weight can increase stress levels. Laboratory studies have also demonstrated that infections of 0.75 lice per gramme fish weight, or approximately eleven sea lice per fish, can kill a recently emigrated wild salmon smolt of about 15 g if all the sea lice develop into pre-adult and adult stages.
- A number of studies in Norway and Ireland have estimated the relative marine survival of smolts treated to provide lice resistance and control groups. All studies have reported an overall improved return rate for treated salmon, but all showed significant spatial and temporal variability in the magnitude of the treatment effect.

- The survival of Atlantic salmon during their marine phase has fallen in recent decades. This downturn in survival is evident over a broad geographical area and is associated with large-scale oceanographic changes. Viewed against current marine mortality rates commonly at or above 95%, the 'additional' mortality attributable to sea lice has been estimated at around 1%.
- In some studies, the impact of sea lice has also been estimated as losses of returning adult salmon to rivers. These estimates indicate marked variability, with losses in individual experiments ranging from 0.6% to 39%. These results suggest that sea lice induced mortality has an impact on Atlantic salmon returns, which may influence the achievement of conservation requirements for affected stocks.
- Much of the heterogeneity among trials comparing the survival to adulthood of juvenile salmon administered sea lice medicines and control groups could be explained by the release location, time period and baseline (i.e. marine) survival. In a recent meta-analysis of Norwegian data, baseline survival was reported to be the most important predictor variable. When this was low, the effect of treatment was high. In contrast, when baseline survival was high, the effect of treatment was undetectable. However, it is unclear whether baseline survival is affected by sea lice exposure.

2.6 Knowledge gaps and research priorities

- Factors influencing marine mortality of Atlantic salmon need to be identified and quantified.
- Efficacious salmon lice management procedures need to be further developed for farmed salmon.
- Transmission dynamics of salmon lice between farmed fish and wild salmonids in time and space need to be better understood.
- Long-term effects of sea lice impact on the stability of wild salmon stocks need to be assessed, relative to the number of returning adults, their condition and age.
- Improved methods are needed to assess the risk of sea lice impacts from salmon aquaculture on wild salmon, particularly during their early marine migration.
- The impact of salmon farming on wild salmon production has been relatively poorly researched, and it is timely to increase the knowledge within this area.

3 Escapees, genetic interactions and effects on wild Atlantic salmon

3.1 Numbers of escapees and observations in rivers

Although aquaculture technology and fish-farm safety has significantly increased over the past decade or more, each year, large numbers of Atlantic salmon still escape from aquaculture installations into the wild. While many of these are reported, for example see the statistics from the Norwegian Directorate of Fisheries for reported escapes from Norwegian farms (http://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemmingsstatistikk), in many circumstances, escapes go unnoticed. Therefore, the numbers of escapees are likely to be significantly higher than the reported numbers and, in Norway, the true numbers escaping from farms have been estimated to be 2–5 times higher than the official statistics (Skilbrei *et al.*, 2015). In other salmon producing countries, for example Scotland http://aquaculture.scotland.gov.uk/data/fish_escapes.aspx, eastern Canada and USA http://www.nasco.int/pdf/reports_annual/2015%20Commissions%20Report.pdf the numbers of farmed escapees are also reported. The degree of underreporting in these regions remains unquantified.

Farmed salmon may escape at both the freshwater (Clifford *et al.*, 1998a; Carr and Whoriskey, 2006; Uglem *et al.*, 2013) and marine stages of production (Clifford *et al.*, 1998b; Webb *et al.*, 1991; Carr *et al.*, 1997a). Most known escapes occur from sea cages (Jensen *et al.*, 2010). However, due to differences in rearing practices between countries and regions, the extent of freshwater escapes may differ. In some countries, such as Scotland, it is likely to be higher than, for example, in Norway. In Scotland, in the order of 20 million smolts are produced annually from freshwater pens (Franklin *et al.*, 2012). In Norway, most smolts are produced in land-based tanks from which escape is less likely.

Although the probability of surviving to adulthood and maturing vary between the different life-history stages at which the salmon escape, the great majority of salmon that escape from farms disappear never to be seen again (Skilbrei, 2010a; Skilbrei, 2010b; Hansen, 2006; Whoriskey *et al.*, 2006). Nevertheless, some of the escapees are in or enter into rivers where native salmon populations exist. While not all escapees in rivers are sexually mature (Carr *et al.*, 1997b; Madhun *et al.*, 2015) or indeed in the process of maturing, most are, and these may attempt to spawn with wild salmon (this includes both parr and adults). Farmed escaped salmon have been observed in rivers in all regions where Atlantic salmon farming occurs; Norway (Gausen and Moen, 1991; Fiske *et al.*, 2006), UK (Youngson *et al.*, 1997; Webb *et al.*, 1991; Green *et al.*, 2012), eastern Canada and USA (Morris *et al.*, 2008; Carr *et al.*, 1997a), and Chile (Sepulveda *et al.*, 2013). Furthermore, farmed salmon can migrate great distances post escape (Hansen and Jacobsen, 2003; Jensen *et al.*, 2013), and have been observed in rivers outside farming dense regions for example Iceland (Gudjonsson, 1991). Still, the incidence of farmed escaped salmon in rivers is likely to be correlated with the volume of farming within the region, as determined by a study conducted in Norway (Fiske *et al.*, 2006), and in Scotland (where there are differences between the east and west coasts) (Green *et al.*, 2012).

While the incidence of farmed escaped salmon has been investigated in a number of rivers in Norway in the period 1989 to 2013 (Fiske *et al.*, 2006), a new national monitoring programme for farmed escaped salmon was established in Norway in 2014, and based upon data from angling catches, dedicated autumn angling and diving surveys 30 out of the 140 rivers surveyed displayed a frequency of >10% escapees (http://www.imr.no/publikasjoner/andre_publikasjoner/romt_oppdrettslaks_i_vassdrag/nb-no). These surveys demonstrate that the number of escapees within rivers varies in time and space (Gausen and Moen, 1991; Fiske *et al.*, 2006).

Farmed salmon escapees may attempt to partake in spawning with wild salmon or among themselves. Several studies have reported observations of farmed salmon spawning with wild fish in rivers. This has for example been reported in rivers in Scotland (Webb *et al.*, 1991; Webb *et al.*, 1993; Butler *et al.*, 2005), Norway (Lura and Saegrov, 1991; Saegrov *et al.*, 1997) and Canada (Carr *et al.*, 1997a). However, experiments demonstrate that the spawning success of farmed salmon is significantly reduced (Fleming *et al.*, 1996; Fleming *et al.*, 2000; Weir *et al.*, 2004), perhaps just 1–3% and <30% of the success of wild males and females respectively (Fleming *et al.*, 1996). However, the relative spawning success is likely to also vary with the life-stage at which the fish escaped (Fleming *et al.*, 1997; Weir *et al.*, 2005). Therefore, if a river has for example 10% farmed escapees observed on the spawning grounds, the genetic contribution to the next generation is likely to be significantly lower than 10%.

3.2 Identification of escapees

Farmed salmon escapees are typically identified using external morphological characteristics and growth patterns on fish scales (Fiske *et al.*, 2006; Lund and Hansen, 1991). In Norway, genetic methods to identify farmed escaped salmon back to their farm(s) of origin has been developed and is routinely implemented in cases of unreported escapes (Glover *et al.*, 2008; Glover, 2010). As of 01.01.2016, the method has been used in ~20 cases of unreported escape and has resulted in initiation of legal investigations successfully resulting in fines for companies found in breach of regulations (Glover, 2010). Since 2003, all aquaculture salmon in Maine must be marked before placement into marine net pens so that in the event of an escape the fish can be traced to the farm of origin (NMFS, 2005). Maine's marking programme utilises a genetic pedigree based approach to identify fish. In other countries, no formal active identification programmes are in place. There are ongoing efforts to develop other genetic and non-genetic tagging methods to permit the routine identification of escapees back to their farms of origin.

3.3 Intraspecific hybridisation and introgression

There are still just a few published studies that have addressed genetic changes in wild populations following invasion of escaped farmed salmon. This may be due to the fact that such studies are often challenging. For example, they often require representative samples of the wild populations ideally before and after invasion, and access to representative farmed samples, as well as informative set of molecular genetic markers (Besnier *et al.*, 2011; Karlsson *et al.*, 2011).

The first studies of introgression were conducted in Ireland (Clifford *et al.*, 1998b; Clifford *et al.*, 1998a) and Northern Ireland (Crozier, 1993; Crozier, 2000) demonstrating introgression of farmed salmon in rivers as a response to escapes from local farms. These escapees originated from both cage escapes in salt water, as well as escapes from freshwater smolt rearing facilities located within rivers. Later on, a set of experiments looking at genetic changes in Norwegian populations was conducted. The first of these studies demonstrated temporal genetic changes in three out of seven populations located on the west and middle parts of Norway, and concluded that introgression of farmed salmon was the primary driver (Skaala *et al.*, 2006). Later, a spatio-temporal investigation of 21 populations across Norway revealed significant temporal genetic changes in several rivers caused by introgression of farmed salmon, and importantly, observed an overall reduction in interpopulation genetic diversity (Glover *et al.*, 2012). The latter observation is consistent with predictions of population homogenization as a result of farmed salmon interbreeding (Mork, 1991). Importantly, all rivers that displayed temporal genetic changes due to spawning of farmed escapees, displayed an increase in genetic variation revealed as total number of alleles observed in the population. This is consistent with introgression from fish of a non-local source. The final published study in Norway used recently developed diagnostic genetic markers for identification of farmed and wild salmon (Karlsson *et al.*, 2011) to estimate cumulative introgression of farmed salmon escapees in 20 wild populations (Glover *et al.*, 2013). In this study, cumulative introgression over 2–3 decades was estimated between 0–47% among rivers. Differences in introgression levels between populations was positively linked with the observed proportions of escapees in the rivers, but it was also suggested that the density of the wild population, and therefore level of competition on the spawning grounds and during juvenile stages, also influenced introgression (Glover *et al.*, 2013). A recent study conducted in the Magaguadavic River in eastern Canada demonstrated introgression of farmed escapees with the native population (Bourret *et al.*, 2011).

The most recent and by far the most extensive investigation of introgression of farmed salmon was recently published as a report in Norwegian by researchers from NINA and IMR (http://www.nina.no/english/News/News-article/ArticleId/3984). Here, a total of 125 Norwegian salmon populations were classified using a combination of the estimate of wild genome P(wild) (Karlsson *et al.*, 2014) and the introgression estimates from the study by Glover *et al.* (2013). These authors established four categories of introgression: green = no genetic changes observed; yellow = weak genetic changes indicated but less than 4% farmed salmon introgression; orange = moderate genetic changes documented 4–10% farmed salmon introgression; red = large genetic changes demonstrated >10% farmed salmon introgression. Based upon these analyses, 44, 41, nine and 31 of the populations studied fell into categories green–red respectively. This huge volume of data therefore provides a comprehensive status for many Norwegian populations but is lacking for all other regions.

3.4 Domestication and divergence from wild salmon

From the very start of the Atlantic salmon aquaculture industry in the early 1970s, breeding programmes to select salmon for higher performance in culture were initiated (Gjedrem *et al.*, 1991; Ferguson *et al.*, 2007; Gjoen and Bentsen, 1997). The largest and most significant of these programmes globally are those initiated in Norway which are based upon material originating from >40 Norwegian rivers (Gjedrem *et al.*, 1991). Other programmes in Norway were also established from wild salmon, and in other countries salmon breeding programmes have also been established. Farmed salmon originating from the three main breeding companies in Norway: Marine Harvest - Mowi strain, Aqua Gen AS, and SalmoBreed AS, dominate global production although this varies from country to country. For example, in eastern Canada only the St John River domesticated strain (Friars *et al.*, 1995) is permitted for use in commercial aquaculture, and in Scotland some locally based strains e.g. Landcatch (Powell *et al.*, 2008) are also being used.

Initially, salmon breeding programmes concentrated on increasing growth, but rapidly expanded to include other traits that are also of commercial importance, such as flesh characteristics, age at maturation and disease resistance (Gjedrem, 2000; Gjedrem, 2010). Today, breeding programmes have advanced to 12+ generations, and genome-assisted selection is being utilised in several of the breeding programmes. QTL selected sub-strains are now commercially available displaying characteristics such as reduced sensitivity to specific diseases (Moen *et al.*, 2009) and increased growth. It is likely that full utilisation of genomic selection will increase the diversity of traits that can be accurately targeted by selection for rapid gains in breeding. For example, the recently identified strong influence of the vgll3 locus on age in maturation in salmon (Ayllon *et al.*, 2015; Barson *et al.*, 2015) could represent an effective target to inhibit grilsing (i.e. early maturation) in aquaculture.

As a result of: (1) directional selection for commercially important traits, (2) inadvertent domestication selection (the widespread genetic changes associated with adaptation to the human-controlled environment and its associated reduction in natural selection pressure), (3) non-local origin, and (4) random genetic changes (drift), farmed salmon display a range of genetic differences to wild salmon (Ferguson *et al.*, 2007). Examples of these differences include growth rate under controlled conditions (Glover *et al.*, 2006; Glover *et al.*, 2009; Solberg *et al.*, 2013 a and b; Thodesen *et al.*, 1999), gene transcription patterns (Bicskei *et al.*, 2014; Roberge *et al.*, 2006; Roberge *et al.*, 2008), stress tolerance (Solberg *et al.*, 2013a), and behavioural traits including predator avoidance and dominance (Einum and Fleming, 1997). In addition, farmed salmon strains typically display lower levels of allelic variation when compared to wild salmon strains (Norris *et al.*, 1999; Skaala *et al.*, 2004), although not all classes of genetic marker reveal the same trends (Karlsson *et al.*, 2010). Looking at the level of genetic variation coding for phenotypic traits such as growth, some data are emerging suggesting a possibly reduced variation in farmed strains (Solberg *et al.*, 2013a; Reed *et al.*, 2015). The latter observation is expected given the fact that farmed fish have been selected for this trait since the early 1970s.

3.5 Fitness studies

Thus far, only three published studies have addressed survival of farmed, hybrid and wild salmon in the natural environment. Such studies are exceptionally demanding on logistics, and require experimental periods extending beyond what typical funding sources permit.

The first study was conducted in the River Burrishoole in Ireland, and involved planting eggs of farmed, hybrid and wild parentage into a natural river system (McGinnity *et al.*, 1997). These fish were identified using DNA profiling and followed through a two-generation experiment. The authors concluded that the lifetime fitness of farmed fish was just 2% of wild fish, and that the relative-fitness increased along a gradient towards the offspring of a F1 hybrid survivor spawning together with a wild salmon (= back cross) that displayed a lifetime survival of 89% compared to the offspring of a wild salmon (McGinnity *et al.*, 2003). The authors concluded that repeated invasions of farmed salmon in a wild population may cause the fitness of the native population to seriously decline, and potentially enter an “extinction-vortex” in extreme cases.

In Norway, a slightly different but complimentary experiment was conducted in the River Imsa (Fleming *et al.*, 2000). Here, the authors permitted migrating adult salmon of farmed and wild native origin entry to the River Imsa, once they had been sampled in the upstream trap. They thereafter spawned naturally and their offspring were monitored until adulthood. This study reported a lifetime fitness of farmed salmon (i.e. escaped adult to adult) of 16% compared with wild salmon (Fleming *et al.*, 2000). Important additional data from this study was the fact that productivity of the wild salmon from the river decreased, following the permitted invasion of farmed salmon, both with respect to the total smolt production and when smolt production from native females was considered alone (Fleming *et al.*, 2000). This is because the offspring of the farmed and hybrid salmon competed with wild salmon for both territory and resources, and the dynamics of this may vary across life-history stages (Sundt-Hansen *et al.*, 2015).

The most recently published study to address the relative fitness of farmed and wild Atlantic salmon in a natural environment was conducted in the River Guddal in Norway (Skaala *et al.*, 2012). Here, these authors used a similar design to the Irish study, releasing large numbers of farmed, hybrid and wild salmon eggs into the river and following their survival. The study included planting out eggs across three cohorts, and permitted for the first time, comparisons of family as well as group fitness (farmed hybrid and wild) in freshwater. The study did not use a local wild fish, but salmon from the Norwegian gene bank as a wild fish proxy. While these authors reported reduced genetic fitness of farmed salmon offspring compared to the non-local wild salmon, egg size was closely related to family survival in the river. Therefore, some farmed salmon families with large eggs displayed surprisingly high survival rates in freshwater (higher than some wild families), although when egg size was adjusted for, farmed salmon offspring displayed significantly lower survival in freshwater compared to the wild salmon. To illustrate this, in 15 of 17 pairwise comparisons of maternal half-sib groups, families sired with wild males performed better compared with families sired with farmed fish. The study also revealed that farmed and wild salmon overlapped in diet in the river, an observation also reported from an earlier small-scale planting study (Einum and Fleming, 1997) and from the full-generation study in the River Imsa (Fleming *et al.*, 2000).

Studies cross-examining the underlying details, mechanisms, and genomics of the observed survival differences between farmed and wild salmon in natural habitats have also been published (Besnier *et al.*, 2015; Reed *et al.*, 2015), although the exact mechanisms still remain elusive. For example, attempts at quantifying predation in the wild (Skaala *et al.*, 2014), and predation susceptibility in semi-natural contests (Solberg *et al.*, 2015) have not revealed greater predation of farmed salmon offspring than wild salmon offspring, despite earlier studies suggesting reduced predation awareness caused by domestication (Einum and Fleming, 1997).

Collectively, the results of the whole-river studies outlined above are supported by the widespread literature demonstrating the reduced fitness of hatchery reared salmonids, as part of supplementation programmes, in the wild (Araki *et al.*, 2007; Araki *et al.*, 2009).

3.6 Short-term consequences of introgression for wild salmon populations (i.e. a few salmon generations)

In natural habitats such as rivers, territory and food resources are typically limited, and survival is often controlled by density-dependent factors, and habitats have carrying capacities (Jonsson *et al.*, 1998; Bacon *et al.*, 2015). Studies have demonstrated that the offspring of farmed salmon compete with wild salmon for resources such as food and space (Skaala *et al.*, 2012; Fleming *et al.*, 2000). Therefore, when farmed salmon manage to spawn, and their offspring constitute a component of a given river's juvenile population, the production of juveniles with a pure wild background will be depressed though competition for these resources. In addition, data from controlled studies have indicated that the total productivity of smolts in the river following introgression of farmed salmon can decrease (Fleming *et al.*, 2000; McGinnity *et al.*, 1997).

As discussed in the section above, farmed salmon display a range of genetic differences to wild populations, which includes various life-history and behavioural traits. In controlled experiments with farmed and wild salmon (McGinnity *et al.*, 1997; McGinnity *et al.*, 2003; Fleming *et al.*, 2000; Fraser *et al.*, 2010 a; Skaala *et al.*, 2012) differences in freshwater growth and body shape, timing of hatching and smolt migration, age of smoltification, incidence of male parr maturation, sea age-at-maturity and growth in the marine environment have been observed, with some variation across farmed–wild comparisons (Fraser *et al.*, 2010 b). Therefore, where farmed salmon have introgressed in natural populations, it is likely that recipient populations will display changes in life-history traits in the direction of the farmed strains. Given that life-history traits are likely to be associated with fitness in the wild and local adaptation (Garcia de Leaniz *et al.*, 2007; Taylor, 1991; Fraser *et al.*, 2011; Barson *et al.*, 2015), these changes in life-history characteristics are likely to be associated with a loss of fitness (which will also contribute to an overall reduction in productivity). These changes will be difficult to detect against the background of natural variability in stock abundance and require long-term studies to quantify accurately, and at the present, there is a lack of empirical data demonstrating such changes in effected wild populations.

The short-term consequences for wild populations will scale with the magnitude and frequency of interbreeding events. For example, in rivers where density of wild spawners is low, spawning success of escapees will increase compared with locations where density of wild spawners is high. Similarly, low density of wild juveniles with relaxed competition, will give farm offspring better survival opportunities than they will have in locations with high density of wild juveniles. Thus, when populations are under stress and density of individuals goes down, impact from escapees is expected to increase, which is in agreement with studies on observed introgression rates in salmon (Glover *et al.*, 2012; Heino *et al.*, 2015; Glover *et al.*, 2013), but also supported for example by studies on brown trout supplemented by non-local hatchery fish (Hansen and Mensberg, 2009).

Atlantic salmon river stocks are characterized by widespread structuring into genetically distinct and differentiated populations (Ståhl, 1987; Verspoor *et al.*, 2005). This is conditioned by the evolutionary relationships among populations (Dionne *et al.*, 2008; Perrier *et al.*, 2011; Dillane *et al.*, 2008) and adaptive responses to historical and contemporary to environmental differences (Garcia de Leaniz *et al.*, 2007; Taylor, 1991). A spatio-temporal genetic study of 21 populations in Norway revealed an overall reduction in interpopulation diversity caused by interbreeding of farmed escaped salmon (Glover *et al.*, 2012). It is likely that further introgression of farmed salmon will continue to erode this diversity.

3.7 Long-term consequences of introgression for wild salmon populations (i.e. more than a few generations)

The conservation of genetic variation within and among populations (as outlined in the UN Convention on Biological Diversity, 1992) is important for the resilience of local stocks to human or natural disturbances (Ryman, 1991; Schindler *et al.*, 2010), and in the long term, reduced genetic variability will affect the species' ability to cope with a changing environment (McGinnity *et al.*, 2009; Lande and Shannon, 1996). Therefore, one way gene flow, as occurs through the successful spawning of farmed escapees potentially represents a powerful evolutionary force. It erodes genetic variation among wild populations (Glover *et al.*, 2012), and in the long run, may also erode the genetic variation within populations under certain situations (Tufto and Hindar, 2003) as the recipient wild populations become more similar to the less variable farmed populations.

Although evolutionary theory permits us to outline general trajectories, it remains difficult to predict and demonstrate the evolutionary fate of specific wild populations receiving farmed immigrants. The severity and nature of the effect depends on a number of factors, including the magnitude of the differences between wild and farmed populations (both historical and adaptive differences), the mechanisms underlying genetic differences between wild and farmed salmon, the frequency of intrusions of farmed fish, and the numbers of intruding farmed fish relative to wild spawning population sizes (Hutchings and Fraser, 2008). Furthermore, wild populations that are already under evolutionary strain from other challenges such as disease pressure, sea lice infection, overharvest, habitat destruction and poor water quality, etc. are more likely to be sensitive to the potential negative effects of genetic introgression and loss of fitness. Therefore, genetic introgression has to be seen in the context of other challenges also.

Taken collectively, existing understanding makes it clear that the long-term consequences of introgression across river stocks can be expected to lead to reduced productivity and decreased resilience to future impacts such as climate change (i.e. less fish and more fragile stocks). Therefore, a substantial reduction or even total elimination of escaped farmed salmon in the wild is essential in order to minimize or avoid negative effects on native populations.

3.8 Summary

- Each year, large numbers of domesticated salmon escape from commercial fish farms. While many of these are reported, the true number of escapees is likely to be significantly higher. Escapees are observed in rivers in all regions where farming occurs, although the numbers of escapees vary both spatially and temporally. It has been noted that in some rivers in some years, the numbers of escapees have approached 50% or more of the spawning population.
- The spawning success of escaped farmed salmon is much lower than wild salmon. Despite this, genetic studies have demonstrated that farmed salmon have displayed widespread introgression in a large number of Norwegian populations where this has been investigated. Introgression has also been shown in other countries, but the full extent of introgression remains to be investigated.
- Farmed salmon are domesticated and display significant genetic differences to wild salmon in a wide range of fitness related traits. Whole-river experimental studies have demonstrated that the offspring of farmed and cultured salmon in general, display lower fitness than their wild counterparts in the wild.
- Juvenile escapees and the offspring of farmed salmon compete with wild salmon for territory and food. Therefore, their presence in the natural habi-

tat will reduce the total production of wild fish. Studies have also shown this can result in a decreased overall productivity of the population.

- Where farmed salmon have successfully interbred with natural populations, it is likely that recipient populations will display changes in life-history traits. These changes are likely to be maladaptive for the wild population.
- The long-term consequences of introgression across river stocks can be expected to lead to reduced productivity and decreased resilience to future impacts such as climate change (i.e. less fish and more fragile stocks).
- The evidence from studies in the wild, and the extensive literature relating to salmonids in general, demonstrates that the offspring of farmed salmon display reduced fitness in the wild. However, the results of these studies suggest that the relative success of farmed salmon and, likewise, the relative potential negative effect on a native population, is likely to vary in time and space. Wild populations that are already under evolutionary strain from other challenges such as disease pressure, sea lice infection, over exploitation, habitat destruction and poor water quality are more likely to be sensitive to the potential negative effects of genetic introgression and loss of fitness. Therefore, such effects have to be seen in the context of other challenges.
- While recognising that there were still uncertainties, WKCULEF considered that the evidence relating to the impacts of escapees / genetic introgression provided a clear indication of impacts on wild salmon populations. A substantial reduction of escaped farmed salmon in the wild, or sterilization of farmed salmon, would be required in order to minimize effects on native populations.

3.9 Knowledge gaps and research priorities

- To increase the level of monitoring and dedicated studies looking into the numbers of escapees and their genetic introgression in native populations, especially in knowledge poor regions. This will also include further characterisation of aquaculture strains and development of monitoring tools across countries through international collaboration.
- To increase understanding of the environmental and biological factors that influence levels of farmed salmon introgression and their ecological consequences including productivity.
- To understand the genomic architecture of domestication and the underlying genetic differences between farmed and wild salmon in both the hatchery and natural environments, and how this affects fitness.
- To identify and quantify adaptive genetic changes in wild populations that have been subject to introgression of farmed escaped salmon. This includes quantification of natural selection and fitness.

Annex 1: Working documents submitted to the Workshop on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic, 1–3 March, 2016

WP No.	Authors	Title
1	Glover, K.A., Skaala, Ø., Solberg, M., Skilbrei, O.T., Svåsand, T. and Wennevik, V.	Salmon escapees and status of knowledge.
2	Jackson, D.	Sea Lice - introduction, background and current state of knowledge.
3	Lillehammer, M.	Stochastic simulations of introgression of farmed salmon into wild populations.
4	Finstad, B. and Gargan, P.	Effects of sea lice on Atlantic salmon - from individual- to population effects.
5	Jaffa, M.	Sea lice in context.
6	Hindar, K.	Genetic introgression from farmed to wild salmon.
7	Coulson, M.	Fish-farm escapes to stay or go? Imlications for the River Polla.
8	Karlsbakk, E.	Microbial diseases in aqauculture and impact on wild salmonids.
9	McGinnity, P.	Effects of farm escapees on salmon production.
10	Svasand, T.	Risk asessment - environmental impacts of Norwegan fish farming.
11	Verspoor, E.	Assessment of interbreeding and introgression of farm genes in a small Scottish Atlantic salmon (*Salmo salar*) stock: *ad hoc* samples - *ad hoc* results?
12	Gargan, P.	Sea lice - perspectives on studies in Ireland.
13	Svasand, T.	Sea lice monitoring and modelling in Norway.
14	Kvamme, B.O.	National sea lice monitoring programme.

Annex 2: References cited

Amundrud, T.L. and Murray, A.G. 2009. Modelling sea lice dispersion under varying environmental forcing in a Scottish sea loch. Journal of Fish Diseases, 32: 27–44.

Araki, H., Cooper, B., and Blouin, M. S. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science, 318: 100–103.

Araki, H., Cooper, B., and Blouin, M. S. 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. Biology Letters, 5: 621–624.

Ayllon, F., Kjaerner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M. F., Dahle, G., Taranger, G. L., *et al*. 2015. The vgll3 Locus Controls Age at Maturity in Wild and Domesticated Atlantic Salmon (*Salmo salar* L.) Males. Plos Genetics, 11.

Bacon, P. J., Malcolm, I. A., Fryer, R. J., Glover, R. S., Millar, C. P., and Youngson, A. F. 2015. Can Conservation Stocking Enhance Juvenile Emigrant Production in Wild Atlantic Salmon? Transactions of the American Fisheries Society, 144: 642–654.

Barson, N. J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G. H., Fiske, P., Jacq, C., *et al*. 2015. Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. Nature, 528: 405–408.

Besnier, F., Glover, K. A., and Skaala, Ø. 2011. Investigating genetic change in wild populations: modelling gene flow from farm escapees. Aquaculture Environment Interactions, 2: 75–86.

Besnier, F., Glover, K. A., Lien, S., Kent, M., Hansen, M. M., 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.

Beaugrand, G. and Reid, F.C. 2003. Long term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology 9: 801–817.

Bicskei, B., Bron, J. E., Glover, K. A., and Taggart, J. B. 2014. A comparison of gene transcription profiles of domesticated and wild Atlantic salmon (*Salmo salar* L.) at early life stages, reared under controlled conditions. BMC Genomics, 15:884.

Bjørn, P.A., Finstad, B., Kristoffersen, R., Mckinley, R.S. and Rikardsen, A.H. 2007. Differences in risks and consequences of salmon louse, *Lepeophtheirus salmonis* (Krøyer), infestation on sympatric populations of Atlantic salmon, brown trout, and Arctic charr within northern fjords. ICES Journal of Marine Science, 64, 386–393.

Bjørn, P.A., Sivertsgård, R., Finstad, B., Nilsen, R., Serra-Llinares, R.M. and Kristoffersen, R. 2011. Area protection may reduce salmon louse infection risk to wild salmonids. Aquaculture Environment Interactions, 1: 233–244.

Bourret, V., Bernatchez, L., O'Reilly, P. T., Carr, J. W., and Berg, P. R. 2011. Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. *Heredity*, *106*, 3, 500–510.

Butler, J. R. A., Cunningham, P. D. and Starr, K. 2005. The prevalence of escaped farmed salmon, *Salmo salar* L., in the River Ewe, western Scotland, with notes on their ages, weights and spawning distribution. Fisheries Management and Ecology, 12: 149–159.

Carr, J.W., Anderson, J.M., Whoriskey, F.G. and Dilworth, T. 1997a. The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. ICES Journal of Marine Science, 54: 1064–1073.

Carr, J.W., Lacroix, G.L., Anderson, J.M. and Dilworth, T. 1997b. Movements of non-maturing cultured Atlantic salmon (*Salmo salar*) in a Canadian river. ICES Journal of Marine Science, 54: 1082–1085.

Carr, J.W., and Whoriskey, F.G. 2006. The escape of juvenile farmed Atlantic salmon from hatcheries into freshwater streams in New Brunswick, Canada. ICES Journal of Marine Science, 63: 1263–1268.

Chaput, G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. ICES Journal of Marine Science, 69: 1538–1548.

Clifford, S.L., McGinnity, P. and Ferguson, A. 1998a. Genetic changes in an Atlantic salmon population resulting from escaped juvenile farm salmon. Journal of Fish Biology, 52: 118–127.

Clifford, S.L., McGinnity, P. and Ferguson, A. 1998b. Genetic changes in Atlantic salmon (*Salmo salar*) populations of northwest Irish rivers resulting from escapes of adult farm salmon. Canadian Journal of Fisheries and Aquatic Sciences, 55: 358–363.

Connors, B.M., Braun, D.C., Peterman, R.M. *et al.* 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. Conservation Letters 5, 304–312.

Crozier, W. W. 1993. Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L) in a Northern Irish river. Aquaculture, 113: 19–29.

Crozier, W. W. 2000. Escaped farmed salmon, *Salmo salar* L., in the Glenarm River, Northern Ireland: genetic status of the wild population 7 years on. Fisheries Management and Ecology, 7: 437–446.

Dillane, E., McGinnity, P., Coughlan, J. P., Cross, M. C., de Eyto, E., Kenchington, E., Prodohl, P., *et al*. 2008. Demographics and landscape features determine intra-river population structure in Atlantic salmon (*Salmo salar* L.): the case of the River Moy in Ireland. Molecular Ecology, 17: 4786–4800.

Dionne, M., Caron, F., Dodson, J. J., and Bernatchez, L. 2008. Landscape genetics and hierarchical genetic structure in Atlantic salmon: the interaction of gene flow and local adaptation. Molecular Ecology, 17: 2382–2396.

Einum, S., and Fleming, I. A. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology, 50: 634–651.

FAO. 2013. FishStat J, www.fao.org

Ferguson, A., Fleming, I. A., Hindar, K., Skaala, Ø., McGinnity, P., Cross, T., and Prodohl, P. 2007. Farm escapees. In The Atlantic salmon. Genetics, Conservation and Management, pp. 357–398. Ed. by E. Verspoor, L. Stradmeyer, and J. L. Nielsen. Blackwell, Oxford, UK.

Finstad, B., Bjørn, PA., Grimnes, A., and Hvidsten, N.A. 2000. Laboratory and field investigations of salmon lice [(*Lepeophtheirus salmonis* (Krøyer)] infestation on Atlantic salmon (*Salmo salar* L.) post-smolts. Aquaculture Research, 31: 795–803.

Finstad B., Kroglund F., Strand R., Stefansson S.O., Bjørn P.A., Rosseland B.O., Nilsen T.O. and Salbu B. 2007. Salmon lice or suboptimal water quality - reasons for reduced postsmolt survival? Aquaculture 273, 374–383.

Finstad, B. and Bjørn, P.A. 2011. Present status and implications of salmon lice on wild salmonids in Norwegian coastal zones. In: Salmon Lice: An Integrated Approach to Understanding Parasite Abundance and Distribution. (Jones, S. and Beamish, R. Eds.). Wiley-Blackwell, Oxford, UK, 281–305.

Fiske, P., Lund, R.A., and Hansen, L.P. 2006. Relationships between the frequency of farmed Atlantic salmon, *Salmo salar* L., in wild salmon populations and fish farming activity in Norway, 1989–2004. ICES Journal of Marine Science, 63: 1182–1189.

Fleming, I.A., Jonsson, B., Gross, M.R., and Lamberg, A. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). Journal of Applied Ecology, 33: 893–905.

Fleming, I.A., Lamberg, A., and Jonsson, B. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. Behavioural Ecology, 8: 470–480.

Fleming, I.A., Hindar, K., Mjolnerod, I.B., Jonsson, B., Balstad, T. and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. Proceedings of the Royal Society of London Series B-Biological Sciences, 267: 1517–1523.

Franklin, P., Verspoor, E. and Slaski, R. 2012. Study into the impacts of open pen freshwater aquaculture production on wild fisheries. Report for Marine Scotland by Homarus Ltd., Beaulieu, Hampshire, UK. Final Report P/SFWP/286, 160 pp.

Fraser D.J., Minto, C., Calvert, A.M., Eddington, J.D. and Hutchings, J.A. 2010 a. Potential for domesticated-wild interbreeding to induce maladaptive phenology across multiple populations of wild Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences, 67, 1768–1775.

Fraser, D.J., Houde, A.L.S., Debes, P.V., O'Reilly, P., Eddington, J.D. and Hutchings, J.A. 2010b. Consequences of farmed-wild hybridization across divergent populations and multiple traits in salmon. Ecological Applications, 20, 935–953.

Fraser, D.J., Weir, L.K., Bernatchez, L., Hansen, M.M. and Taylor, E.B. 2011. Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. Heredity, 106: 404–420.

Friars, G. W., Bailey, J. K., and Oflynn, F. M. 1995. Applications of selection for multiple traits in cage-reared Atlantic salmon (*Salmo salar*). Aquaculture, 137: 213–217.

Friedland, K., Hansen, D.L.P., Dunkley, D.A. and MacLean, J.C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. ICES Journal of Marine Science 57: 419–429.

Friedland, K.D., Chaput, G. and Maclean, J.C. 2005. The emerging role of climate in post-smolt growth of Atlantic salmon. ICES Journal of Marine Science 62: 1338–1349.

Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Ó Maoiléidigh, N. and McCarthy, J.L. 2009. The recruitment of Atlantic salmon in Europe. ICES Journal of Marine Science 66: 289–304.

Friedland, K.D., Shank, B.V., Todd, C.D., McGinnity, P. and Nye, J.A. 2014. Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal oscillation. Journal of Marine Systems 133, 77–87.

Garcia de Leaniz, C., Fleming, I. A., Einum, S., Verspoor, E., Jordan, W. C., Consuegra, S., Aubin-Horth, N., *et al.* 2007. A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. Biological Reviews, 82: 173–211.

Gargan, P. G., Forde, G., Hazon, N., F., R. D. J. and Todd, C. D. 2012. Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. Canadian Journal of Fish and Aquatic Sciences, 69: 343–353.

Gausen, D., and Moen, V. 1991. Large-scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. Canadian Journal of Fisheries and Aquatic Sciences, 48: 426–428.

Gjedrem, T., Gjoen, H. M., and Gjerde, B. 1991. Genetic-Origin of Norwegian Farmed Atlantic Salmon. Aquaculture, 98: 41–50.

Gjedrem, T. 2000. Genetic improvement of cold-water fish species. Aquaculture Research, 31: 25–33.

Gjedrem, T. 2010. The first family-based breeding program in aquaculture. Reviews in Aquaculture, 2: 2–15.

Gjoen, H. M., and Bentsen, H. B. 1997. Past, present, and future of genetic improvement in salmon aquaculture. ICES Journal of Marine Science, 54: 1009–1014.

Glover, K.A., Bergh, O., Rudra, H., and Skaala, Ø. 2006. Juvenile growth and susceptibility to *Aeromonas salmonicida* subsp *salmonicida* in Atlantic salmon (*Salmo salar* L.) of farmed, hybrid and wild parentage. Aquaculture, 254: 72–81.

Glover, K.A., Skilbrei, O.T., and Skaala, Ø. 2008. Genetic assignment identifies farm of origin for Atlantic salmon *Salmo salar* escapees in a Norwegian fjord. ICES Journal of Marine Science, 65: 912–920.

Glover, K.A., Ottera, H., Olsen, R.E., Slinde, E., Taranger, G.L., and Skaala, Ø. 2009. A comparison of farmed, wild and hybrid Atlantic salmon (*Salmo salar* L.) reared under farming conditions. Aquaculture, 286: 203–210.

Glover, K.A. 2010. Forensic identification of fish farm escapees: The Norwegian experience. Aquaculture Environment Interactions, 1: 1–10.

Glover, K.A., Quintela, M., Wennevik, V., Besnier, F., Sørvik, A.G.E., and Skaala, Ø. 2012. Three decades of farmed escapees in the wild: A spatio-temporal analysis of population genetic structure throughout Norway. Plos One, 7(8) e43129.

Glover, K.A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M., and Skaala, Ø. 2013. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genetics, 14:4.

Godwin, S.C., Dill, L.M., Reynolds, J.D. and Krkošek, M. 2015. Sea lice, sockeye salmon, and foraging competition: lousy fish are lousy competitors. Canadian Journal of Fisheries and Aquatic Sciences 72, 8.

Green, D. M., Penman, D. J., Migaud, H., Bron, J. E., Taggart, J. B., and McAndrew, B. J. 2012. The Impact of Escaped Farmed Atlantic Salmon (*Salmo salar* L.) on Catch Statistics in Scotland. Plos One, 7.

Gudjonsson, S. 1991. Occurrence of reared salmon in natural salmon rivers in Iceland. Aquaculture, 98: 133–142.

Hansen, L.P., Håstein, T., Naevdal, G., Saunders, R.L., and Thorpe, J.E. (Eds). 1991. Interactions between cultured and wild Atlantic salmon. Proceedings of a symposium hosted by the Directorate for Nature Management and Norwegian Institute for Nature Research, held in the Hotel Alexandria, Loen, Norway, 23–26 April 1990. Aquaculture, 98: 1–324.

Hansen, L. P., and Jacobsen, J. A. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. ICES Journal of Marine Science, 60: 110–119.

Hansen, L.P. 2006. Migration and survival of farmed Atlantic salmon (*Salmo salar* L.) released from two Norwegian fish farms. ICES Journal of Marine Science, 63: 1211–1217.

Hansen, L.P. and Windsor, M. 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. NINA Special Report 34. 74 pp. Trondheim, October, 2006.

Hansen, M.M., and Mensberg, K.L.D. 2009. Admixture analysis of stocked brown trout populations using mapped microsatellite DNA markers: indigenous trout persist in introgressed populations. Biology Letters, 5: 656–659.

Heino, M., Svåsand, T., Wennevik, V., and Glover, K. A. 2015. Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. Aquaculture Environment Interactions, 6: 185–190.

Helland, I.P., Finstad, B., Uglem, I., Diserud, O.H., Foldvik, A., Hanssen, F., Bjørn, P.A., *et al*. 2012. What determines salmon lice infections on wild salmonids? Statistical calculations of data from the national salmon lice surveillance program 2004–2010 (in Norwegian). NINA Report, 891. 51 pp.

Helland, I.P., Uglem, I., Jansen, P.A., Diserud, O, H., Bjørn, P.A. and Finstad, B. 2015. Statistical and ecological challenges of monitoring parasitic sea lice infestations in wild salmonid fish stocks. Aquaculture Environment Interactions, 7: 267–280.

Heuch, P.A., Bjorn, P.A., Finstad, B., Holst, J.C., Asplin, L. and Nilsen, F. 2005. A review of the Norwegian 'National Action Plan against Salmon Lice on Salmonids': The effect on wild salmonids. Aquaculture, 246, 79–92.

Holm, M., Holst J. C. and Hansen L. P. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. ICES Journal of Marine Science, 57, 955–964.

Holst, J.C., Jakobsen, P.J., Nilsen, F., Holm, M., Asplin, L. and Aure, J. 2003. Mortality of seaward-migrating post-smolts of Atlantic salmon due to Salmon lice infection in Norwegian salmon stocks. In: Salmon at the Edge. (Mills, D. Ed). Wiley-Blackwell, Oxford, UK. Pp. 136–137.

Hutchings, J. A., and Fraser, D. J. 2008. The nature of fisheries- and farming-induced evolution. Molecular Ecology, 17: 294–313.

Hutchinson, P. (Ed). 1997. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. ICES Journal of Marine Science, 54: 963–1225.

Hutchinson, P. (Ed). 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. ICES Journal of Marine Science, 63: 1159–1371.

ICES. 2010. Effect of mariculture on populations of wild fish. ICES Advice 2010, Book 1, 195–208.

ICES. 2014. OSPAR request on interactions between wild and captive fish stocks. ICES Advice 2014, Book 1, 1–6.

ICES. 2015. Report of the Working Group on North Atlantic Salmon (WGNAS), 17–26 March 2014, Moncton, Canada. ICES CM 2015/ACOM:09. 330 pp.

Jackson, D., Cotter, D., O'Maoileidigh, N., O'Donohoe, P., White, J., Kane, F., Kelly, S., McDermott, T., McEvoy, S., Drumm, A. and Cullen, A. 2011a. Impact of early infestation with the salmon louse *Lepeophtheirus salmonis* on the subsequent survival of outwardly migrating Atlantic salmon smolts from a number of rivers on Ireland's south and west coast. Aquaculture 319, 37–40.

Jackson, D., Cotter, D., O'Maoileidigh, N., O'Donohoe, P., White, J., Kane, F., Kelly, S., McDermott, T., McEvoy, S., Drumm, A., Cullen, A. and Rogan, G. 2011b. An evaluation of the impact of early infestation with the salmon louse *Lepeophtheirus salmonis* on the subsequent survival of outwardly migrating Atlantic salmon, *Salmo salar* L., smolts. Aquaculture 320, 159–163.

Jackson, D., Cotter, D., Newell, J., McEvoy, S., O'Donohoe, P., Kane, F., McDermott, T., Kelly, S. and Drumm, A. 2013. Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar* L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. Journal of Fish Diseases 36 (3), 273–281.

Jensen, Ø., Dempster, T., Thorstad, E.B., Uglem, I. and Fredheim, A. 2010. Escapes of fishes from Norwegian Sea cage aquaculture: causes, consequences and prevention. Aquaculture Environment Interactions, 1, 71–83.

Jensen, A.J., Karlsson, S., Fiske, P., Hansen, L.P., Hindar, K. and Østborg, G. 2013. Escaped farmed Atlantic salmon in the Arctic Ocean. Aquaculture Environment Interactions, 3, 223–229. Jensen *et al*., 2010.

Johnsen, I.A., Asplin, L.C., Sandvik, A.D. and Serra-Llinares, R.M. 2016. Salmon lice dispersion in a northern Norwegian fjord system and the impact of vertical movements. Aquaculture Environment Interactions, 8, 99–116.

Jones, S.R.M., Bruno, D., Madsen, L., and Peeler, E.J. 2015. Disease management mitigates risk of pathogen transmission from maricultured salmonids. Aquaculture Environment Interactions, 6, 119–134.

Jonsson, N., Jonsson, B., and Hansen, L. P. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. Journal of Animal Ecology, 67: 751–762.

Karlsen, Ø. *et al.* In preparation. The effect of salmon lice infections on wild caught Atlantic salmon (*Salmo salar*) - a laboratory study.

Karlsson, S., Moen, T., and Hindar, K. 2010. Contrasting patterns of gene diversity between microsatellites and mitochondrial SNPs in farm and wild Atlantic salmon. Conservation Genetics, 11: 571–582.

Karlsson, S., Moen, T., Lien, S., Glover, K.A., and Hindar, K. 2011. Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. Molecular Ecology Resources, 11: 247–253.

Karlsson, S., Diserud, O.H., Moen, T. and Hindar, K. 2014. A standardized method for quantifying unidirectional genetic introgression. Ecology and Evolution, 4: 3256–3263.

Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B., and Todd, C.D. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B: Biological Sciences 280: 20122359. (a) http://dx.doi.org/10.1098/rspb.2012.2359.

Lande, R., and Shannon, S. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution, 50: 434–437.

Lund, R. A., and Hansen, L. P. 1991. Identification of wild and reared Atlantic salmon, *Salmo salar* L., using scale characters. Aquaculture and Fisheries Management, 22: 499–508.

Lura, H., and Saegrov, H. 1991. Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. Aquaculture, 98: 151–159.

Madhun, A.S., Karlsbakk, E., Ischsen, C.H., Omdal, L.M., Sørvik, A.G.E., Skaala, Ø., Barlaup, B.T., *et al.* 2015. Potential disease interaction reinforced: double-virus infected escaped farmed Atlantic salmon, *Salmo salar* L., recaptured in a nearby river. Journal of Fish Diseases, 38: 209–219.

McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., *et al.* 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES Journal of Marine Science, 54: 998–1008.

McGinnity, P., Prodohl, P., Ferguson, K., Hynes, R., O'Maoileidigh, N., Baker, N., Cotter, D., *et al*. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London Series B-Biological Sciences, 270: 2443–2450.

McGinnity, P., Jennings, E., DeEyto, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K., *et al*. 2009. Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. Proceedings of the Royal Society B-Biological Sciences, 276: 3601–3610.

Middlemas, S.J., Raffell, J.A., Hay, D.W., Hatton-Ellis, M. and Armstrong, J.D. 2010. Temporal and spatial patterns of sea lice levels on sea trout in western Scotland in relation to fish farm production cycles. Biology Letters 6, 548–551.

Middlemas, S.J., Fryer, R.J., Tulett, D. and Armstrong, J.D. 2013. Relationship between sea lice levels on sea trout and fish farm activity in western Scotland. Fisheries Management and Ecology, 20: 68–74.

Moen, T., Baranski, M., Sonesson, A.K. and Kjøglum, S. 2009. Confirmation and fine-mapping of a major QTL for resistance to infectious pancreatic necrosis in Atlantic salmon (*Salmo salar*): population-level associations between markers and trait. BMC Genomics, 10 (368).

Mork, J. 1991. One-generation effects of farmed fish immigration on the genetic differentiation of wild Atlantic salmon in Norway. Aquaculture, 98: 267–276.

Morris, M. R. J., Fraser, D. J., Heggelin, A. J., Whoriskey, F. G., Carr, J. W., O'Neil, S. F., and Hutchings, J. A. 2008. Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. Canadian Journal of Fisheries and Aquatic Sciences, 65: 2807–2826.

NASCO. 2006. Resolution by the Parties to the Convention for the Conservation of Salmon in the North Atlantic Ocean to Minimize Impacts from Aquaculture, Introductions and Transfers, and Transgenics on the Wild Salmon Stocks, the Williamsburg Resolution (Adopted at the Twentieth Annual Meeting of NASCO in June 2003 and amended at the Twenty-First Annual Meeting of NASCO in June 2004, and at the Twenty-Third Annual Meeting of NASCO in June 2006). North Atlantic Salmon Conservation Organization (NASCO), Edinburgh, Scotland, UK. Council document CNL(06)48. 44 pp.

National Marine Fisheries Service and US Fish and Wildlife Service. 2005. Final Recovery Plan for the Gulf of Maine Distinct Population Segment of Atlantic Salmon (*Salmo salar*). National Marine Fisheries Service, Silver Spring, Maryland. 325 pp.

Norris, A. T., Bradley, D. G., and Cunningham, E. P. 1999. Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. Aquaculture, 180: 247–264.

Penston, M.J. and Davies, I.M. 2009. An assessment of salmon farms and wild salmonids as sources of *Lepeophtheirus salmonis* (Krøyer) copepodids in the water column in Loch Torridon, Scotland. Journal of Fish Diseases, 32: 75–88.

Perrier, C., Guyomard, R., Bagliniere, J. L., and Evanno, G. 2011. Determinants of hierarchical genetic structure in Atlantic salmon populations: environmental factors vs. anthropogenic influences. Molecular Ecology, 20: 4231–4245.

Powell, J., White, I., Guy, D., and Brotherstone, S. 2008. Genetic parameters of production traits in Atlantic salmon (*Salmo salar*). Aquaculture, 274: 225–231.

Reed, T. E., Prodohl, P., Hynes, R., Cross, T., Ferguson, A. and McGinnity, P. 2015. Quantifying heritable variation in fitness-related traits of wild, farmed and hybrid Atlantic salmon families in a wild river environment. Heredity, 115: 173–184.

Roberge, C., Einum, S., Guderley, H., and Bernatchez, L. 2006. Rapid parallel evolutionary changes of gene transcription profiles in farmed Atlantic salmon. Molecular Ecology, 15: 9–20.

Roberge, C., Normandeau, E., Einum, S., Guderley, H. and Bernatchez, L. 2008. Genetic consequences of interbreeding between farmed and wild Atlantic salmon: insights from the transcriptome. Molecular Ecology, 17: 314–324.

Ryman, N. 1991. Conservation genetics considerations in fishery management. Journal of Fish Biology, 39: 211–224.

Saegrov, H., Hindar, K., Kalas, S., and Lura, H. 1997. Escaped farmed Atlantic salmon replace the original salmon stock in the River Vosso, western Norway. ICES Journal of Marine Science, 54: 1166–1172.

Salama, N.K.G., Collins, C.M., Fraser, J.G., Dunn, J., Pert, C.C., Murray, A.G. and Rabe, B. 2013. Development and assessment of a biophysical dispersal model for sea lice. Journal of Fish Diseases, 36, 323–337.

Salama, N.K.G., Murray, A.G. and Rabe, B. 2015. Simulated environmental transport distances of *Lepeophtheirus salmonis* in Loch Linnhe, Scotland, for informing aquaculture area management structures. Journal of Fish Diseases, doi:10.1111/jfd.12375.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., and Webster, M. S. 2010. Population diversity and the portfolio effect in an exploited species. Nature, 465: 609–612.

Sepulveda, M., Arismendi, I., Soto, D., Jara, F., and Farias, F. 2013. Escaped farmed salmon and trout in Chile: incidence, impacts, and the need for an ecosystem view. Aquaculture Environment Interactions, 4: 273–283.

Serra-Llinares, R.M., Bjørn, P.A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M. and Asplin, L. 2014. Salmon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. Aquaculture Environment Interactions, 5, 1–16.

Serra-Llinares, R.M., Bjørn, P.A., Sandvik, A.D., Lindstrom, N.M., Johnsen, I.A., Halttunen, E., Nilsen, R., Finstad, B., Skardhamar, J. and Asplin, L. Submitted. The effectiveness of synchronized fallowing for the control of salmon lice infestations on wild salmonids. Aquaculture Environment Interactions.

Skaala, Ø., Hoyheim, B., Glover, K., and Dahle, G. 2004. Microsatellite analysis in domesticated and wild Atlantic salmon (*Salmo salar* L.): allelic diversity and identification of individuals. Aquaculture, 240: 131–143.

Skaala, Ø., Wennevik, V., and Glover, K.A. 2006. Evidence of temporal genetic change in wild Atlantic salmon, *Salmo salar* L., populations affected by farm escapees. ICES Journal of Marine Science, 63: 1224–1233.

Skaala, Ø., Glover, K.A., Barlaup, B.T., Svåsand, T., Besnier, F., Hansen, Michael, M., and Borgstrøm, R. 2012. Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. Canadian Journal of Fisheries and Aquatic Sciences, 69: 1994–2006.

Skaala, Ø., Glover, K.A., Barlaup, B.T. and Borgstrøm, R. 2014. Microsatellite DNA used for parentage identification of partly digested Atlantic salmon (*Salmo salar*) juveniles through non-destructive diet sampling in salmonids. Marine Biology Research, 10: 323–328.

Skilbrei, O. T. 2010a. Adult recaptures of farmed Atlantic salmon post-smolts allowed to escape during summer. Aquaculture Environment Interactions, 1: 147–153.

Skilbrei, O.T. 2010b. Reduced migratory performance of farmed Atlantic salmon post-smolts from a simulated escape during autumn. Aquaculture Environment Interactions, 1: 117–125.

Skilbrei, O.T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F. and Strand, R. 2013. Impact of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 1997–2009. Journal of Fish Diseases 36: 249–260. doi:10.1111/jfd.12052.

Skilbrei, O.T., Heino, M. and Svåsand, T. 2015. Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages, from farms sites in Norway. ICES Journal of Marine Science, 72: 670–685.

Solberg, M.F., Glover, K.A., Nilsen, F. and Skaala, Ø. 2013a. Does Domestication Cause Changes in Growth Reaction Norms? A Study of Farmed, Wild and Hybrid Atlantic Salmon Families Exposed to Environmental Stress. Plos One, 8 (1) e54469.

Solberg, M.F., Zhang, Z.W., Nilsen, F. and Glover, K.A. 2013b. Growth reaction norms of domesticated, wild and hybrid Atlantic salmon families in response to differing social and physical environments. BMC Evolutionary Biology, 13 (234).

Solberg, M.F., Zhang, Z. and Glover, K.A. 2015. Are farmed salmon more prone to risk than wild salmon? Susceptibility of juvenile farm, hybrid and wild Atlantic salmon *Salmo salar* L. to an artificial predator. Applied Animal Behaviour Science, 162: 67–80.

Ståhl, G. 1987. Genetic population structure of Atlantic salmon. In Population genetics and fishery management, pp. 121–140. Ed. by N. Ryman, and F. Utter. University of Washington press, Seattle.

Sundt-Hansen, L., Huisman, J., Skoglund, H., and Hindar, K. 2015. Farmed Atlantic salmon *Salmo salar* L. parr may reduce early survival of wild fish. Journal of Fish Biology, 86: 1699–1712.

Taranger, G.L., Karlsen, Ø., Bannister, R.J., Glover, K.A., Husa, V., Karlsbakk, E., Kvamme, B.O., Boxaspen, K.K., Bjørn, P.A., Finstad, B., Madhun, A.S., Craig Morton, H. and Svåsand, T. 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES Journal of Marine Science, 72(3): 997–1021.

Taylor, E.B. 1991. A review of local adaptation in salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture, 98: 185–207.

Thodesen, J., Grisdale-Helland, B., Helland, S. J., and Gjerde, B. 1999. Feed intake, growth and feed utilization of offspring from wild and selected Atlantic salmon (*Salmo salar*). Aquaculture, 180: 237–246.

Thorstad, E.B., Todd, C.D., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kålås, S., Uglem, I., Berg, M. and Finstad, B. 2014. Effects of salmon lice on sea trout - a literature review. NINA Report 1044: 1–162.

Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kålås, S., Berg, M. and Finstad, B. 2015. Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta*-a literature review. Aquaculture Environment Interactions, 7: 91–117.

Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Horsberg, T.E. and Jackson, D. 2013. Salmon lice - impact on wild salmonids and salmon aquaculture. Journal of Fish Diseases, 36: 171–194.

Tufto, J. and Hindar, K. 2003. Effective size in management and conservation of subdivided populations. Journal of Theoretical Biology, 222: 273–281.

Tveiten, H., Bjørn, P. A., Johnsen, H. K., Finstad, B. and McKinley, R. S. 2010. Effects of the sea louse *Lepeophtheirus salmonis* on temporal changes in cortisol, sex steroids, growth and reproductive investment in Arctic charr *Salvelinus alpinus*. Journal of Fish Biology, 76: 2318–2341.

Uglem, I., Økland, F., and Rikardsen, A. H. 2013. Early marine survival and movements of escaped Atlantic salmon *Salmo salar* L. juveniles from a land-based smolt farm during autumn. Aquaculture Research, 44: 1824–1834.

Verspoor, E., Beardmore, J.A., Consuegra, S., De Leaniz, C.G., Hindar, K., Jordan, W.C., Koljonen, M.L., *et al*. 2005. Population structure in the Atlantic salmon: insights from 40 years of research into genetic protein variation. Journal of Fish Biology, 67: 3–54.

Vollset, K.W., Barlaup, B.T., Skoglund, H., Normann, E.S., Skilbrei, O.T. 2014. Salmon lice increase the age of returning Atlantic salmon. Biology Letters, 10: 20130896. http://dx.doi.org/10.1098/rsbl.2013.0896.

Vollset, K.W., Krontveit, R. I., Jansen, P., Finstad, B., Barlaup, B.T., Skilbrei, O.T., Krkošek, M., Romunstad, P., Aunsmo, A., Jensen, A.J. and Dahoo, I. 2015. Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish and Fisheries; doi:10.1111/faf.12141.

Wagner, G.N., Fast, M.D. and Johnson, S.C. 2008. Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. Trends in Parasitology, 24(4): 176–183.

Webb, J.H., Hay, D.W., Cunningham, P.D., and Youngson, A.F. 1991. The spawning behaviour of escaped farmed and wild adult Atlantic salmon (*Salmo salar* L) in a Northern Scottish river. Aquaculture, 98: 97–110.

Webb, J.H., Youngson, A.F., Thompson, C.E., Hay, D.W., Donaghy, M.J., and I.S., M. 1993. Spawning of escaped farmed Atlantic salmon, *Salmo salar* L., in western and northern Scottish rivers; egg deposition by females. Aquaculture and Fisheries Management, 24: 557–561.

Weir, L.K., Hutchings, J.A., Fleming, I.A., and Einum, S. 2004. Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, *Salmo salar*. Journal of Animal Ecology, 73: 1069–1079.

Weir, L.K., Hutchings, J.A., Fleming, I.A. and Einum, S. 2005. Spawning behaviour and success of mature male Atlantic salmon (*Salmo salar*) parr of farmed and wild origin. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1153–1160.

Whoriskey, F.G., Brooking, P., Doucette, G., Tinker, S., and Carr, J.W. 2006. Movements and survival of sonically tagged farmed Atlantic salmon released in Cobscook Bay, Maine, USA. ICES Journal of Marine Science, 63: 1218–1223.

Youngson, A. F., Webb, J. H., MacLean, J. C., and Whyte, B. M. 1997. Frequency of occurrence of reared Atlantic salmon in Scottish salmon fisheries. ICES Journal of Marine Science, 54: 1216–1220.

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Annex 4: Technical minutes from the Review Group on Possible effects of salmonid aquaculture

- RGAQUA
- Deadline: 21 April 2016
- Participants: Martin Krkošek, Robin Waples and Einar E. Nielsen (Chair)
- Expert Group: WKCULEF

Review of: Report of the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF).

The review group would like to compliment the workshop participants for a very clear, well-structured, insightful and comprehensive report. In our view only very few points have been missed and we agree with the vast majority of the conclusions presented. We still have a few suggestions for amendment in relation to issues that may be unclear, could be treated in more detail or are missing altogether in the draft report. We hope that our comments/suggestions can help to improve the report and look forward to work with you in relation to completing the final draft advice.

Similar to the report, we have split our comments and suggestions into two sections, relating to sea-lice and genetic interactions respectively. Our main comments are outlined below. However for both sections we think that the link between the main text and the sections on "Knowledge gaps and research priorities" is relatively weak. It is difficult to find a direct justification for the outlined research priorities. We suggest numbering the priorities, and subsequently provide direct appropriate reference to each of them in the main text.

There is a general bias in the published literature and available data with respect to effects on wild salmon populations from salmonid aquaculture (both sea lice and genetics) in countries and areas that have intensive salmon farming industries. This is a consequence of the importance of the parasite to management of farmed salmon and the expected magnitude of interactions. However, it also presents a challenge to understand the scale of sea lice and genetic effects on wild salmon in salmon farming areas relative to areas without salmon farms. Likewise, it is mentioned (page 19)… " the great majority of salmon that escape from farms disappear never to be seen again". That could well be true, especially given how hard it is to track escapees. But just because they are never seen again, does not mean they have no effects on wild populations in regions which are not subject to intense monitoring and/or reported in the scientific literature. Thus, a general recommendation to also investigate effects in geographic regions without intensive aquaculture could be warranted.

Sea lice

The review presents two different interpretations of % mortality caused by sea lice that are reported in the literature, but that give different representations of the effect of sea lice on salmon populations (Jackson *et al.*, 2013; Krkošek *et al.*, 2013). The interpretations seem incompatible, which can be confusing, and more effort is needed to clarify how the interpretations are related and how they differ. In one view (Jackson *et al.*, 2013), the emphasis is placed on the absolute difference in marine mortality between fish treated with parasiticides and those that are not. The example given in the review is a difference of one percent, where mortality in treated groups is 95% compared to 96% in untreated groups. The additional one percent mortality between groups is attributed to sea lice, which is interpreted as a small number compared to the 95% mortality from the treatment groups. The other interpretation of this same example is in terms of the percent loss of recruitment or abundance of adult salmon due to exposure to sea lice. In this interpretation, the same example corresponds to a 20% loss in adult salmon abundance due to sea lice; for every five fish that return as adults in the treated groups (95% mortality), there are four fish that return as adults in the untreated group (96% mortality). In other words, one in five fish are lost to sea lice effects. These differences in interpretation of the same data differ by 20x and reflect the nuances of interpreting survival data. It is therefore important to clarify for non-expert readers how to interpret the results. It is true that natural marine mortality of salmon is high and multiple factors are involved, but it is also true that a small incremental increase in marine mortality due to sea lice (or any other factor) can result in losses of salmon abundance that are relevant for fisheries and conservation management.

The review has an emphasis on the physiological responses to sea lice infection as well as experimental data on lethal infection loads. However, there could be more discussion and explanation of the environmental/biological stressors and ecological processes that mediate the relationship between lice and marine survival of Atlantic salmon. While laboratory estimates of lethal loads and physiological responses are attractive to predict impacts on wild populations, this is likely an over-simplified view because natural ecological processes such as predation and competition are likely to remove infected fish before the lice kill the fish directly. In this view, sublethal effects seen in the lab may increase or decrease mortality in the field (e.g. Pacific salmon) (Peacock *et al.*, 2014), and so laboratory results need to be connected with behavioural changes in the fish that alter predator–prey interactions between the smolts and their predators as well as the smolts and their prey (e.g. migration behaviour) (Birkeland and Jakobsen, 1997). Also, early marine growth is important for smolts to escape predation and also access a more diverse prey field and so it is therefore particularly relevant under resource-limited or parasitized conditions. Finally, there are also abiotic stressors such as pollutants that may affect the effects of sea lice on salmon smolts. These potentially interactive effects of multiple factors are likely to be important for explaining the result from meta-analysis that the effect of sea lice on salmon survival depends on the baseline survival of untreated fish (Vollset *et al.*, 2015). However, in that work, the baseline survival used is that from untreated groups, which is itself likely to be affected by louse abundance, introducing a circularity that leaves the interactive effects between lice and other factors on salmon survival poorly characterized.

There is little mention of recent difficulties in controlling sea lice on salmon farms in some areas. The difficulties are because lice have evolved resistance to the common chemical treatments. This presents a challenge to controlling lice on farms, and therefore is relevant to the wild salmon that migrate through those areas. Alternative methods and technologies are needed to provide more effective and sustainable control of sea lice on salmon farms. Work in this area includes alternative medicines, biocontrol using wrasse, and hydrogen peroxide bath treatments in specialized vessels that service farms.

The literature reviewed mixes results from Pacific salmon together with results from Atlantic salmon (as also done in this review). It is unclear to what extent the mechanisms of lice effects on wild salmon are the same between these two areas. There are key differences between Pacific and Atlantic situations, including differences in the genome of the lice themselves as well as the ecological context of the salmon. In the

Pacific, salmonids are more diverse in their life-history traits, species composition, and abundance. Also, the salmon farming industry is smaller. Thus, the extent to which the results from the Pacific on sea lice effects on wild salmon are transferable to the Atlantic situation should be at least briefly discussed.

Genetic effects

There is little reference to previous attempts to model the persistence of wild salmon populations interbreeding with farmed conspecifics. Early modelling work by Hutchings (1991) predicted that the extinction risk of native genomes is largest when interbreeding occurs and when farmed fish occur frequently and at high densities. The risk is largest in small wild populations, which is related to both demographic and genetic effects. Hindar *et al.* (2006) refined this work by using life-stage specific fitness and narrowing the modelling to realistic scenarios based on experimental data. They found that under high intrusion scenarios the recovery of the wild population is not likely under all circumstances even when interbreeding has been ceased for many decades. Baskett *et al.* (2013) used a model with coupled demographic and genetic dynamics to evaluate how genetic consequences of aquaculture escapes depend on how divergent the captive and wild populations are. They found negative genetic consequences increased with divergence of the captive population, unless strong selection removes escapes before they reproduce. Recent modelling work by Castellani *et al.* (2015) has focused on using individual based eco-genetic models, which are parameterized taking processes such as growth, mortality and maturation as well environmental and genotypic variation into account. This should allow improved power for predicting the outcome of genetic and ecological interactions between wild and farmed salmon.

“3.9 Knowledge gaps.” A key issue that was not discussed involves the timing and pace of escapes. For example, given a fixed number N of escapes over a fixed time period T, is it worse for the wild population if they come in one big pulse, or gradually in small amounts of "leakage"? Hindar *et al.* (2006) concluded that large pulses of escapes are more damaging, while Baskett *et al.* (2013) reached the opposite conclusion; that constant, small-scale leakage created greater fitness losses to the wild population. The different conclusions can be largely explained by different time frames of reference: Hindar *et al.* focused on short-term effects, while Baskett *et al.* evaluated mean effects over long periods of time. However, this topic merits more detailed study. Also, Baskett *et al.* did not explicitly consider overlapping generations. So, more work is needed in order to evaluate results as a function of escapes across generations in species with age structure like Atlantic salmon. This is important to resolve; as it is convenient to ignore low-level leakage because it is very difficult to eliminate or even monitor, but some results at least suggest it can have extremely important effects on wild populations.

Regarding variable estimates of relative spawning success of escapes: Apart from natural variability and sampling error, a logical explanation for the wide range of estimates is that the lower estimates apply to escapes from aquaculture stocks that are the most strongly domesticated. If so, then those interbreeding events likely have more serious per capita consequences than interbreeding events involving less domesticated stocks. This would mean that simply focusing on the rate of interbreeding will not necessarily provide a full picture of the genetic consequences of escapes. For discussion see Basket and Waples (2013).

Regarding the text on page 23 that mentions reduced fitness of hatchery fish used in salmon supplementation, the review paper of Christie *et al*. (2014) on this topic could be cited.

References

Baskett, M. L. and Waples, R. S. 2013. Minimizing unintended fitness consequences of cultured individuals on wild populations: keep them similar or make them different? Conservation Biology 27:83–94.

Baskett, M. L., Burgess, S. C. and Waples, R. S. 2013. Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. Evolutionary Applications **6**:1090–1108.

Birkeland, K. and Jakobsen P. J. 1997. Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. Environmental Biology of Fishes **49**:129–137.

Castellani, M., Heino, M., Gilbey, J., Araki, H., Svåsand, T. and Glover, K. A. 2015. IBSEM: An Individual-Based Atlantic Salmon Population Model. PLoS ONE 10: e0138444.

Christie, M. R., Ford, M. J. and Blouin, M. 2014. On the reproductive success of early-generation hatchery fish in the wild. Evolutionary Applications **7**:883–896.

Hutchings, J. A. 1991. The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. Aquaculture **98**: 119–132.

Jackson, D., Cotter, D., Newell, McEvoy, J. S., O'Donohoe, P., Kane, F. McDermott, T. Kelly, S and Drumm, A. 2013. Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar* L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. Journal of Fish Diseases **36**:273–281.

Krkošek, M., Revie, C., Gargan, P., Skilbrei, O. T., Finstad, B. and Todd, C. D. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B **280**: 2012.2359.

Hindar, K., Fleming, I. A., McGinnity, P., and Diserud, O. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. ICES Journal of Marine Science, **63**: 1234–1247.

Peacock, S., B. Connors, M. Krkošek, J. Irvine, and M. A. Lewis. 2014. Can reduced predation offset negative effects of sea louse parasites on chum salmon? Proceedings of the Royal Society B **281**:2013.2913.

Vollset, K., R. Krontveit, P. Jansen, B. Finstad, B. Barlaup, O. Skilbrei, M. Krkošek, A. Romunstad, A. Aunsmo, A. Jansen, and I. Doohoo. 2015. Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish and Fisheries **7**:91–113.