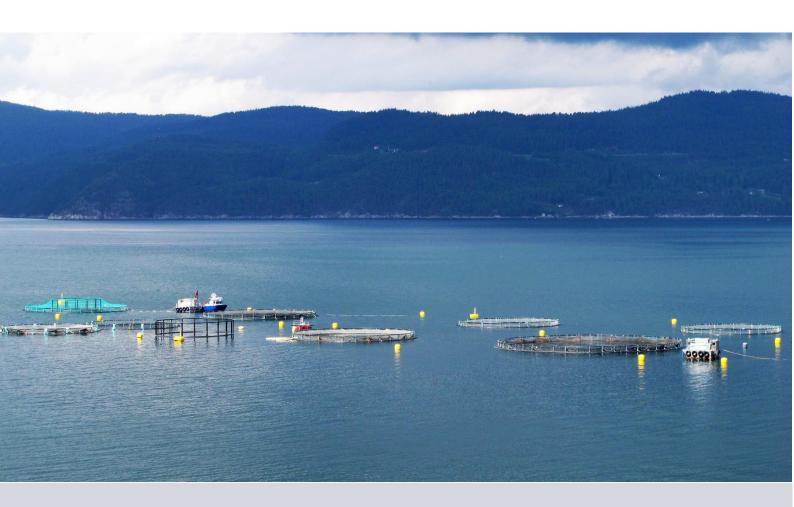
NINA Report

1449 Impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout

Eva B. Thorstad Bengt Finstad





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Impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout

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Abstract

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Results from scientific studies on the impacts of salmon lice on Atlantic salmon and sea trout are summarized here. Considerable evidence exists that that there is a link between farm-intensive areas and the spread of salmon lice to wild Atlantic salmon and sea trout. Several studies have shown that the effects of salmon lice from fish farms on wild salmon and sea trout populations can be severe; ultimately reducing the number of adult fish due to salmon lice induced mortality, resulting in reduced stocks and reduced opportunities for fisheries. Depending on the population size, elevated salmon lice levels can also result in too few spawners to reach conservation limits.

Salmon lice are external parasites on salmon and trout at sea. They feed on fish's mucus, skin and muscle. Mortality due to salmon lice primarily occurs in young fish after they enter the sea from fresh water (11 mobile lice per fish is lethal level for a 15 g wild salmon), but severely infested sea trout can also die from salmon lice later in life. Mortality occurs because salmon lice can cause severely damaged fins and skin lesions, and thereby physiological stress, problems with salt regulation, increased susceptibility to other infections and reduced disease resistance in individual fish. Salmon lice can also cause reduced swimming performance, feeding and growth and altered behaviour of the fish.

Salmon farming increases the spread and abundance of salmon lice in marine habitats, and thereby the risk of infection and mortality among wild salmon and sea trout in areas with fish farms. These facts are both verified by field monitoring of salmon lice on wild fish and by the fact that salmon lice on wild fish in farm-intensive areas have lice with the same resistance to chemicals as used in farms. Wild fish in farm-free areas generally show low lice levels. In farm-intensive areas, lice levels on wild fish are typically higher, but variable. With the expansion of fish farming, marked salmon lice outbreaks on salmonids have been reported from Canada, Ireland, Norway and Scotland.

Studies indicate an annual loss of 50 000 adult wild Atlantic salmon to Norwegian rivers because of salmon lice, which corresponds to an overall loss of 10% of the wild salmon because of salmon lice on a national level (i.e., including both farm-free and farm-intensive areas, based on data from the years 2010-2014). Salmon lice from fish farms are identified as one of the two largest threats to wild salmon in Norway.

Population-level effects of salmon lice in Ireland and Norway have been quantified in large-scale studies in nature by comparing the survival of individually tagged fish chemically protected against salmon lice with untreated control fish. These studies show that lice-induced mortality in farm-intensive areas can lead to an average of 12-29% fewer adult salmon. To exemplify this loss, a 20% reduction due to salmon lice in a river where 4000 Atlantic salmon spawn each year equals a loss of 800 spawners, which means that 3200 salmon spawners will return to the river in a given year instead of 4000. Mortality of sea trout is likely to be higher than in Atlantic salmon, because unlike the ocean-migrating Atlantic salmon, they usually remain in coastal waters, where fish farms are situated.

There are a large number of scientific studies on the impacts of salmon lice on Atlantic salmon and sea trout, ranging from laboratory and field investigations of the effects of salmon lice on individual fish, to analyses of impacts on wild populations. There is year-to-year and local variation in the population effects of salmon lice, and abilities to estimate effects in different areas depend on sufficient resolution of the monitoring of wild fish and salmon lice levels.

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Foreword

Results from scientific studies on the impacts of salmon lice on Atlantic salmon and sea trout have been summarized in several earlier reviews (e.g. Finstad & Bjørn 2011, Finstad et al. 2011). The most recent review summarized the impacts on sea trout (Thorstad et al. 2015). In this report, we summarize the impacts on both Atlantic salmon and sea trout based on earlier reviews and new publications from recent years. The report was commissioned by Salmon and Trout Conservation Scotland.

January 2018

Eva B. Thorstad Bengt Finstad

1 Introduction

This is a summary of the knowledge of impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout. Atlantic salmon and brown trout are in general among the most studied fish species. The impacts of salmon lice on Atlantic salmon and sea trout is also a well-studied topic compared to many other anthropogenic impacts on natural resources (e.g. reviews by Pike & Wadsworth 1999, Todd 2007, Wagner et al. 2008, Costello 2009, Revie et al. 2009, Finstad & Bjørn 2011, Finstad et al. 2011, Torrissen et al. 2013, Thorstad et al. 2015).

Atlantic salmon and sea trout



Atlantic salmon (*Salmo salar*) and sea trout (which is the sea run form of brown trout, *Salmo trutta*) spawn and stay in freshwater as juveniles. After one to eight years in freshwater, when they are about 10-20 cm long, they migrate to sea. When migrating to the sea for the first time, they are termed smolts as long as they are in freshwater and post-smolts as soon as they have entered the sea.

Atlantic salmon. Photo Eva B. Thorstad

Atlantic salmon perform long-distance feeding migrations in the Atlantic Ocean, before returning to the rivers to spawn after one or several years. On their way to ocean feeding areas, they spend up to a few weeks migrating through coastal waters, where fish farms are situated and lice levels may be high. In contrast, sea trout typically remain feeding in coastal waters (usually within 80 km of their home river, although some migrate further). Sea trout spend a variable amount of time at sea, from a few months during summer, to periods lasting a year or more. Some sea trout return to freshwater to spend the winter there, whereas some stay at sea.



Sea trout. Photo Eva B. Thorstad

2 Effects of salmon lice on individual fish in laboratory and field studies

The development of salmon lice and impacts on individual Atlantic salmon and sea trout have been extensively investigated in several laboratory and field studies (see references in Finstad & Bjørn 2011, Finstad et al. 2011, Thorstad et al. 2015, Karlsen et al. 2016, Nilsen et al. 2017a). Similar tissue damage (**fig. 1 and 3**) and responses are found in salmon and trout. Laboratory and field studies show similar results. Sea trout may be more susceptible to acquire lice than Atlantic salmon (Bui et al. 2017).

Laboratory and field studies have shown that salmon lice may induce osmoregulatory dysfunction (i.e. problems with the salt balance), physiological stress responses, anaemia, reduced feeding and growth, increased susceptibility to secondary microbial infections, reduced disease resistance and increased mortality in individual fish (see references in Finstad & Bjørn 2011, Finstad et al. 2011, Thorstad et al. 2015). Mortality starts to occur in the most severely infested fish within 10-20 days of exposure to lice larvae, when the lice have developed into preadult and adult stages.

Atlantic salmon and sea trout experience a challenging environmental shift when they migrate from freshwater to the sea and must adapt to the increased salinity, and problems with the salt balance induced by salmon lice may ultimately lead to mortality. Problems with the salt balance are likely caused by both the mechanical damage of the skin and tissue per se and to the overall physiological stress responses (see references in Thorstad et al. 2015). The damage of the skin, mucus surfaces and dermal tissue caused by salmon lice impairs the physical barrier between the fish body and seawater, and results in increased leakage of water from the fish and thereby osmotic and ionic imbalance.

Salmon lice-infested fish have shown a reduced body mass and condition factor compared to control fish (see references in Finstad & Bjørn 2011, Finstad et al. 2011, Thorstad et al. 2015). This may be due to harmful stress responses, dehydration, and reduced feeding activity. Sublethal levels of salmon lice may also reduce the swimming performance of the fish (Wagner et al. 2003, 2004).



Figure 1. Salmon lice grazing on wild sea trout (upper and lower left) and a resulting cranial lesion (lower right) Salmon lice feed on the mucus, skin and underlying tissue including blood. The mobile preadult and adult stages of salmon lice (fig. 2) cause more severe tissue erosion than earlier stages. Tissue damage by the mobile stages ultimately causes mortality of the most heavily infested fish. Photos: Eva B. Thorstad (upper) and Steinar Kålås (lower)



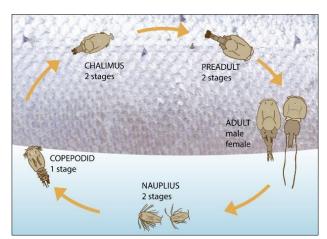


Figure 2. Life cycle of salmon lice

Salmon lice are external parasites on salmonids in the sea (scientific name *Lepeophtheirus salmonis*). They occur naturally on wild fish in the North Atlantic and North Pacific Oceans. Aquaculture activities have not extended the geographic distribution range, but because farmed salmon also act as hosts, open net cage farms have increased the production of larvae in coastal areas. Salmon lice are free-living in the sea during the first life-stages (lower part of the figure), before they attach externally to the host fish (upper part).

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Figure 3. Wild sea trout with dorsal fin damaged from salmon lice

Salmon lice larvae tend to show a preference for gills and fins, especially the dorsal fin. The damage caused by the chalimus larvae is typically rather minor except in dorsal fin areas, where damage may be severe. The mobile preadult and adult lice cause more severe skin damage, especially on the preferred head and dorsal areas, but also in more anterior regions. Photo: Bengt Finstad

3 Lethal levels of salmon lice in individual fish

Lethal levels of salmon lice in Atlantic salmon and sea trout are examined from laboratory studies and used to develop classification systems (Grimnes & Jakobsen 1996, Bjørn & Finstad 1997, Finstad et al. 2000, Finstad & Bjørn 2011, Finstad et al. 2011, Taranger et al. 2015). Eleven attached/mobile salmon lice can cause death of an Atlantic salmon post-smolt of 15 g. Further, 50 attached/mobile lice may cause death of a sea trout post-smolt of 60 g. In sea trout post-smolts (fish body mass 19-70 g), the critical level for a sublethal stress response was found to be 12-13 mobile lice per fish (Wells et al. 2006).

These threshold levels are based on effects in relatively short-term laboratory studies, and values are indicative and not absolute. For instance, density dependent mortality by lice may affect estimates of threshold values, and in some cases lead to overestimates. On the other hand, mortality in the natural environment may be higher than in laboratory studies because of additive effects. The effects of salmon lice have, for example, been shown to be more severe for Atlantic salmon post-smolts impaired also by other influences such as suboptimal water quality (Finstad et al. 2007, 2012). Furthermore, compromised fish may in general experience an elevated mortality risk from predators (e.g. Thorstad et al. 2013).

Lethal levels from laboratory studies are supported from field observations by Holst et al. (2003). They sampled more than 3000 wild salmon post-smolts in the Norwegian Sea, and found none carrying more than 10 adult salmon lice, suggesting a lethal dose around this level.

4 Premature return to freshwater by sea trout due to salmon lice

Premature return of salmon lice-infested sea trout from the sea to freshwater has repeatedly been documented in Ireland, Norway and Scotland (Whelan 1991, Tully & Whelan 1993, Tully et al. 1993ab, Birkeland 1996, Birkeland & Jakobsen 1997, Gargan 2000, Bjørn et al. 2001, Butler & Walker 2006, Hatton-Ellis et al. 2006, Pert et al. 2009, Gjelland et al. 2014, Halttunen et al. 2017). This is interpreted as an adaptive response by the fish to salmon lice-induced problems with salt regulation in seawater (Birkeland 1996, Birkeland & Jakobsen 1997, Bjørn et al. 2001, Wells et al. 2007).

Return to freshwater may in the short term enable the fish to regain osmotic homeostasis and survive. Return to freshwater also allows short-term recovery from salmon lice infestation, because salmon lice have a low tolerance to and survive only for short periods in freshwater. In the long term, however, growth opportunities and future reproduction of individuals may be greatly reduced by a shortened sea migration caused by salmon lice infestation.

5 Links between fish farming and salmon lice levels in wild fish

Salmon lice generally occur in low numbers on wild salmonids in areas lacking fish farming (Tingley et al. 1997, Schram et al. 1998, Heuch et al. 2002, Rikardsen 2004, Bjørn et al. 2007, Urquhart et al. 2010, Bjørn et al. 2011, Gargan et al. 2016b). Salmon lice have historically been observed in low numbers on wild salmonids, and few adverse effects on the host have been reported. However, since the late 1980s, in parallel with the expansion of fish farming, there have been several reports of marked sea lice outbreaks on salmonids in Norway, Canada, Ireland and Scotland (summarized by Revie et al. 2009, Finstad et al. 2011, Thorstad et al. 2015). Salmon lice epizootics are not a common phenomenon for wild salmonids in farm-free areas (Thorstad et al. 2015).

Salmon lice levels on wild fish vary considerably among studies in farm-intensive areas, ranging from lice levels resembling those recorded in farm-free areas to those indicating a risk of significant lice-induced mortality (Finstad et al. 2000, Bjørn et al. 2007, 2011, summarized by Thorstad et al. 2015, Gargan et al. 2017, Nilsen et al. 2017bc). This is to be expected because studies vary considerably in the time of the year of the survey, fish sizes collected, sampling methods and sample sizes. It should also be noted that in field sampling studies, only fish that survived infestation will be caught.



Salmon farm. Photo Eva. B. Thorstad

9



Hatchery-reared Atlantic salmon with preadult salmon lice. Photo: Bengt Finstad

The increased host density in areas with fish farming promotes transmission and population growth in salmon lice (Jansen et al. 2012, Torrissen et al. 2013). In coastal areas with intensive Atlantic salmon farming, the large disparity in abundance between cultured and wild hosts means that larval production of salmon lice must originate primarily from farmed salmon and not from wild fish (Tully & Whelan 1993, Heuch & Mo 2001, Butler 2002, Heuch et al. 2005, Penston & Davies 2009). This is verified in a new study showing that salmon lice on wild fish in farm-intensive areas have lice with the same resistance to chemicals used in farms (Fjørtoft et al. 2017).

A number of field studies in Ireland, Norway and Scotland have demonstrated a link between Atlantic salmon farms and salmon lice levels in wild Atlantic salmon and sea trout, with increased salmon lice levels on wild fish closer to salmon farms (Tully et al. 1999, Gargan 2000, Bjørn et al. 2001, Bjørn & Finstad 2002, Gargan et al. 2003, Bjørn et al. 2007, 2011, Middlemas et al. 2013, Serra-Llinares et al. 2014, Helland et al. 2015, Shephard et al. 2016, Gargan et al. 2017, Nilsen et al. 2017bc). Studies in Ireland, Norway and Scotland have shown elevated salmon lice levels on wild sea trout particularly within 30 km of the nearest farms (Gargan et al. 2003, Middlemas et al. 2013, Serra-Llinares et al. 2014, 2016, Gargan et al. 2017). Elevated salmon lice levels on wild sea trout also may be recorded at distances exceeding 25-30 km (Bjørn & Finstad 2002, Bjørn et al. 2011). Numerical models have shown that salmon lice larvae can be passively dispersed on currents to distances >15 km (Salama et al. 2016) and even >100 km (Asplin et al. 2011, 2014). The results from these studies correspond with others showing increased concentrations of salmon lice larvae in the water column near salmon farms (Gillibrand et al. 2005, Penston et al. 2008ab). Moreover, there is support for a correlation between salmon lice larvae in the water column and the number of gravid salmon lice at the local salmon farms (Penston & Davies 2009).

The correlation between salmon farming and lice production is even more apparent in farmed areas employing synchronized production cycles. Where salmon farms operate on a synchronised 2-year production cycle, biomass of the fish increases with time during the production cycle, and thereby the potential for salmon lice larval production (Butler 2002, Revie et al. 2002b, Gillibrand et al. 2005, Gargan et al. 2016a, Harte et al. 2017). Several studies have shown a relationship between the production cycle in salmon farms and salmon lice levels on wild sea trout, with higher lice levels on trout in the second year of the production cycle (Butler 2002, Marshall 2003, Hatton-Ellis et al. 2006, Middlemas et al. 2010, 2013, Gargan et al. 2016a), which supports a link between aquaculture farms and salmon lice burdens in wild sea trout. This has also been shown as a relationship between density of salmon lice larvae in the water and production year on the west coast of Scotland (Harte et al. 2017).

6 Effects of salmon lice on wild fish populations

There are several types of studies showing effects by salmon lice on wild fish populations. The first indications of population effects by salmon lice were Atlantic salmon and sea trout collapses and declines in several farm-intensive areas in Ireland, Scotland and Norway, which have been attributed to increased salmon lice production from fish farms (Northcott & Walker 1996, Poole et al. 1996, Whelan & Poole 1996, Gargan 2000, Butler 2002, Gargan et al. 2003, Butler & Walker 2006, Gargan et al. 2006ab, Ford & Myers 2008, Vøllestad et al. 2009, Otero et al. 2011, Skaala et al. 2014ab, Vollset et al. 2014, Gargan et al. 2016a). Several of these studies indicate severe effects by salmon lice on wild fish on a population level. However, populations effects of salmon lice from catch statistics data and comparisons between farm-intensive and less farm-intensive or farm-free areas are difficult to quantify because field data on salmon lice have been lacking. Other factors may also contribute to variation between years, rivers and regions in size of spawning stocks.

Indications of population-level effects on Atlantic salmon and sea trout have also been based on monitoring of lice levels on wild fish in nature in relation to threshold levels known to induce physiological compromise and mortality of individual fish (Finstad et al. 1994, 2000, Bjørn et al. 2001, Gargan et al. 2003, Taranger et al. 2015, Gargan et al. 2017). Bjørn et al. (2001) found that 32% of the sea trout post-smolts captured at their study site in northern Norway exhibited relative densities of salmon lice above the level that caused mortality in experimentally infested fish in the laboratory. In a large-scale Irish study, including 4600 sea trout sampled at 15-52 sites, 3.4% of the sea trout in bays without farms had salmon lice levels above a critical threshold of 0.7 chalimi per gram fish mass, whereas in bays with farms, 31% of the sea trout had salmon lice levels above this level (Gargan et al. 2003). Taranger et al. (2015) investigated sea trout at 109 stations along the Norwegian coast for salmon lice infestation, and found that data from 67 stations indicated moderate-to-high mortality of wild sea trout. In a large-scale Scottish study, including nearly 5000 sea trout sampled from 48 different sites along the Scottish west coast and Outer Hebrides during 2003-2009, 13% of the sea trout carried salmon lice levels above the critical threshold of 13 mobile lice per sea trout (Middlemas et al. 2013, applying threshold levels proposed by Wells et al. 2006). Gargan et al. (2017) found that lice loads on sea trout were reduced in recent years compared to the early years of monitoring in farm-intensive areas. These large-scale field studies from Ireland, Norway and Scotland indirectly indicate an elevated risk of salmon liceinduced mortality of sea trout in areas with high salmon lice levels. However, it is not known to what degree threshold levels based on laboratory results are directly applicable to field data, and there are uncertainties in how well the sampled fish represent entire populations, and it is therefore difficult to extrapolate these data to a quantitative estimate of the population effects for sea trout in farm-intensive areas. One problem is that the most severely attacked individuals will die, and therefore never will be sampled in studies like this. Also, some severely infested sea trout may prematurely return to freshwater due to salmon lice infestations, and therefore not be included.

Large-scale experimental studies on salmon lice induced mortality in Atlantic salmon postsmolts have been conducted in nature by comparing individually tagged fish chemically protected from salmon lice with unprotected fish. The purpose is to quantify the impact of salmon lice by releasing parallel groups of smolts treated with anti-parasitic medication and non-treated control groups, recapturing the returning adults, and monitoring survival differences between the groups (Vollset et al. 2016). Higher survival at sea of protected salmon smolts have been found in all these studies, but not in every location or in each year. The estimated average risk ratio of protected fish returning to the rivers to spawn compared to unprotected fish ranged from an average 1.14:1 to 1.41:1 (Jackson et al. 2011a,b, Gargan et al. 2012, Jackson et al. 2013, Krkošek et al. 2013, Skilbrei et al. 2013, Jackson et al. 2014, Krkošek et al. 2014, Vollset et al. 2014). Within any given release group a risk ratio of 1.14-1.41:1 reflects that 12-29% fewer unprotected than protected fish ultimately are recaptured as adults, which is an indication of the effect of salmon lice at these localities at the time the fish were released. A meta-analysis including all the Norwegian studies showed an overall risk ratio of 1.18:1, but the effect varied strongly between groups (Vollset et al. 2016).



Wild Atlantic salmon male in spawning colours. Photo Eva B. Thorstad

The variation in fish survival in the studies described above may reflect both the variation in treatment efficacy and the variation in actual exposure of the released fish to salmon lice (Skilbrei & Wennevik 2006, Gargan et al. 2012). The effect of such treatments is only temporary for the first few weeks of the marine migration, the acquired dose of the active component will vary among individuals, and mortality for treated fish may therefore underestimate the impact of salmon lice. We should, therefore, be cautious in extrapolating data from single studies to a population level. Nonetheless, comprehensive meta-analyses and long-term studies, and similar results from an increasing number of experimental studies, support that 12-29% fewer returning adult spawners can be expected for Atlantic salmon populations because of salmon lice induced mortality in farm-intensive areas. In Ireland, it was even found that the reduction in adult spawners due to salmon lice may be more than 50% in high lice years (based on spawners returning to the Erriff after one year at sea, Shephard & Gargan 2017). They found that there had been a general declining trend in Atlantic salmon returning to the Erriff, likely due to a general decline in marine survival, but that the salmon lice induced reduction came in addition to that.

To exemplify the losses due to salmon lice indicated in the studies referred to above, a 20% reduction due to salmon lice in a river where 4000 Atlantic salmon spawn each year equals a loss of 800 spawners, which means that 3200 salmon spawners will return to the river in a given year instead of 4000. (In the same example, a 10% reduction means a loss of 400 spawners, a 30% reduction means a loss of 1200 spawners and a 50 % reduction means a loss of 2000 spawners.) Hence, impacts on salmon populations due to salmon lice in farm-intensive areas can be severe, ultimately reducing the number of adult fish due to salmon lice induced mortality, resulting in reduced stocks and reduced opportunities for fisheries. Depending on the population size, elevated salmon lice levels can also result in too few spawners to reach conservation limits.

Jackson et al. (2013) reported a level of marine mortality attributable to salmon lice infestation of 1%, and pointed out that this is small in absolute terms and as a proportion of the overall marine mortality and therefore stated that at these levels it is unlikely to influence the conservation status of stocks. However, to understand the consequences of an increased mortality at this level for populations, it is necessary to calculate what this percentage equals in terms of reduced spawning stocks. The return rates of 1SW wild salmon smolts to the Southern North East Atlantic Commission area of NASCO area averaged around 6% during the period 2000 to 2008 (Anon. 2014), when the majority of the experimental releases in the study of Jackson et al. (2013) were undertaken. As pointed out by Thorstad et al. (2014), precisely because natural mortality rates of salmon are high, even a proportionally small additional mortality from salmon lice can amount to a large loss in adult salmon returning. Hence, if the natural survival is 6%, an additional mortality of 1% due to salmon lice as estimated by Jackson et al. (2013), equals a survival of 5% instead of 6%. To put this reduction in return rates into the same context as in the paragraph above, if a return of 4000 salmon to a river represents a 6% return rate, a reduction in the return rate to 5% translates into a reduction of 17% of the adult salmon, or 680 fewer fish returning.

All these results mentioned above have been summarized in ICES (2016), agreed upon and these estimates indicate marked variability with losses in individual experiments ranging from 0.6% to 39%. The 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 (ICES 2016).

In Norway, the Norwegian Scientific Advisory Committee for Atlantic Salmon has estimated the likely effect of salmon lice on the population level in an analysis that - for the first time - covered the entire country, including both farm-free and farm-intensive areas (Anon. 2017). The annual loss of wild salmon to Norwegian rivers due to salmon lice was estimated at 50 000 adult salmon for the years 2010-2014. This corresponds to an annual loss of 10% of wild salmon due to salmon lice, on a national level (i.e., 10% of the total pre-fishery abundance). Salmon lice from fish farms are identified as one of the two largest threats to wild Atlantic salmon in Norway (Forseth et al. 2017).

Atlantic salmon post-smolts migrate through farm-intensive areas in near-coastal areas on their way to ocean feeding grounds (Thorstad et al. 2011, 2012, Halttunen et al. 2018). The results from studies of Atlantic salmon should therefore be regarded as minimum estimates for sea trout mortality (Thorstad et al. 2015). Sea trout normally remain for extended periods (weeks, months or sometimes even a year or more) in near coastal areas. If those coastal areas are characterised by high salmon lice levels, sea trout post smolts are likely to be more affected by salmon lice than Atlantic salmon. Since sea trout remain in coastal areas later in the spring and summer than Atlantic salmon, they are also exposed to seasonally higher risks of salmon lice infestation.

In addition to reduced growth and increased mortality, studies in Ireland, Norway and Scotland have shown that salmon lice infestations may alter fish sizes and life history traits in both Atlantic salmon and sea trout (Skilbrei et al. 2013, Vollset et al. 2014, Thorstad et al. 2015, Gargan et al. 2016a, Shephard et al. 2016). In sea trout, reduced growth and increased mortality will reduce the benefits of marine migrations, and may also result in selection against anadromy in areas with high lice levels, and possibly to the local loss of sea trout and establishment of exclusively freshwater resident populations (Thorstad et al. 2015).

7 A model-based prediction system for salmon lice infestation pressure

The number of lice eggs spread from fish farms and hatched into the water masses, the pelagic life stages of nauplii and copepodites and the high spatiotemporal variability of ocean currents all have a major influence on the local lice infestation pressure on salmonids (Sandvik et al. 2016). A model-based prediction of salmon lice infestation pressure matches well the field observation of lice in sentinel cages, as presented in Sandvik et al. (2016). Models have been developed to quantify lice induced mortality in Norwegian fjords by taking into account timing of smolt migration, duration of postsmolts in fjords, lice pressure in fjords and as a sum the total modelled lice induced mortality due to these factors (Taranger et al. 2015, Vollset et al. 2017). Such models have recently been developed for the Norwegian government for use as first generation management advice for fish farming along the Norwegian coast (Nilsen et al. 2017a). Methods from these studies may well be implemented in other countries.



Salmon farm. Photo Eva. B. Thorstad

8 Conclusions

Scientific studies indicate that salmon farming increases the abundance of salmon lice in the marine habitat and that salmon lice in the most intensively farmed areas have negatively impacted wild Atlantic salmon and sea trout populations. The effects of salmon lice on Atlantic salmon and sea trout include increased marine mortality, reduced marine growth, and for sea trout as changes in migratory behaviour. Published studies range from those investigating the effects of salmon lice on individual fish, both in the laboratory and the field, to analyses of their impacts on wild populations.

Conclusions are based on comprehensive studies of the effects by salmon lice, which include:

1) Studies of individual fish in laboratory and field studies documenting (i) tissue damage, (ii) problems with salt regulation and other physiological stress responses, (iii) reduced growth, and (iv) increased susceptibility to secondary infections and reduced disease resistance. One or more of these effects have frequently been reported to occur as the result of heavy salmon lice infestations.

2) Studies documenting premature migratory return to freshwater of sea trout with high levels of salmon lice. Premature migratory return may facilitate individual survival and recovery from infestation, but reduce growth and thereby future reproduction by reducing the time spent feeding at sea. Sea trout with excessive skin lesions also may be more vulnerable to fungal and bacterial infection in fresh-water.

3) Studies based on catch statistics and routine population monitoring utilizing in-river traps that have indicated salmon lice-induced changes in population abundance, age structure and altered life history characteristics.

4) Monitoring of salmon lice levels on wild fish.

5) Comparisons of salmon lice levels in farm-intensive and less farm-intensive (or farm-free) areas.

6) Indications of population-level effects on sea trout based on monitoring of salmon lice levels on wild fish in relation to experimentally determined threshold levels known to induce physiological compromise and mortality of individual fish.

7) Quantification of Atlantic salmon mortality due to salmon lice in large-scale field studies by comparing growth and marine survival of salmon treated with prophylactic chemicals against salmon lice with un-protected control groups.

In sum, the combined knowledge from scientific studies provides evidence of a general and pervasive negative effect of salmon lice on salmonid populations in intensively farmed areas of Ireland, Norway and Scotland. Premature migratory return, increased marine mortality and reduced growth of survivors that are induced by elevated salmon lice levels inevitably imply a reduction in numbers and body size of fish returning to freshwater for spawning, and hence in number of fish available to fisheries. Levels of additional mortality by salmon lice as indicated in several scientific studies may result in salmon stocks not achieving river specific conservation limits and, if sustained over time, could result in significant cumulative reductions in adult salmon recruitment.

This summary is based on an earlier reviews (Finstad & Bjørn 2011, Finstad et al. 2011, Thorstad et al. 2015) and new studies on the effects of salmon lice. New studies have confirmed and strengthened conclusions in previous reviews. Sea lice Caligus elongatus is another parasite species that may occur on farmed and wild salmonids, but is not covered here. A full list of earlier references to the scientific literature is not included, but extensive reference lists can be found in the previous reviews.

9 References

- Anon 2014. Report of the Working Group on North Atlantic Salmon (WGNAS), 19-28 March 2014, Copenhagen, Denmark. ICES CM 2014/ACOM:09. 433 pp.
- Anon. 2017. Status for norske laksebestander i 2017. Rapport fra Vitenskapelig råd for lakseforvaltning nr 10, 152 s. English summary: http://www.vitenskapsradet.no/Portals/vitenskapsradet/Pdf/Status%20of%20wild%20Atlantic%20salmon%20in%20Norway%202017.pdf
- Asplin, L., Boxaspen, K.K. & Sandvik, A.D. 2011. Modeling the distribution and abundance of planktonic larval stages of *Lepeophtheirus salmonis* in Norway. In: Salmon lice: An integrated approach to understanding parasite abundance and distribution (eds. S. Jones & R. Beamish), pp. 31-50. Wiley-Blackwell, Oxford.
- Asplin, L., Johnsen, I.A., Sandvik, A.D., Albretsen, J., Sundfjord, V., Aure, J. & Boxaspen, K. 2014. Dispersion of salmon lice in the Hardangerfjord. Marine Biology Research 10, 216-225.
- Birkeland, K. 1996. Consequences of premature return by sea trout (*Salmo trutta*) infested with the salmon louse (*Lepeophtheirus salmonis* Krøyer): migration, growth, and mortality. Canadian Journal of Fisheries and Aquatic Sciences 53, 2808-2813.
- Birkeland, K. & 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. 1997. The physiological effects of salmon lice infection on sea trout post smolts. Nordic Journal of Freshwater Research 73, 60-72.
- Bjørn, P.A. & Finstad, B. 2002. Salmon lice, *Lepeophtheirus salmonis* (Krøyer), infestation in sympatric populations of Arctic char, *Salvelinus alpinus* (L.), and sea trout, *Salmo trutta* (L.), in areas near and distant from salmon farms. ICES Journal of Marine Science 59, 131-139.
- Bjørn, P.A., Finstad, B. & Kristoffersen, R. 2001. Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. Aquaculture Research 32, 947-962.
- Bjørn, P.A., Finstad, B., Kristoffersen, R., McKinley, R.S. & 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. & Kristoffersen, R. 2011. Area protection may reduce salmon louse infection risk to wild salmonids. Aquaculture Environment Interactions 1, 233-244.
- Bui, S., Halttunen, E., Mohn, A.M., Vågseth, T. & Oppedal, F. 2017. Salmon lice evasion, susceptibility, retention, and development differ amongst host salmonid species. ICES Journal of Marine Science doi:10.1093/icesjms/fsx222.
- Butler, J.R.A. 2002. Wild salmonids and sea louse infestations on the west coast of Scotland: sources of infection and implications for the management of marine salmon farms. Pest Management Science 58, 595-608.
- Butler, J.R.A. & Walker, A.F. 2006. Characteristics of the sea trout Salmo trutta (L.) stock collapse in the River Ewe (Wester Ross, Scotland), in 1988-2001. In: Sea Trout: Biology, Conservation and Management (eds. G. Harris & N. Milner), pp. 45-59. Blackwell Publishing, Oxford.
- Costello, M.J. 2009. How sea lice from salmon farms may cause wild salmonid declines in Europa and North America and be a threat to fishes elsewhere. Proceedings of the Royal Society B 276, 3385-3394.
- Finstad, B. & 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 (eds. S. Jones & R. Beamish), pp. 281-305. Wiley-Blackwell, Oxford.

- Finstad, B., Johnsen, B.O. & Hvidsten, N.A. 1994. Prevalence and mean intensity of salmon lice, *Lepeophtheirus salmonis* Krøyer, infection on wild Atlantic salmon *Salmo salar* L., postsmolts. Aquaculture and Fisheries Management 25, 761-764.
- Finstad, B., Bjørn, PA., Grimnes, A. & Hvidsten, N.A. 2000. Laboratory and field investigations of salmon lice [*Lepeophtheirus salmonis* (Krøyer)] infestation on Atlantic salmon (*Salmo salar* L.) postsmolts. Aquaculture Research 31, 795-803.
- Finstad, B., Bjørn, P.A., Todd, C.D., Whoriskey, F., Gargan, P.G., Forde, G. & Revie, C. 2011. The effect of sea lice on Atlantic salmon and other salmonid species. In: Atlantic salmon ecology (eds. Ø. Aas, S. Einum, A. Klemetsen & J. Skurdal), pp. 253-276. Wiley-Blackwell, Oxford.
- Finstad, B., Kroglund, F., Strand, R., Stefansson, S.O., Bjørn, P.A., Rosseland, B.O., Nilsen, T.O. & Salbu, B. 2007. Salmon lice or suboptimal water quality - Reasons for reduced postsmolt survival? Aquaculture 273, 374-383.
- Finstad, B., Kroglund, F., Bjørn, P.A., Nilsen, R., Pettersen, K., Rosseland, B.O., Teien, H.-C., Nilsen, T.O., Stefansson, S., Salbu, B., Fiske, P. & Ebbesson, L.O.E. 2012. Salmon lice-induced mortality of Atlantic salmon postsmolts experiencing episodic acidification and recovery in freshwater. Aquaculture 362, 193-199.
- Fjørtoft, H.B., Besnier, F., Stene, A., Nilsen, F., Bjørn, P.A., Tveten, A.-K., Finstad, B., Aspehaug, V. & Glover, K.A. 2017. The Phe362Tyr mutation conveying resistance to organophosphates occurs in high frequencies in salmon lice collected from wild salmon and trout. Scientific Reports 7, 14258.
- Ford, J.S. & Myers, R.A. 2008. A global assessment of salmon aquaculture impacts on wild salmonids. PLoS Biology 6(2).
- Forseth, T., Barlaup, B.T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T.A., Rikardsen, A.H., Thorstad, E.B., Vøllestad, A. & Wennevik, V. 2017. The major threats to Atlantic salmon in Norway. ICES Journal of Marine Science 74, 1496-1513.
- Gargan, P. 2000. The impact of the salmon louse (*Lepeophtheirus salmonis*) on wild salmonid stocks in Europe and recommendations for effective management of sea lice on salmon farms. In: Aquaculture and the Protection of Wild Salmon (eds. P. Gallaugher & C. Orr), pp. 37-46. Workshop Proceedings, July 2000, Simon Fraser University, Vancouver, British Columbia, Canada.
- Gargan, P.G., Poole, W.R. & Forde, G. 2006a. A review of the status of Irish sea trout stocks. In: Sea trout: Biology, conservation and management (eds. G. Harris & N. Milner), pp. 25-44. Blackwell Publishing, Oxford.
- Gargan, P.G., Shephard, S & MacIntyre, C. 2017. Assessment of the increased mortality risk and population regulating effect of sea lice (*Lepeophtheirus salmonis*) from marine salmon farms on wild sea trout in Ireland and Scotland. In: Sea trout: science & management (ed. G. Harris), pp. 538-554. Proceedings of the 2nd International Sea Trout Symposium, Ireland.
- Gargan, P.G., Tully, O. & Poole, W.R. 2003. The relationship between sea lice infestation, sea lice production and sea trout survival in Ireland, 1992-2001. In Salmon at the edge (ed. D. Mills), chapter 10, pp. 119-135. Proceedings of the 6th International Atlantic Salmon Symposium, Edinburgh, UK, July 2002. Atlantic Salmon Trust/Atlantic Salmon Federation.
- Gargan, P.G., Kelly, F.L., Shephard, S., & Whelan, K.F. 2016a. Temporal variation in sea trout *Salmo trutta* life history traits in the Erriff River, western Ireland. Aquaculture Environment Interactions 8, 675-689.
- Gargan, P.G., Roche, W.K., Forde, G.P. & Ferguson, A. 2006b. Characteristics of the sea trout (*Salmo trutta* L.) stocks from the Owengowla and Invermore fisheries, Connemara, Western Ireland, and recent trends in marine survival. In: Sea Trout: Biology, Conservation and Management (eds. G. Harris & N. Milner), pp. 60-75. Blackwell Publishing, Oxford.
- Gargan, P.G., Forde, G., Hazon, N., Russel, D.F. & 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.

- Gargan, P., Karlsbakk, E., Coyne, J., Davies, C. & Roche, W. 2016b. Sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) infestation levels on sea trout (*Salmo trutta* L.) around the Irish Sea, an area without salmon aquaculture. ICES Journal of Marine Science 73, 2395-2407.
- Gillibrand, P., Hay, D., Penston, M. & Murray, A. 2005. Sea lice and sea trout. Are salmon farms causing increased parasitism on wild salmonids in Scotland? Ocean Challenge 14, 24-30.
- Gjelland, K.Ø., Serra-Llinares, R.M., Hedger, R.D., Arechavala-Lopez, P., Nilsen, R., Finstad, B., Uglem, I., Skilbrei, O.T. & Bjørn, P.A. 2014. How does salmon lice affect the marine phase of sea trout behaviour? Aquaculture Environment Interactions 5, 221-233.
- Grimnes, A. & Jakobsen, P. 1996. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon (*Salmo salar*). Journal of Fish Biology 48, 1179-1194.
- Halttunen, E., Gjelland, K.Ø., Hamel, S., Serra-Llinares, R.-M., Nilsen, R., Arechavala-Lopez, P., Skarðhamar, J., Johnsen, I.A., Asplin, L., Karlsen, Ø., Bjørn, P.A. & Finstad, B. 2017. Sea trout adapt their migratory behaviour in response to high salmon lice concentrations. Journal of Fish Diseases DOI: 10.1111/jfd.12749.
- Halttunen, E., Gjelland, K.Ø., Glover, K., Johnsen, I.A., Serra-Llinares, R.M., Skaala, Ø., Nilsen, R., Bjørn P.A., Karlsen, Ø., Finstad, B. & Skilbrei, O. 2018. Migration of Atlantic salmon post-smolts in a fjord system with a high infestation pressure of salmon lice. Marine Ecology Progress Series DOI:10.3354/meps12403.
- Harte, A.J., Bowman, A.S., Salama, N.K.G. & Pert, C.C. 2017. Factors influencing the long-term dynamics of larval sea lice density at east and west coast locations in Scotland. Diseases of Aquatic Organisms 123: 181-192.
- Hatton-Ellis, M., Hay, D.W., Walker, A.F. & Northcott, S.J. 2006. Sea lice *Lepeophtheirus salmonis* infestations of post-smolt sea trout in Loch Shieldaig, Wester Ross, 1999-2003. In: Sea Trout: Biology, Conservation and Management (eds. G. Harris & N. Milner), pp. 372-376. Blackwell Publishing, Oxford.
- Helland, I.P., Uglem, I., Jansen, P.A., Diserud, O.H., Bjørn, P.A. & Finstad, B. 2015. Statistical and ecological challenges of monitoring parasitic salmon lice infestations in wild salmonid fish stocks. Aquaculture Environment Interactions 7, 267-280.
- Heuch, P.A. & Mo, T.A. 2001. A model of salmon louse production in Norway: effects of increasing salmon production and public management measures. Diseases of Aquatic Organisms 45, 145-152.
- Heuch, P.A., Knutsen, J.A., Knutsen, H. & Schram, T. 2002. Salinity and temperature effects on sea lice over-wintering on sea trout (*Salmo trutta*) in coastal areas of the Skagerrak. Journal of the Marine Biological Association U.K 82, 887-892.
- Heuch, P.A., Bjørn, P.A., Finstad, B., Holst, J.C., Asplin, L. & 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.
- Holst, J.C., Jakobsen, P., Nilsen, F., Holm, M., Asplin, L. & 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 (ed D. Mills). Blackwell Science, Oxford, UK.
- ICES 2016. 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.
- Jackson, D., Cotter, D., Newell, J., O'Donohoe, P., Kane, F., McDermott, T., Kelly, S. & Drumm, A. 2014. Response to M Krkošek, C W Revie, B Finstad and C D Todd's 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, 419-421.
- Jackson, D., Cotter, D., Newell, J., McEvoy, S., O'Donohoe, P., Kane, F., McDermott, T., Kelly, S. & 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.

- Jackson, D., Cotter, D., Ó'Maoilédigh, N., O'Donohoe, P., White, J., Kane, F., Kelly, S., McDermott, T., McEvoy, S., Drumm, A. & Cullen, A. 2011b. 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 coasts. Aquaculture 319, 37-40.
- Jackson, D., Cotter, D., Ó'Maoilédigh, N., O'Donohoe, P., White, J., Kane, F., Kelly, S., McDermott, T., McEvoy, S., Drumm, A., Cullen, A. & Rogan, G. 2011a. An evaluation of the impact of early infestation with the salmon louse *Lepeophtheirus salmonis* on the subsequent survival of outward migration Atlantic salmon *Salmo salar* L., smolts. Aquaculture 320, 159-163.
- Jansen, P.A., Kristoffersen, A.B., Viljugrein, H., Jimenez, D., Aldrin, M. & Stien, A. 2012. Sea lice as a density-dependent constraint to salmonid farming. Proceedings of the Royal Society B 279, 2330-2338.
- Karlsen, Ø., Finstad, B., Ugedal., O & Svåsand, T. 2016. Kunnskapsstatus som grunnlag for kapasitetsjustering innen produksjonsområder basert på lakselus som indikator. Rapport fra Havforskningen Nr.14-2016 (ISSN 1893-4536 online).
- Krkošek, M., Revie, C.W., Finstad, B. & 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, 415-417.
- Krkošek, M., Revie, C., Gargan, P., Skilbrei, O.T., Finstad, B. & Todd, C.D. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B 280, 20122359.
- Marshall, S. 2003. The incidence of sea lice infestations on wild sea trout compared to farmed salmon. Bulletin of the European Association of Fish Pathologists 23, 72-79.
- Middlemas, S.J., Fryer, R.J., Tulett, D. & 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.
- Middlemas, S.J., Raffell, J.A., Hay, D.W., Hatton-Ellis, M. & 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.
- Nilsen, F., Ellingsen, I., Finstad, B., Jansen, P.A., Karlsen, Ø., Kristoffersen, A., Sandvik, A.D., Sægrov, H., Ugedal, O., Vollset, K.W. & Myksvoll, M.S. 2017a. Vurdering av lakselusindusert villfiskdødelighet per produksjonsområde i 2016 og 2017. Rapport fra ekspertgruppe for vurdering av lusepåvirkning. ISBN 978-82-8088-414-5.
- Nilsen, R., Serra Llinares, R.M., Schrøder Elvik, K.M., Sandvik, A.D., Johnsen, I.A., Kvamme, B.O., Karlsen, Ø., Finstad, B. & Lehmann, G. B. 2017c. Lakselusinfestasjon på vill laksefisk vår og sommer 2017 – Fremdriftsrapport til Mattilsynet september 2017. Rapport fra havforskningen nr. 26-2017 (ISSN-4536 online).
- Nilsen, R., Serra Llinares, R.M., Sandvik, A.D., Schrøder Elvik, K.M., Asplin, L., Bjørn, P.A., Johnsen, I.A., Karlsen, Ø., Finstad, B., Berg, M., Uglem, I., Wiik Vollset, K. & Lehmann, G.B. 2017b. Lakselusinfestasjon på vill laksefisk langs Norskekysten i 2016. Med vekt på modellbasert varsling og tilstandsbekreftelse. Sluttrapport til Mattilsynet. Rapport fra havforskningen nr. 1-2017 (ISSN 1893-4536 online).
- Northcott S.J. & Walker A.F. 1996. Farming salmon, saving sea trout: a cool look at a hot issue. In: Aquaculture and Sea Lochs (ed. K.D. Black), pp. 72-81. The Scottish Association for Marine Science, Dunstaffnage.
- Otero, J., Jensen, A.J., L'Abée-Lund. J.H., Stenseth, N.C., Storvik, G.O. & Vøllestad, L.A. 2011. Quantifying the ocean, freshwater and human effects on year-to-year variability of one-sea-winter Atlantic salmon angled in multiple Norwegian rivers. PLoS ONE 6(8): e24005.

- Penston, M.J. & 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.
- Penston, M.J., Millar, C.P. & Davies, I.M. 2008a. Reduced *Lepeophtheirus salmonis* larval abundance in a sea loch on the west coast of Scotland between 2002 and 2006. Diseases of Aquatic Organisms 81, 109-117.
- Penston, M.J., Millar, C.P., Zuur, A. & Davies, I.M. 2008b. Spatial and temporal distribution of *Lepeophtheirus salmonis* (Krøyer) larvae in a sea loch containing Atlantic salmon, *Salmo salar* L., farms on the northwest coast of Scotland. Journal of Fish Diseases 31, 361-371.
- Pert, C.C., Raffell, J., Urquhart, K., Weir, S.J., Kantola, K.M.H. & Bricknell, I.R. 2009. The pathogen burden of early returning sea trout (*Salmo trutta* L.) infected with *Lepeophtheirus salmonis* (Krøyer, 1837), in the River Shieldaig, Scotland. Bulletin of the European Association of Fish Pathologists 29, 210-216.
- Pike, A.W. & Wadsworth, S.L. 1999. Sea lice on salmonids: their biology and control. Advances in Parasitology 44, 253-337.
- Poole, W.R., Whelan, K.F., Dillane, M.G., Cooke, D.J. & Matthews, M. 1996. The performance of sea trout, *Salmo trutta* L., stocks from the Burrishoole system western Ireland, 1970-1994. Fisheries Management and Ecology 3, 73-92.
- Revie, C.W, Dill, L., Finstad, B. & Todd, C. 2009. Sea Lice Working Group Report. NINA Special Report 39, 1-117.
- Revie, C.W., Gettingby, G., Treasurer, J.W., Rae, G.H. & Clark, N. 2002. Temporal, environmental and management factors influencing the epidemiological patterns of sea lice (*Lepeophtheirus salmonis*) infestations on farmed Atlantic salmon (*Salmo trutta*) in Scotland. Pest Management Science 58, 576-584.
- Rikardsen, A.H. 2004. Seasonal occurrence of sea lice *Lepeophtheirus salmonis* on sea trout in two north Norwegian fjords. Journal of Fish Biology 65, 711-722.
- Salama, N.K.G., Murray, A.G. & Rabe, B. 2016. Simulated environmental transport distances of *Lepeophtheirus salmonis* in Loch Linnhe, Scotland, for informing aquaculture area management structures. Journal of Fish Diseases 39: 419-428.
- Sandvik, A.D., Bjørn, P.A., Ådlandsvik, B., Asplin, L., Skarðhamar, J., Johnsen, I.A., Myksvoll, M.S.
 & Skogen, M.D. 2016. Toward a model-based prediction system for salmon lice infestation pressure. Aquaculture Environment Interactions 8, 527-542.
- Schram, T.A., Knutsen, J.A., Heuch, P.A. & Mo, T.A. 1998. Seasonal occurrence of Lepeophtheirus salmonis and Caligus elongatus (Copepoda: Caligidae) on sea trout (Salmo trutta), off southern Norway. ICES Journal of Marine Science 55, 163-175.
- Serra-Llinares, R.M., Bjørn, P.A., Finstad, B., Nilsen, R. & Asplin, L. 2016. Nearby farms are a source of lice for wild salmonids: a reply to Jansen et al. 2016. Aquaculture Environment Interactions 8: 351-356.
- Serra-Llinares, R.M., Bjørn, P.A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M. & 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.
- Shephard, S. & Gargan, P. 2017. Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. Aquaculture Environment Interactions 9, 181-192.
- Shephard, S., MacIntyre, C. & Gargan, P. 2016. Aquaculture and environmental drivers of salmon lice infestation and body condition in sea trout. Aquaculture Environment Interactions 8: 597-610.

- Skaala, Ø., Kålås, S. & Borgstrøm, R. 2014a. Evidence of salmon lice-induced mortality of anadromous brown trout (*Salmo trutta*) in the Hardangerfjord, Norway. Marine Biology Research 10, 279-288.
- Skaala, Ø., Johnsen, G.H., Lo, H., Borgstrøm, R., Wennevik, V., Hansen, M.M., Merz, J.E., Glover, K.A. & Barlaup, B.T. 2014b. A conservation plan for Atlantic salmon (*Salmo salar*) and anadromous brown trout (*Salmo trutta*) in a region with intensive industrial use of aquatic habitats, the Hardangerfjord, western Norway. Marine Biology Research 10, 308-322.
- Skilbrei, O.T. & Wennevik, V. 2006. Survival and growth of sea-ranched Atlantic salmon treated against sea lice prior to release. ICES Journal of Marine Science 63, 1317-1325.
- Skilbrei, O.T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F. & 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 Fish Diseases 36, 249-260.
- 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. & Svåsand, T. 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES Journal of Marine Science 72, 997-1021.
- Thorstad, E.B., Whoriskey, F.G., Rikardsen, A.H. & Aarestrup, K. 2011. Aquatic nomads: the life and migrations of the Atlantic salmon. In: Atlantic Salmon Ecology (eds. Ø. Aas, S. Einum, A. Klemetsen & J. Skurdal), pp. 1-32. Wiley-Blackwell, Oxford.
- Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H. & Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*. behaviour and survival during the smolt and initial post-smolt migration. Journal of Fish Biology 81, 500-542.
- Thorstad, E.B., Todd, C.D., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kålås, S., Uglem, I., Berg, M. & 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., Finstad, B. 2015. Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta* a literature review. Aquaculture Environment Interactions 7, 91-113.
- Thorstad, E.B., Uglem, I., Finstad, B., Kroglund, F., Einarsdottir, I.E., Kristensen, T., Diserud, O., Arechavala-Lopez, P., Mayer, I., Moore, A., Nilsen, R., Björnsson, B.T. & Økland, F. 2013. Reduced marine survival of hatchery Atlantic salmon post-smolts exposed to aluminium and moderate acidification in freshwater. Estuarine, Coastal and Shelf Science 124, 34-43.
- Tingley, G.A., Ives, M.J. & Russell, I.C. 1997. The occurrence of lice on sea trout (*Salmo trutta* L.) captured in the sea off the East Anglian coast of England. ICES Journal of Marine Science 54, 1120-1128.
- Todd, C.D. 2007. The copepod parasite (*Lepeophtheirus salmonis* (Krøyer), *Caligus elongatus* Nordmann) interactions between wild and farmed Atlantic salmon (*Salmo salar* L.) and wild sea trout (*Salmo trutta* L.): a mini review. Journal of Plankton Research 29, i61-i71.
- Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Horsberg, T.E. & Jackson, D. 2013. Salmon lice - impact on wild salmonids and salmon aquaculture. Journal of Fish Diseases 36, 171-194.
- Tully, O. & Whelan, K.F. 1993. Production of nauplii of *Lepeophtheirus salmonis* (Krøyer) (Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (*Salmo trutta* L.) off the west coast of Ireland in 1991. Fisheries Research 17, 187-200.
- Tully, O., Poole, W.R. & Whelan, K.F. 1993b. Infestation parameters for *Lepeophtheirus salmonis* (Krøyer) (Copepoda: Caligidae) parasitic on sea trout, *Salmo trutta* L., off the west coast of Ireland during 1990 and 1991. Aquaculture and Fisheries Management 24, 545-557.

- Tully, O., Gargan, P., Poole, W.R. & Whelan, K.F. 1999. Spatial and temporal variation in the infestation of sea trout (*Salmo trutta* L.) by the caligid copepod *Lepeophtheirus salmonis* (Krøyer) in relation to sources of infection in Ireland. Parasitology 119, 41-51.
- Tully, O., Poole, W.R., Whelan, K.F. & Merigoux, S. 1993a. Parameters and possible causes of epizootics of *Lepeophtheirus salmonis* (Krøyer) infesting sea trout (*Salmo trutta* L.) off the west coast of Ireland. In: Pathogens of Wild and Farmed Fish: Sea Lice (eds. G.A. Boxhall & D. Defaye), pp. 202-213. Ellis Horwood, Chichester.
- Urquhart, K., Pert, C.C., Fryer, R.J., Cook, P., Weir, S., Kilburn, R., McCarthy, U., Simons, J., McBeath, S.J., Matejusova, I. & Bricknell, I.R. 2010. A survey of pathogens and metazoan parasites on wild sea trout (*Salmo trutta*) in Scottish waters. ICES Journal of Marine Science 67, 444-453.
- Vøllestad, L.A., Hirst, D., L'Abée-Lund, J.H., Armstrong, J.D., MacLean, J.C., Youngson, A.F. & Stenseth, N.C. 2009. Divergent trends in anadromous salmonid populations in Norwegian and Scottish rivers. Proceedings of the Royal Society B 276, 1021-1027.
- Vollset, K.W., Skoglund, H., Barlaup, B.T., Pulg, U., Gabrielsen, S.E. & Wiers, T. 2014. Can the river location within a fjord explain the density of Atlantic salmon and sea trout? Marine Biology Research, 10, 268-278.
- Vollset, K.W., Krontveit, R.I., Jansen, P.A., Finstad, B., Barlaup, B.T., Skilbrei, O.T., Krkošek, M., Romundstad, P., Aunsmo, A., Jensen, A.J. & Dohoo, I. 2016. Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish and Fisheries 17: 714-730.
- Vollset, K.W., Dohoo, I., Karlsen, Ø., Halttunen, E., Kvamme, B.O., Finstad, B., Wennevik, V., Diserud, O.H., Bateman, A., Friedland, K.D., Mahlum, S., Jørgensen, C., Qviller, L., Krkošek, M, Åtland, Å. & Barlaup, B.T. 2017. Food for thought: Disentangling the role of sea lice on the marine survival of Atlantic salmon. ICES Journal of Marine Science doi:10.1093/icesjms/fsx104.
- Wagner, G.N., Fast, M.D. & Johnson, S.C. 2008. Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. Trends in Parasitology 24, 176-183.
- Wagner, G.N., McKinley, R.S., Bjørn, P.A. & Finstad, B. 2003. Physiological impact of sea lice on swimming performance of Atlantic salmon. Journal of Fish Biology 62, 1000-1009.
- Wagner, G.N., McKinley, R.S., Bjørn, P.A. & Finstad, B. 2004. Short-term freshwater exposure benefits sea lice-infected Atlantic salmon. Journal of Fish Biology 64, 1593-1604.
- Wells, A., Grierson, C.E., MacKenzie, M., Russon, I.J., Reinardy, H., Middlemiss, C., Bjørn, P., Finstad, B., Wendelaar Bonga, S.E., Todd C.D. & Hazon, N. 2006. The physiological effects of simultaneous, abrupt seawater entry and sea lice (*Lepeophtheirus salmonis*) infestation of wild, sea-run brown trout (*Salmo trutta*) smolts. Canadian Journal of Fisheries and Aquatic Sciences 63, 2809-2821.
- Wells, A., Grierson, C.E., Marshall, L., MacKenzie, M., Russon, I.J., Reinardy, H., Sivertsgård, R., Bjørn, P.A., Finstad, B., Wendelaar Bonga, S.E., Todd, C.D. & Hazon, N. 2007. Physiological consequences of "premature freshwater return" for wild sea-run brown trout (*Salmo trutta*) postsmolts infested with sea lice (*Lepeophtheirus salmonis*). Canadian Journal of Fisheries and Aquatic Sciences 64, 1360-1369.

Whelan, K. 1991. Disappearing sea trout: Decline or collapse. The Salmon Net 23, 24-31.

Whelan, K.F. & Poole, W.R. 1996. The sea trout stock collapse, 1989-1992. In: The conservation of aquatic systems, proceedings of a seminar held on 18-19 February 1993 (ed. J. Reynolds), pp. 101-110. Royal Irish Academy.

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