

10.1.8* NASCO has asked ICES to 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

Advice summary

ICES advises that there is substantial and growing evidence that salmon aquaculture activities can affect wild Atlantic salmon, through the impacts of sea lice as well as and farm escapees. Both factors can reduce the productivity of wild salmon populations and there is marked temporal and spatial variability in the magnitude of reported effects.

Effects of sea lice on wild Atlantic salmon

- The sea louse (*Lepeophtheirus salmonis*) is a parasite of salmonids that has widespread geographic distribution. Salmon farming has been shown to increase the abundance of lice in the marine environment and the risk of infection among wild salmon populations. There is considerable spatial and temporal variability in the extent of affected areas.
- Lice are also a serious problem for the Atlantic salmon farming industry and have been so since the 1970s.
- Laboratory studies show that 0.04–0.15 lice per gram fish weight can increase stress levels and that infections of 0.75 lice per gram fish weight can kill hatchery-reared smolts if all the lice develop into pre-adult and adult stages. This is the equivalent of 11 lice per smolt. This is also supported by field studies.
- Current marine mortality rates for salmon are often at or above 95%, the causes of which are largely unknown.
- There are differing perspectives on the impact of lice. In one perspective, the “additional” marine mortality attributable to lice is estimated at around 1%. In another perspective of the same data, losses are expressed at between 0.6% and 39% reduction in adult returns to rivers. The most important factor causing this variability is the level of total marine mortality. The greatest impact from lice is likely to occur on post smolts during the early period of marine migration.

Effects of escapees and genetic interactions on wild Atlantic salmon

- Farmed salmon are domesticated and display substantial differences to wild salmon in a wide range of fitness-related traits.
- Very large numbers of domesticated salmon escape from fish farms each year. Escapees are observed in rivers in all regions where farming occurs, although the number of escapees varies both spatially and temporally. The numbers of escapees have approached 50% or more of the spawning population in some rivers in some years. There is limited monitoring in rivers away from fish-farming regions.
- The spawning success of escaped farmed salmon is much lower than in wild salmon. Despite this, a large number of Norwegian wild salmon populations exhibit widespread introgression of farmed salmon genomes. Introgression has also been shown in other countries.
- The introgression of farmed salmon reduces the viability of the populations in rivers, caused by maladaptive changes in life history traits.
- The presence of farmed salmon and their offspring in a river has been shown to result in a decreased overall productivity of the wild population through competition for territory and food.
- The long-term consequences of introgression across river stocks can be expected to lead to erosion of genetic diversity and therefore to decreased resilience.

Request

1. With respect to Atlantic salmon in the North Atlantic area:

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1.4 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 production⁴;

Notes:

* This advice is part of ICES 2016 advice on North Atlantic salmon stocks (ICES, 2016b).

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⁴ In response to question 1.4, ICES is requested to review and update the findings of the ICES/NASCO symposium on the impacts of aquaculture and the request for advice from OSPAR in June 2010.

The ICES Secretariat asked NASCO for further clarification via email and received the following from NASCO on 23 September 2015. These clarifications were consequently incorporated into the Terms of Reference for a Workshop to address the request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF; ICES, 2016a).

Clarification 1: *The request is referring to the most recent of the series of international symposia organised by NASCO and ICES in 2005. These symposia focused on both the scientific and management issues concerning interactions between aquaculture and wild salmon and other diadromous fish. The advice sought should focus on the effects of sea lice, genetic interactions and the impact on wild salmon production and not on the management approaches to addressing these. Furthermore, this request relates to impacts of salmonid farming and not other forms of aquaculture such as stocking. NASCO is holding a Theme-based Special Session on the topic of developments in relation to minimising the impacts of farmed salmon on wild salmon stocks and the advice will provide a very useful input to that process.*

Clarification 2: *Updating of the 2014 advice provided to OSPAR would be appreciated; there was no intention to request that ICES review its advice to OSPAR in the sense of assessing its quality but rather that ICES consider the advice already provided and update it as necessary in the light of new information. In the case of the advice to NASCO, the focus should be on the effects of sea lice, genetic interactions and impacts on wild salmon production whereas the advice to OSPAR also covered introduction of antibiotics and other pharmaceuticals; release of nutrients and other organic matter; effects on small cetaceans and introduction of non-indigenous species.*

Basis of the advice

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 current needs of industry with the need to safeguard wild stocks. The topic remains an area of continued intensive research interest.

This request for advice was addressed by a workshop, (Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic, WKCULEF). This enabled experts in aquaculture effects, wild Atlantic salmon, disease transmission, and genetic interactions to share and discuss relevant information and recent findings. WKCULEF was convened in Copenhagen, 1–3 March 2016, and was attended by 25 representatives from five ICES Member Countries.

Methods

The WKCULEF terms of reference were addressed through a comprehensive review of recent peer-reviewed literature, presentations from participants, reviews of working documents prepared ahead of the meeting, as well as the development of documents and text for the report during the meeting. 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. Information pertaining to population level effects was incorporated into the sections dealing with these main issues.

The published literature with respect to the effects of lice and genetic interactions on wild salmon populations from salmonid aquaculture is inevitably focused on countries that have established salmon farming industries. This is a consequence of the importance of both farmed salmon production and wild stocks to national interests. However, relatively little is known about the scale of possible effects of lice and genetic changes on wild salmon in areas without salmon farms in the immediate vicinity.

The terms of reference for WKCULEF focus on interactions between salmon farming and Atlantic salmon. However, salmon farming activities can impact on other salmonid species, in particular sea trout, Arctic char, and species of Pacific salmon, and selected references relating to these species have been included where considered relevant.

Elaboration on the advice

The effects of sea lice on Atlantic salmon

The sea louse (*Lepeophtheirus salmonis*) has a widespread geographic distribution, is a specific parasite of salmonids, and has been a serious problem for the Atlantic salmon farming industry since the 1970s (Thorstad *et al.*, 2015). 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. In recent years, lice have also developed resistance to one or more of the chemicals commonly used to manage lice levels and resistant lice have been reported in all areas of Norway, except Finnmark County in northernmost Norway (Aaen *et al.*, 2015; Besnier *et al.*, 2014). The high density of salmon in cages has provided a high 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 lice on wild salmon collected from coastal areas in the vicinity of salmon farms have been regarded as evidence that mariculture is a main source of the infections and studies have demonstrated a link between fish farming activity and lice infestations on wild salmonids (Helland *et al.*, 2012, 2015; 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 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 characterized 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 summarize the current state of knowledge in relation to the impact of lice on Atlantic salmon. The literature reviewed includes some results from studies on Pacific salmon. This is considered to provide added insight, but needs interpreting with some caution since there are differences between the situation in the Pacific and the Atlantic, including 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; the salmon farming industry is also smaller.

Physiological effects

Several laboratory studies have presented the effect of lice on the 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 (e.g. high levels of plasma cortisol and glucose, reduced osmoregulatory ability, and reduced non-specific immunity) occur when the lice develop from the sessile chalimus second stage to the mobile first pre-adult stage. Reduced growth, reproduction, swimming performance, and impaired immune defence have also been reported (Finstad and Bjørn, 2011). The susceptibility and response to louse infection varies among individuals, populations, and species of salmonid.

It has been shown in laboratory studies that 0.04–0.15 lice per gram fish weight can increase stress levels, reduce swimming ability, and affect the water and salt balance in Atlantic salmon (Finstad *et al.*, 2000). In sea trout, the same authors found around 50 mobile lice are likely to give direct mortality, and 13 mobile lice, or approximately 0.35 lice per gram fish weight might cause physiological stress in sea trout (weight range 19–70 grams). Around 0.05–0.15 lice per gram fish weight were found to affect growth, condition, and reproductive output in sexually maturing Arctic charr (Tveiten *et al.*, 2010).

Finstad *et al.* (2000) also found that infections of 0.75 lice per gram fish weight, or approximately 11 lice per fish, can kill a recently emigrated wild salmon smolt of about 15 gram if all the lice develop into pre-adult and adult stages. This is consistent with field studies on 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 10 adult lice (Holst *et al.*, 2003). Fish with up to 10 mobile lice were observed to be in poor condition with a low haematocrit level and poor growth. These authors also conducted 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 11 mobile lice or less survived. The results have been further verified in the laboratory on wild-caught Atlantic salmon post-smolts infected with lice and showing the same level of tolerance for lice infections (Karlsen *et al.*, in prep.).

These results have been used to provide estimates of death rates according to lice densities on migrating salmon smolts 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 gram fish weight, 50% in the group 0.2–0.3 lice per gram fish weight, 20 % in the group 0.1–0.2 lice per gram fish weight and 0% in the group < 0.1 lice per gram 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.

In practice, numerous biotic and abiotic stressors (e.g. pollutants) and ecological processes are likely to mediate the relationship between lice and the 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 will probably remove infected fish before lice kill the fish directly. Early marine growth is important for smolts to enable them to reduce the risk of predation and to allow access to more diverse prey fields, and reduced growth rates will affect fish under resource-limited or parasitized conditions. Furthermore, studies with Pacific salmon (Peacock *et al.*, 2014) have demonstrated that sub-lethal effects seen in laboratory trials may increase or decrease observed mortality in the field. As such, laboratory results ideally need to be connected with behavioural changes (e.g. migration behaviour; Birkeland and Jakobsen, 1997) in the fish that alter predator–prey interactions between the smolts and their predators as well as the smolts and their prey.

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 may in some cases be used as a proxy for potential levels on salmon (Thorstad *et al.*, 2014).

In Norway, 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 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). Sentinel cages have also been used to investigate infestation rates (Bjørn *et al.*, 2011).

The results of monitoring indicate considerable variation in the risk of lice-related mortality (low: < 10%, moderate 10–30%, and high: > 30%) between years and sampling locations. 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. It was low at most sites in Norway in 2010 and 2013, but moderate or 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 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 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).

As noted previously, research effort on interactions between farmed and wild salmon is concentrated in areas where salmon farming is most prevalent. The same applies to monitoring efforts and little, if any, monitoring is undertaken in many areas more remote from salmon farming areas, representing a potential gap in our knowledge.

Population effects

Population-level impacts of 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.*, 2011a, 2011b; 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 louse treatments were efficacious and that released smolts were exposed to 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. In addition, the baseline marine survival from untreated groups, which is used as a comparator for treated groups, is itself likely to be affected by louse abundance, introducing an element of circularity that leaves the interactive effects between lice and other factors on salmon survival poorly characterized.

Survival estimates have been based on a statistical analysis of differential survival to adults among release groups (Gargan *et al.*, 2012; Jackson *et al.*, 2011a, 2011b, 2013), including odds ratios (Jackson *et al.*, 2013; Skilbrei *et al.*, 2013; Krkošek *et al.*, 2013, 2014; 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 improved return rate for treated versus control salmon, but all showed significant spatial and temporal variability.

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 (3 989 recaptured out of 657 624 released), reported an odds ratio of 1.18:1 (95% CI: 1.07–1.30) in favour of treated fish. Untreated returning salmon were on average older and had a lower weight than 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 outmigrating smolts returning to their home rivers for the majority of wild stocks and with even lower levels for hatchery-origin fish (ICES, 2015).

The scientific literature provides differing perspectives of the mortality attributable to lice (Jackson *et al.*, 2013; Krkošek *et al.*, 2013). 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. In this instance, viewed against marine mortality rates at or above 95% for fish in the wild, the mortality attributable to lice has been estimated at around 1% (i.e. mortality in treated groups is 95% compared to 96% in untreated groups). This “additional” mortality between groups is interpreted as a small number compared to the 95% mortality from the treatment groups.

The other perspective of this same example is in terms of the percent loss of recruitment, or abundance of returning adult salmon, due to exposure to sea lice. In this perspective, 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), four fish return as adults in the untreated group (96% mortality). In other words, one in five fish is lost to sea lice effects. These perspectives are solely differences in interpretation of the same data. Where impacts of lice have been estimated as losses of returns to rivers, these indicate marked variability, ranging from 0.6% to 39% (Gargan *et al.*, 2012; Krkošek *et al.*, 2013; Skilbrei *et al.*, 2013). These results suggest that a small incremental increase in marine mortality due to lice (or any other factor) can result in losses of Atlantic salmon that are relevant for fisheries and conservation management and 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. Total marine survival was reported to be the most important predictor variable. When marine survival was low (few recaptures from the control group), the effect of treatment was relatively high (odds ratio of 1.7:1). However, when marine 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, and the findings of other studies support this hypothesis (Finstad *et al.*, 2007; Connors *et al.*, 2012;

Jackson *et al.*, 2013; Godwin *et al.*, 2015). Potential interactive effects of multiple factors are likely to be important for explaining the result from meta-analysis where the effect of sea lice on salmon survival depends on the baseline survival of untreated fish (Vollset *et al.*, 2015). In conclusion the authors cautioned that though their study supported the hypothesis that lice contribute to the mortality of salmon, the effect was not consistently present and strongly modulated by other risk factors, suggesting that population-level effects of lice on wild salmon stocks cannot be estimated independently of the other factors that affect marine survival.

Escapees, genetic interactions and effects on wild Atlantic salmon

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. Although many of these are reported (e.g. <http://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemningsstatistikk>), in many circumstances, escapes go unnoticed. 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). The numbers of farmed escapees are also reported in Scotland (http://aquaculture.scotland.gov.uk/data/fish_escapes.aspx) and in eastern Canada and the United States (NASCO, 2015), but the degree of underreporting in these regions has not been estimated.

Farmed salmon may escape from both the freshwater (Clifford *et al.*, 1998a; Carr and Whoriskey, 2006; Uglem *et al.*, 2013) and the 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 magnitude 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, 2010b; Hansen, 2006; Whoriskey *et al.*, 2006). Nevertheless, some escapees enter rivers where native salmon populations exist and other fish escape direct to river systems. While not all escapees are sexually mature (Carr *et al.*, 1997b; Madhun *et al.*, 2015), some may attempt to spawn with wild salmon (this can include both precocious 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), United Kingdom (Youngson *et al.*, 1997; Webb *et al.*, 1991; Green *et al.*, 2012), eastern Canada and the United States (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 at a considerable distance from the main concentrations of salmon farming, for example in Iceland (Gudjonsson, 1991). Still, the incidence of farmed escaped salmon in rivers has been correlated with the volume of farming in Norway (Fiske *et al.*, 2006), and in Scotland (where there are differences between the east and west coasts; Green *et al.*, 2012). Relatively little is known about possible levels of spawning by escapees in river systems away from centres of aquaculture production. Numbers of escapees in such areas are typically assumed to be low (ICES, 2015), but can be subject to temporal variation (e.g. higher in rivers at spawning time than evidenced from in-season catches).

The incidence of farmed escaped salmon has been investigated in a number of rivers in Norway (Fiske *et al.*, 2006). A new national monitoring programme for farmed escaped salmon was established in Norway in 2014 based upon data from angling catches, dedicated autumn angling, and diving surveys. The results for 30 of the 140 rivers surveyed exceeded a frequency of 10% escapees (see http://www.imr.no/publikasjoner/andre_publicasjoner/romt_oppdrettslaks_i_vassdrag/nb-no). These studies 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 spawn with wild salmon or among themselves. Observations of farmed salmon spawning with wild fish have been reported in rivers in Scotland (Webb *et al.*, 1991, 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%. One explanation for the wide range of estimates of the relatively low spawning success of escapees is that they originate from aquaculture stocks that have been changed the most by domestication. If so, these interbreeding events likely have more serious consequences

than interbreeding events of a similar magnitude 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 escapees (Baskett and Waples, 2013).

The life stage of the escapees affects potential impact. Escapes of smolts are believed to assume a normal migration pattern, few immature adults return to rivers, maturing fish have a higher tendency to return to nearby rivers (Skilbrei *et al.*, 2015). This is also affected by the time of year relative to migration patterns in the wild. Thus smolts that escape when natural migration is occurring in the spring have a greater tendency to return than those escaping at other times of the year (Skilbrei *et al.*, 2015).

The rate at which escapes occur may also have implications for the possible impact. Hindar *et al.* (2006) concluded that large pulses of escapes are more damaging than small amounts of gradual "leakage". However, 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.* (2006) focused on short-term effects, while Baskett *et al.* (2013) evaluated mean effects over long periods of time. However, this topic merits more detailed study. Baskett *et al.* also did not explicitly consider overlapping generations, and so more work is needed in order to evaluate results as a function of escapes across generations in 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.

Identification of escapees

Farmed salmon escapees are typically identified using external morphological characteristics, including 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 have been developed and are routinely implemented in cases of unreported escapes (Glover *et al.*, 2008; Glover, 2010). By the start of 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 utilizes 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.

Intraspecific hybridization and introgression

Only few published studies have addressed genetic changes in wild populations following the invasion of escaped farmed Atlantic 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 an 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, 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. The first studies in Norway demonstrated temporal genetic changes in three out of seven populations located on the west and middle parts of the country, and concluded that introgression of farmed salmon was the primary driver (Skaala *et al.*, 2006). A more recent 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 breeding with wild fish (Mork, 1991). Importantly, all rivers that displayed temporal genetic changes due to spawning of farmed escapees displayed an increase in genetic variation, revealed as the 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 ranged from 0% to 47% between rivers. Differences in introgression levels between populations were 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 has also demonstrated introgression of farmed escapees with the native population (Bourret *et al.*, 2011).

The most recent and extensive investigations of introgression of farmed salmon were recently published as a report in Norwegian by researchers from NINA and IMR (<http://www.nina.no/english/News/News-article/ArticleId/3984>). 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). The latter authors established four categories of introgression: green = no genetic changes observed; yellow = weak genetic changes indicated – i.e. less than 4% farmed salmon introgression; orange = moderate genetic changes documented – i.e. 4–10% farmed salmon introgression; red = large genetic changes demonstrated – i.e. >10% farmed salmon introgression. Based upon these analyses, 44, 41, 9, and 31 of the populations studied fell into categories green to red, respectively. There are no similar estimates in other countries.

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 have been those initiated in Norway, 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 then expanded to include other traits that are also of commercial importance, such as flesh characteristics, age-at-maturation, and disease resistance (Gjedrem, 2000, 2010). Currently, breeding programmes have advanced to 12+ generations, and genome-assisted selection is being utilized in several of the breeding programmes. Quantitative Trait Loci (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 utilization of genomic selection will increase the number of traits that can be accurately targeted by selection for rapid gains in breeding. For example, the recently identified strong influence of the *vgl13* locus on age-at-maturation in salmon (Ayllon *et al.*, 2015; Barson *et al.*, 2015) could represent an effective target to inhibit grilising (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.*, 2013a, 2013b; Thodesen *et al.*, 1999), gene transcription patterns (Bicskei *et al.*, 2014; Roberge *et al.*, 2006, 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 that suggest 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.

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 unusually long and costly experimental periods.

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 survival from fertilization to adult return (life-time success) of farmed fish was just 2% of wild fish (McGinnity *et al.*, 2003). The relative life-time success increased along a gradient towards the offspring of F1 hybrid survivors spawning together with wild salmon (i.e. back crosses) that displayed life-time success of 89% compared to pure offspring of wild salmon. 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 investigation 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 a river that had no native Atlantic salmon population 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. As there were no local wild fish, salmon from the Norwegian gene-bank were used 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 relatively high survival rates in freshwater (higher than some wild families). When these studies were controlled for egg size, farmed salmon offspring displayed significantly lower survival in freshwater compared to the wild salmon. To illustrate this, in 15 of 17 pair-wise comparisons of maternal half-sib groups, families sired with wild males performed better than 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 release study (Einum and Fleming, 1997) and from the full-generation study in the river Imsa (Fleming *et al.*, 2000).

Studies 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, including those fish used in stocking programmes (Araki *et al.*, 2007, 2009; Christie *et al.*, 2014).

Short-term (few generation) consequences of introgression for wild salmon populations

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 rivers' juvenile population, the production of juveniles with a pure wild background will be depressed through 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 whole-river experiments with farmed and wild salmon (McGinnity *et al.*, 1997, 2003; Fleming *et al.*, 2000; Fraser *et al.*, 2010a; Skaala *et al.*, 2012) differences in freshwater growth and body shape, timing of 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.*, 2010b). 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. At present, there is a lack of empirical data demonstrating such changes in affected wild populations.

The short-term consequences for wild populations is expected to be dependent on the magnitude and frequency of interbreeding events. For example, in rivers where density of wild spawners is low, spawning success of escapees should increase compared with locations where density of wild spawners is high. Similarly, low density of wild juveniles with reduced ability to compete should give farm offspring better survival opportunities than they will have in locations with a high density of wild juveniles. Thus, when populations are under stress and the density of individuals goes down, impact from escapees is expected to increase. These expectations are supported both by modelling (Hutchings, 1991; Hindar *et al.*, 2006; Castellani *et al.*, 2015) and by studies on observed introgression rates in salmon (Glover *et al.*, 2012; Heino *et al.*, 2015; Glover *et al.*, 2013), and also 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 (Dillane *et al.*, 2008; Dionne *et al.*, 2008; Perrier *et al.*, 2011) and adaptive responses to historical and contemporary environmental differences (Taylor, 1991; Garcia de Leaniz *et al.*, 2007). A spatio-temporal genetic study of 21 populations in Norway revealed an overall reduction in inter-population 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.

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

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 (Lande and Shannon, 1996; McGinnity *et al.*, 2009). Therefore, gene flow into wild populations caused by successful spawning of farmed escapees potentially represents a powerful evolutionary force. It erodes genetic variation among these 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 and modelling 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. These include:

- 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 pressure from other challenges such as diseases, 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.

There have been a number of 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 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 not occurred 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 escapees 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. Further field studies would be required to verify (or otherwise) these models.

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 changes (i.e., less fish and more fragile stocks).

Knowledge gaps

This advice provides a review of the current evidence based on the latest available information in the peer-reviewed literature. While these recent findings have advanced our understanding of the interactions between salmonid aquaculture and wild salmon, substantial uncertainties remain and further investigations are recommended.

Knowledge gaps in relation to impacts of lice include:

- Natural mortality. In order to put mortality from lice into context, there is a need to better understand the causes underlying the current approximate 95% natural mortality of wild salmon and their interactions.
- Transfer of lice. In order to understand better the variation in infestation rates in wild salmon, there is a need to further explore the temporal and spatial variability in the mechanisms underlying the transfer of lice from farmed fish to wild salmonids.
- Long-term effects. There have been few studies of long-term effects of lice on wild salmon populations.
- Distance effects. Little is known on impacts in areas further away from salmon farming concentrations (applies also to escapees).

Knowledge gaps in relation to impacts of farm escapees include:

- Scale of introgression. Monitoring should continue in order to characterize changes in introgression through time. In addition, further characterization of aquaculture strains would better inform management decisions.
- Factors affecting introgression. There is uncertainty around the environmental and biological factors that influence levels of farmed salmon introgression.
- Consequences of introgression and escapees. There is limited knowledge of the ecological consequences of introgression and escapees. This particularly includes effects on the productivity of fish populations in rivers.
- Effects of escapes on the genetic structure of wild Atlantic salmon populations. There is a need for a better understanding of the underlying genetic differences between farmed and wild salmon and how these affect fitness.
- Timing and pace of escapes. There is conflicting evidence surrounding the long-term differences in impact between escapes resulting from major events and gradual leakage.

References

- Aaen, S. M., Helgesen, K. O., Bakke, M. J., Kaur, K., and Horsberg, T. E. 2015. Drug resistance in sea lice: a threat to salmonid aquaculture. *Trends in Parasitology*, 31(2): 72–81.
- Amundrud, T. L., and Murray, A. G. 2009. Modelling sea lice dispersion under variable 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 *vglI3* 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.
- 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.
- Beaugrand, G., and Reid, F. C. 2003. Long term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, 9: 801–817.
- 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., Kent, M., Skern-Mauritzen, R., Lien, S., Malde, K., Edvardsen, R., Taylor, S., Ljungfeldt, L., Nilsen, F., and Glover, K. 2014. Human-induced evolution caught in action: SNP-array reveals rapid amphi-atlantic spread of pesticide resistance in the salmon ectoparasite *Lepeophtheirus salmonis*. *BMC Genomics*, 15: 937.
- 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.
- 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.
- 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.
- 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., 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.

- 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.
- 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.
- 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.
- 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.
- 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., Cooper, A. B., Reynolds, J. D., Dill, L. M., Ruggerone, G. T. and Krkošek, M. 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., and Cross, T. F. 2008. Demographics and landscape features determine intrariver 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 software. <http://www.fao.org/fishery/statistics/software/fishstatj/en>.
- 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., and Bjørn, P. A. 2011. Present status and implications of sea lice on wild salmonids in Norwegian coastal zones. *In*: Sea lice: An Integrated Approach to Understanding Parasite Abundance and Distribution. S. Jones and R. Beamish (Eds.). Wiley-Blackwell, Oxford, UK, 281–305.
- Finstad, B., Bjørn, P. A., Grimnes, A., and Hvidsten, N. A. 2000. Laboratory and field investigations of sea 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. Sea lice or suboptimal water quality – reasons for reduced postsmolt survival? *Aquaculture*, 273: 374–383.
- 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., Mjølnerod, 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. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*, 1: 535–586.
- Fraser, D. J., Minto, C., Calvert, A. M., Eddington, J. D., and Hutchings, J. A. 2010a. 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 O'Flynn, 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., Russell, D. J. F., 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 Fisheries 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. 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.
- Gjedrem, T., Gjoen, H. M., and Gjerde, B. 1991. Genetic-Origin of Norwegian Farmed Atlantic Salmon. *Aquaculture*, 98: 41–50.
- 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. 2010. Forensic identification of fish farm escapees: The Norwegian experience. *Aquaculture Environment Interactions*, 1: 1–10.
- 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., Otterø, 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., 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. 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 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, 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 sea lice infections on wild salmonids? Statistical calculations of data from the national sea 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., Bjørn, P. A., Finstad, B., Holst, J. C., Asplin, L., and Nilsen, F. 2005. A review of the Norwegian 'National Action Plan Against Sea lice on Salmonids': The effect on wild salmonids. *Aquaculture*, 246: 79–92.
- 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.
- 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 Sea lice infection in Norwegian salmon stocks. *In* *Salmon at the Edge*. D. Mills (Ed.). Wiley-Blackwell, Oxford, UK., 136–137.
- Hutchings, J. A. 1991. The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. *Aquaculture*, 98: 119–132.
- Hutchings, J. A., and Fraser, D. J. 2008. The nature of fisheries- and farming-induced evolution. *Molecular Ecology*, 17: 294–313.
- ICES. 2010. Effect of mariculture on populations of wild fish. *In* Report of the ICES Advisory Committee, 2010. ICES Advice 2010, Book 1, 195–208.
- ICES. 2015. Report of the Working Group on North Atlantic Salmon (WGNAS), 17–26 March 2014, Moncton, Canada. ICES CM 2015/ACOM:09. 332 pp.
- ICES. 2016a. 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 CM 2016/ACOM:42. 44 pp.
- ICES. 2016b. North Atlantic Salmon Stocks. *In* Report of the ICES Advisory Committee, 2016. ICES Advice 2016, Book 10, Section 10.1.

- Jackson, D., Cotter, D., O'Maoileidigh, N., O'Donohoe, P., White, J., Kane, F., Kelly, S., *et al.* 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., *et al.* 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, 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, 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.
- Johnsen, I. A., Asplin, L. C., Sandvik, A. D., and Serra-Llinares, R. M. 2016. Sea 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 prep). The effect of sea 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. DOI: 10.1098/rspb.2012.2359. <http://dx.doi.org/10.1098/rspb.2012.2359>.
- Krkošek, M., Revie, C. W., Finstad, B., and Todd, C. D. 2014. Comment on Jackson *et al.* '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*, 37(4): 415–417.
- 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.
- 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.
- NMFS. 2005. Final Recovery Plan for the Gulf of Maine Distinct Population Segment of Atlantic Salmon (*Salmo salar*). National Marine Fisheries Service and U.S. Fish and Wildlife Service, Silver Spring, Maryland. 325 pp.
- NASCO. 2015. Report of the Thirty-Second Annual Meetings of the Commissions. Happy Valley-Goose Bay, Canada, 2–5 June 2001.
- 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.
- Peacock, S., Connors, B., Krkošek, M., Irvine, J., and Lewis, M. A. 2014. Can reduced predation offset negative effects of sea louse parasites on chum salmon? *Proceedings of the Royal Society B*, 281: 2013–2913.
- 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. Sea 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., Lindstrøm, N. M., Johnsen, I. A., Halttunen, E., Nilsen, R., *et al.* (submitted). The effectiveness of synchronized following for the control of sea 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, Kevin A., Barlaup, Bjørn 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., *et al.* 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., *et al.* 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., *et al.* 2015. Effects of sea lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta*—a literature review. *Aquaculture Environmental Interactions*, 7: 91–117.
- Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Horsberg, T. E., and Jackson, D. 2013. Sea 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., Okland, 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., and Skilbrei, O. T. 2014. Sea lice increase the age of returning Atlantic salmon. *Biological 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., *et al.* 2015. Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. *Fish and Fisheries*, 7: 91–113; 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 McLaren, I. S. 1993. Spawning of escaped farmed Atlantic salmon, *Salmo salar* L., in western and northern Scottish rivers; egg deposition by females. *Aquaculture Research*, 24(5): 663–670.
- 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.