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NINA Report

1044 Effects of salmon lice on sea trout

- a literature review

Eva B. Thorstad, Christopher D. Todd, Pål Arne Bjørn,
Patrick G. Gargan, Knut Wiik Vollset, Elina Halttunen, Steinar Kålås,
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Norwegian Institute for Nature Research

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Sea trout from River Espedalselva in south-western Norway.
Photo Tore Wiers, UNI Research, LFI

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SUMMARY

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Salmon lice are external parasites on salmonids in the marine environment. Farmed salmonids also act as hosts for salmon lice; therefore open net cage farms can increase the production of infective larvae in coastal areas. The aim of this report is to review the existing knowledge on the effects of salmon lice on wild sea trout and focuses on reports in the peer-reviewed primary scientific literature. For this reason, reference to so-called “grey literature” reports has been minimized. The studies reviewed here range from laboratory and field investigations of the effects of salmon lice on individual fish, to analyses of impacts on wild populations.

Salmon lice feed on the host fish mucus, skin and muscle, causing tissue erosion. Laboratory and field studies have demonstrated that salmon lice may induce osmoregulatory dysfunction, physiological stress, anaemia, reduced feeding and growth, increased susceptibility to secondary infections, reduced disease resistance and mortality in individual sea trout.

Sea trout in farm-free areas generally show low levels of salmon lice. In farm-intensive areas, salmon lice levels vary considerably among studies and localities, ranging from low levels similar to farm-free areas to those indicating a risk of significant lice-induced mortality. Several studies have shown elevated salmon lice levels in wild sea trout adjacent to fish farms, particularly within 30 km of the nearest farms. Amongst salmonids, sea trout are especially vulnerable to salmon lice infestation because they typically remain in coastal waters during their marine residence, and coastal waters are the areas where open net cage Atlantic salmon farms typically are situated.

Based on the reviewed studies, it can be concluded that salmon farming increases the abundance of lice in marine habitats and that, despite the control measures routinely applied by the salmon aquaculture industry, salmon lice in intensively farmed areas have negatively impacted wild sea trout populations by reducing growth and increasing marine mortality. However, the resulting reduction of wild sea trout populations cannot in most cases be quantified because of a lack of suitably comprehensive field data and studies of population-level effects of salmon lice.

Population-level effects of salmon lice have been quantified in Atlantic salmon by comparing growth and survival of chemically protected fish with un-treated control groups released in parallel. There are few such studies on sea trout, but the results for Atlantic salmon support that 12-44% fewer spawners are potential levels of extra mortality attributable to salmon lice that can be expected for Atlantic salmon populations in farm-intensive areas. Studies of Atlantic salmon likely represent minimum estimates for sea trout mortality at the same sites because salmon smolts migrate quickly through coastal waters and into the open ocean, whereas sea trout remain throughout in coastal or inshore waters.

Salmon lice do not increase extinction risk of brown trout as a species. Because only components of brown trout populations migrate to sea, reduced growth and increased mortality at sea will reduce the individual benefits of marine migration, and may thereby result in selection against anadromous behaviour in areas with high salmon lice levels. In the extreme, selection could result in the local loss of the marine migratory life history strategy, and perhaps especially so for trout populations exploiting small catchments and that may

depend upon marine refuges in the winter. Large catchments with suitable year-round conditions for freshwater residents face a lower risk of loss of their brown trout populations. However, a severe reduction or loss of sea-migrating individual trout may result in (1) reduced future recruitment of trout, and (2) reduced or eliminated harvestable surplus of trout for fisheries.

Thus, loss of the improved growth opportunities for trout at sea and reduced recruitment to spawning may lead to lower total abundance of brown trout, and loss of the large veteran migrants popular among fishers and which may make a disproportionately large contribution to egg deposition within the overall population. Salmon lice-induced effects also might extend to altered genetic composition and diversity of trout populations, and the establishment of exclusively freshwater resident populations. Some monitoring studies have indicated that such changes may have occurred already in some catchments in farm-intensive areas; but the lack of comprehensive and long-term monitoring of sea trout populations and integrated studies of the effects of salmon lice at the population level make it difficult to draw specific conclusions in this respect.

Whilst the focus of the present report remains with the effects of salmon lice, it has also to be acknowledged that sea trout populations are affected also by a multiplicity of environmental and anthropogenic influences. There is local and regional variation in the importance of these other impact factors, and the status of sea trout varies accordingly across the distribution range. Other human-induced impact factors include climate change effects, pollution, overfishing, diseases caused by viruses, bacteria, fungi and other parasites. Some of these impacts perhaps are attributable to the increased geographic spread and biomass production of fish farming over recent decades, by hydropower development and other river flow regulation, migration obstacles and habitat alterations. The interactive effects of two or more impact factors may be complex and unpredictable. For sea trout populations experiencing negative anthropogenic impacts both in freshwater and at sea, there is need for co-ordinated mitigation measures.

There now is a good understanding of effects of salmon lice at the level of the individual host fish, and the most important knowledge gaps therefore pertain to the effects of salmon lice at the population level. Specifying and quantifying the reduction of wild sea trout populations as a result of increased mortality and reduced growth (and thereby fecundity) should be a priority research topic. In order to fully inform our understanding of population-level effects, more detailed and comprehensive information is required on sea trout marine migration behaviour, the foraging areas exploited by trout at sea and their vulnerability to salmon louse infestation. In contrast to Atlantic salmon, sea trout populations throughout the geographic distribution generally have been rather poorly studied, monitored and mapped. As a consequence, even the status of sea trout populations and a basic understanding of putative anthropogenic factors potentially impacting them are not well known for many catchments or watersheds.

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EXTENDED SUMMARY

This extended summary provides a chapter by chapter summary of the report.

Introduction

Salmon lice (*Lepeophtheirus salmonis*) are external parasites on salmonids in the marine environment. Farmed salmonids also can act as hosts, and open net cage farms can increase the production of infective larvae in coastal areas. Aquaculture activities have not extended the natural geographic distribution range of salmon lice, but the effects of salmon lice on wild salmonid populations are potentially problematic in areas with intensive Atlantic salmon (*Salmo salar*) aquaculture in Ireland, Norway, Scotland and other countries. The aim of this report is to summarize existing knowledge of the effects of salmon lice on sea trout (*Salmo trutta*) based on a literature review of international publications in peer-reviewed journals and books.

Salmon lice hatch from the eggstrings carried by the adult female as planktonic nauplius larvae. There are two planktonic and free-swimming nauplius stages and the third moult is to the copepodid, which is the infective stage when the parasite must find a host fish. Once attached to a host, the copepodid moults into the first of two attached chalimus stages, followed by further moults to the two preadult stages and the definitive adult phase. Salmon lice use rasping mouthparts to feed on the host mucus, skin and tissue, and can cause skin damage and lesions.

Brown trout spawn in freshwater, and there are both freshwater resident and anadromous populations. Anadromous brown trout that migrate to marine habitats for feeding are termed sea trout. In anadromous populations, some or all individuals undertake feeding migrations to marine habitats. Within populations, there is little genetic differentiation between anadromous and resident individuals, and there is significant interbreeding between the two forms. The anadromous life history is a trait that is controlled both by multiple genes and environmental influences.

Life history strategies of sea trout at sea

Information on life history strategies, behaviour and habitat use of sea trout in the marine environment is required to evaluate their vulnerability to salmon lice, to develop and improve monitoring methods, to interpret monitoring results and to develop and evaluate mitigation measures to reduce impacts of salmon lice on wild populations. Understanding how salmon lice affect host life history traits, such as “partial” marine migration, is also important to complement our understanding of the potential effects of salmon lice at the host population level.

There is considerable geographic and within-population variation in sea trout life history strategy, particularly with regard to the timing and duration of marine migrations. Females tend to adopt the anadromous life history strategy more than do males, perhaps because females have more to gain by increasing body size and thereby future fecundity.

Sea trout that undergo smoltification typically emigrate from rivers and enter the sea for the first time in spring or early summer (February-June). Smolts are usually 1-8 years old and 10-25 cm in length and this varies both latitudinally and within and among populations. Sea trout also may enter the sea for the first time at other times of the year. Sea trout post-smolts may remain at sea only for a few months during the summer, and can return to freshwater to over-winter; thereafter these veteran migrants may regularly spend their summers at sea and winters in freshwater. They may spawn after the first summer at sea, but more often do so in their second or third year after smolting.

Sea trout need not return to freshwater after the first summer at sea, but some can remain continuously at sea during the summer and winter until they mature and return to freshwater for spawning the following year or even several years later. Sea trout are frequently recorded at sea during winter, both in southern and northern areas. The duration and timing of marine migration is likely governed by trade-offs between growth opportunities and survival risk associated with the different habitats, and the overall most beneficial strategy may vary both among individuals and populations. The strategy of remaining at sea during winter is likely more common in populations from small catchments with unstable and poor freshwater winter conditions. Sea trout from very small coastal streams with little water flow and periods of droughts may rear quickly through the parr stage in freshwater, and then remain at sea for the rest of their life, excepting brief returns to freshwater for spawning.

Sea trout in the marine environment typically remain in coastal or near-shore areas, and do not undertake long-distance migrations to open ocean areas. However, they may feed offshore in pelagic waters in outer coastal areas and in the Baltic and North seas. Sea trout usually remain within 80 km or less of their river of origin, but a few individuals may undertake longer distance migrations. Some have been recaptured >500 km from the river where they were tagged. The largest numbers of sea trout in the sea are likely to be found within a few kilometres of their river of origin.

Sea trout are found both in estuaries and full salinity sea water. Post-smolts may tend to remain closer to river mouths and nearer to shore, especially during their first weeks at sea. Sea trout remain primarily in the upper 1-5 m of the water column, but with dives down to nearly 30 m depth. Marine mortality seems largely influenced by density-independent factors and not by density-dependent factors.

Sea trout are among the lesser studied salmonids in the marine environment. Sea trout populations therefore have been monitored over the long-term for only a very few catchments. There is little information in many areas of the British Isles and Scandinavia of the status of the sea trout populations. There also is little information on natural variation in marine survival, the major sources of risk and mortality for sea trout, and how and why sea survival may change in space and time.

Anthropogenic impacts other than salmon lice on sea trout populations

The status of sea trout stocks and fisheries varies across the distribution range, according both to local and regional factors. Human-derived impact factors that may act on sea trout in freshwater include acidification, other aquatic pollution (e.g. from agriculture, roads and mining), hydropower development, other river flow regulation, migration obstacles and habitat alterations. In the marine environment, in addition to salmon lice, human-derived impact factors include also the construction and deployment of harbours, piers, bridges, fish farm structures and other industrial developments. However, there is little information on how such structures and their associated activity may impact sea trout. Climate change, overexploitation in fisheries, and increased risk of diseases caused by increased occurrence, or introduction of, new viruses, bacteria, fungi and parasites due to fish farming all are impact factors that may affect sea trout in both the freshwater and marine phases. There is local and regional variation in which human impact factors are the most important.

Several anthropogenic factors can impact sea trout populations simultaneously, and it is often difficult to isolate and analyse the effects of single factors in wild populations. The interactive effects of two or more impact factors may be complex, non-linear and unpredictable.

Climate change is an impact factor that interacts with other anthropogenic influences, including the effects of salmon lice. Negative effects of salmon lice might become more severe over larger geographical areas as a result of climate change, and northerly populations will likely be increasingly impacted. Sea trout populations of reduced population size and genetic variability, and with less variation in life history traits attributable to other impacts, are expected to be less robust in adapting to climate change.

Historical outline of salmon lice studies in sea trout

In the case of the salmon aquaculture industry, the first outbreaks of salmon lice infestation occurred in Norwegian Atlantic salmon farms during the 1960s, soon after cage culture began. Similar outbreaks occurred in Scottish Atlantic salmon farms from the mid-1970s onwards. In Ireland in 1989-1991, heavily salmon lice-infested wild sea trout in poor physical condition were for the first time registered to undergo premature migratory return to freshwater. The same phenomenon was documented in Norway from the early 1990s. Since then, a large number of relevant physiological and ecological studies have been undertaken, and which form the basis for this review. These range from investigations of the effects of salmon lice on individual fish in the laboratory and the field, to analyses of their impacts on populations in the wild.

Evaluation of sampling and monitoring methods

The acquisition of accurate and representative data on salmon lice levels on sea trout is challenging because of the variation in the life history, behaviour and interactions of both the host and the parasite. As is well known for many other parasite species, salmon lice are aggregated on their hosts. Often, this leads to a skewed distribution where a few individuals within a population can have very high numbers of lice. On the other hand, one of the fundamental problems in sampling is that the likelihood of capturing fish is dependent on the levels of salmon lice. For example, highly infested sea trout may have returned to brackish water and freshwater or died at sea and therefore there is a risk of excluding observations of the highest salmon lice levels. Studies based on sampling sea trout in, or close to, river mouths might lead to an overestimation of the salmon lice levels if mainly prematurely returned sea trout are captured. Conversely, river outfalls are also used by fish that only recently entered the sea and are yet to be infested, and data from these fish may in some periods lead to underestimation of salmon lice levels. This natural variability and complex distribution poses requirements on data sampling and data analysis; large amounts of data are needed in order to confidently describe the statistical relationships between the parasite larval pool and occurrence of salmon lice on the wild fish. In addition, there are several methodological issues about the practicalities involved; e.g. sampling gear, counting and analysis methods all require careful consideration when planning and undertaking the sampling and monitoring.

Effects of salmon lice on individual sea trout in laboratory studies

Laboratory studies have shown that salmon lice may induce osmoregulatory dysfunction, physiological stress responses, anaemia, reduced feeding and growth, increased susceptibility to secondary microbial infections, reduced disease resistance and increased mortality in individual sea trout. Osmoregulatory dysfunction is likely caused both by the mechanical damage of the skin and tissue *per se* and is an expression of overall physiological stress responses. Mechanical abrasion and impairment of the barrier between the fish body and seawater results in increased leakage of water from the host individual, and thereby affects its overall osmotic and ionic balance.

Although large numbers of chalimus stages on the fins can cause severe tissue damage, the so-called “mobile” preadult and adult life cycle stages of salmon lice generally cause more severe tissue erosion than do the earlier attached stages. Physiological stress responses may, however, be triggered also by chalimus stages, especially for fish carrying heavy salmon lice burdens. Stress responses therefore typically become more severe when the salmon lice develop into the mobile stages. Salmon lice-induced fish mortality tends to be incurred within 10-20 days of exposure to copepodids in the laboratory, by which time the salmon lice have developed to the preadult and adult stages.

Effects of salmon lice on individual sea trout in field studies
There is concordance between laboratory and field studies regarding the patterns of mechanical damage induced by salmon lice, their physiological impacts on the host fish, and the fact that salmon lice may cause mortality and reduced growth of individual fish. Field studies have confirmed laboratory observations that salmon lice may induce osmoregulatory dysfunction, physiological stress responses, anaemia, reduced growth, increased susceptibility to secondary microbial infections and increased mortality. Field studies also confirm that osmotic imbalance may be detectable at moderate levels of salmon lice. Host fish stress responses increase with increasing salmon lice levels. Chalimus larval stages alone may cause severe erosion of epidermal and dermal host tissues when present in large numbers.

Premature migratory return of salmon lice-infested sea trout to freshwater has been documented in Ireland, Scotland and Norway. Premature return is interpreted as an adaptive response by the host to salmon lice-induced osmoregulatory dysfunction in seawater. Return to freshwater may, in the short term, enable the fish to regain osmotic balance and survive. Return to freshwater also allows short-term recovery from salmon lice infestation, because salmon lice have a low freshwater tolerance. In the long term, however, growth opportunities and future fecundity of individuals may be greatly reduced by an abbreviated sea migration caused by salmon lice.

Salmon lice levels in samples of wild sea trout
Salmon lice on sea trout in areas lacking salmon farming, or in locations sampled prior to the commencement of farming, generally show low intensities (mean density per infested fish), although prevalences (proportion of fish infested) can be high by late summer. The natural background salmon lice intensity on sea trout in farm-free areas may be as low as 0-3 lice per fish and with a prevalence of 0-20% in late winter and spring. This may increase to a peak of up to 4-8 lice per fish and higher prevalence in the late summer and autumn. Even in areas lacking salmon farms, a few host individuals can carry salmon lice burdens that may exert negative impacts on their growth and survival.

There are no published records of salmon lice epizootics on wild sea trout in farm-free areas. There are, however, historical reports of epizootics for other wild salmonid species in Canada in the early 20th century. Salmon lice epizootics seem not to be a common phenomenon for sea trout or other wild salmonids in farm-free areas.

Salmon lice levels on sea trout in farm-intensive areas vary considerably among studies − ranging from levels resembling those recorded in farm-free areas to those indicating a risk of significant lice-induced mortality. In areas where sea trout are heavily infested, individual hosts rarely carry the adult lice stage, and chalimus larval stages accordingly predominate. This may be attributable to high salmon lice levels at that locality. Alternatively, it is possible that heavily infested fish are not effectively sampled because those that had carried preadult and adult lice stages might already have died, or perhaps they had returned prematurely to freshwater before the lice could develop to the mobile stages.

Large-scale field studies from Ireland, Scotland and Norway indicate an elevated risk of salmon lice-induced mortality of sea trout in areas with high salmon lice levels. Due to uncertainties regarding how representative the sampled fish actually are of the entire host population, it is difficult to extrapolate these data to a quantitative estimate of the population effects for sea trout in farm-intensive areas.

Interactions between fish farming activity and salmon lice levels of sea trout in coastal areas

A number of comparative field studies have demonstrated a link between Atlantic salmon farms and salmon lice levels in wild sea trout, with increased salmon lice levels on wild sea trout closer to salmon farms. Several studies have shown elevated salmon lice levels of wild sea trout, particularly within 30 km of the nearest farms. Elevated salmon lice levels also may be recorded at distances >25-30 km, and models have shown that the planktonic stages of salmon lice larvae can be dispersed >100 km. How far, and in which direction, larvae are transported depend upon numerous variables, including their development rate, water temperature, currents and salinity. Several studies have also shown temporal correlations between salmon lice levels in wild sea trout and year of the production cycle and biomass of fish in adjacent farms, with increased salmon lice levels on sea trout with increased total fish biomass in those farms.

Population effects of salmon lice

Large-scale field studies of growth and marine survival, of groups of experimentally tagged salmonids with prophylactic chemical treatment against salmon lice, have permitted quantification of the population effects of salmon lice by comparing treated fish with un-protected control groups released in parallel. There are few such studies on sea trout, but there are several relevant studies on Atlantic salmon. As expected, these studies showed heterogeneity or variation in the effect of salmon lice among years and rivers, but with fewer unprotected fish returning to their natal rivers to spawn compared to protected fish (range in risk ratio 1.14:1-1.41:1). The overall effect is consistently clear; salmon lice have a potential significant and detrimental effect on marine survival of Atlantic salmon. Meta-analyses and long-term studies, and similar results from an increasing number of experimental studies in Ireland and Norway, support that these are levels of extra mortality (i.e., 12-44% fewer spawners) that can be expected for Atlantic salmon in farm-intensive areas. An extensive meta-analysis applied to all the available published data showing that treatment against salmon lice had a significant positive effect on survival to adult recruitment leading to an estimated risk ratio between treated and untreated of 1.29:1, which corresponds to a potential loss of 39% of adult Atlantic salmon spawners.

The salmon louse-induced mortality from Atlantic salmon studies referred to above should likely best be regarded as minimum estimates for sea trout mortality at the same sites. There is only one similar study in sea trout, which showed 3.4% survival of treated fish and 1.8% of un-treated controls. Although these survival levels are low, they are significantly different and indicate the extent to which spawning abundances of adult sea trout may be reduced in local populations, in this case by almost one half.

Elevated marine mortality rates, such as that induced by salmon lice, result in a proportional reduction in the number of spawning adults. Because sea-run brown trout typically are females, any additional marine mortality has the potential to affect egg deposition and hence ultimately recruitment even more negatively than would be the case were there an equal sex ratio.

The widespread and world-wide occurrence of freshwater resident brown trout populations implies that a marine impact factor such as salmon lice does not increase extinction risk of the brown trout as a species. However, because brown trout is a partially migrating species, reduced marine growth and increased marine mortality will reduce the benefit of marine migrations for individuals in anadromous populations, and may thereby result in selection against anadromy in areas with high lice levels.

Sea trout stock collapses and declines in several farm intensive areas in Ireland, Scotland and Norway have been attributed to increased salmon lice production from Atlantic salmon held in farms. However, the reduction of wild sea trout populations arising from increased mortality and reduced growth that may be caused by salmon lice in farm-intensive areas cannot, in most cases, be quantified because of a lack of field data in combination with associated studies of the population-level effects of salmon lice. In concluding a negative effect of salmon lice on wild sea trout populations, it has also to be acknowledged that there may be considerable variation of sea trout spawning populations among years that is attributable to factors other than lice from salmon farms. At present, effects of salmon lice infestations on sea trout populations are demonstrated to be potentially significant, but are difficult to isolate from other potentially confounding influences.

Sea trout as proxy indicator of salmon lice levels in Atlantic salmon

Sampling wild sea trout will provide valuable data on salmon lice levels over time and between different areas that are relevant to assessments of the risks encountered by Atlantic salmon post-smolts. However, the contrasting migratory behaviour and marine habitat utilization of sea trout and Atlantic salmon may result in salmon lice levels impacting the two host species to a differing extent.

In order to use sea trout as a proxy of infestation risk, and to draw quantitative conclusions on salmon lice levels in Atlantic salmon, knowledge of local environmental conditions should be used in ascertaining (1) how the body size of the larger sea trout captured may affect salmon lice levels compared to the smaller Atlantic salmon post-smolts, (2) whether coastal migration of the two species occurs at the same time, (3) the duration of their exposure to salmon lice, (4) the areas that may have been occupied or traversed by sea trout in the period prior to their capture, (5) how freshwater layers and brackish water in the coastal area may have impacted the results regarding vertical habitat use of the fish, and (6) the possibility that sea trout have remained for a longer time in inshore, freshwater-impacted areas.

To improve precision in the use of sea trout as a proxy indicator, there is a need to analyse separately the data on salmon lice levels from post-smolts and larger sea trout, and also to separate between salmon lice life stages. Sea trout as a proxy cannot be used alone to evaluate salmon lice levels in Atlantic salmon post-smolts, but sea trout data can be used in conjunction with other methods to analyse the overall local salmon lice levels.

Conclusions

The studies reviewed indicate that salmon farming increases the abundance of lice in marine habitats and that salmon lice in intensively farmed areas have negatively impacted wild sea trout populations. The effects of salmon lice on sea trout ultimately are manifest as increased marine mortality and reduced marine growth. These conclusions are based on comprehensive studies of the effects by salmon lice which include:

1) Studies of individual sea trout in laboratory and field studies documenting (i) tissue damage, (ii) osmoregulatory dysfunction and other physiological stress responses, (iii) reduced growth, and (iv) an increased susceptibility to secondary microbial infections and reduced disease resistance.
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 does compromise growth potential and thereby future fecundity by reducing the time spent feeding at sea. Sea trout with excessive skin lesions might also be more vulnerable to fungal and bacterial infection in freshwater than would undamaged fish.
3) Studies based on catch statistics and routine population monitoring utilizing in-river traps that have indicated salmon louse-induced changes in population abundance 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 arising from monitoring of salmon lice levels on wild fish in relation to experimentally determined threshold levels known to induce physiological stress and mortality of individual fish.

In sum, the combined knowledge from the reviewed studies provides evidence of a general negative effect of salmon lice on sea trout 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 (1) a reduction in numbers and body size of sea trout returning to freshwater for spawning, and (2) a reduced or eliminated surplus that can be harvested by recreational and commercial fisheries.

In the extreme, reduced marine growth and increased mortality could result in the local loss of anadromous sea trout populations, particularly in catchments with freshwater conditions unsuitable for brown trout during certain periods of the year. Large catchments with suitable year-round conditions may not face a risk of total loss of brown trout, but a severe reduction or loss of the anadromous life history strategy may result in altered population genetic composition, establishment of populations characterised by freshwater residency, and perhaps reduced overall genetic diversity and less variable life-history characteristics. The loss of the enhanced growth opportunities at sea also may lead to lower total abundance of brown trout, lowered recruitment and loss of the large veteran migrants popular among recreational fishers. These large multiple-spawner fish may make a disproportionately large contribution to overall population egg deposition and perhaps should be a focus of conservation strategies. Some ecological changes may have occurred already for some sea trout populations and catchments in farm-intensive areas, as suggested by some monitoring studies; but a general lack of long-term monitoring of sea trout populations and comprehensive population effect studies makes it difficult to make specific judgements.

Knowledge gaps and research needs

The status of sea trout populations and a basic understanding of putative anthropogenic factors potentially impacting them are not well known for many catchments. In contrast to Atlantic salmon, wild sea trout populations generally have been rather poorly studied, monitored and mapped. With specific regard to the marine environment, the behaviour and survival is less well understood for sea trout than for many other salmonid species. More information is required on sea trout marine migration and foraging areas, relative to marine salmon aquaculture.

The effect of salmon lice on sea trout is a relatively well-studied subject, with a large number of published studies, as shown in this review. The effects of salmon lice on individual sea trout are relatively well documented, both through laboratory and field studies, whereas the most important knowledge gaps are related to effects at the population level and in quantifying the reduction in wild sea trout populations as a result of increased mortality and reduced growth of individual fish caused by salmon lice. For robust and informed evaluation of the effects of salmon lice on sea trout populations, more field experiments comparing survival and growth of fish released to the environment following prophylactic treatment against salmon lice should be undertaken.

SAMMENDRAG

(Summary in Norwegian)

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Lakselus er en ekstern parasitt på laksefisk i sjøen. Oppdrettslaks kan også være verter for lakselus, og åpne merder med oppdrettslaks bidrar derfor til økt produksjon av lakselus i kystområdene. Formålet med denne rapporten er å oppsummere kunnskap om effekter av lakselus på sjøørret basert på gjennomgang av internasjonale vitenskapelige publikasjoner i journaler og bøker med fagfellevurdering (peer-review). Referanser til såkalt “grå litteratur”, som tekniske rapporter, er i liten grad inkludert. Undersøkelsene som er gjennomgått omfatter alt fra laboratorie- og feltundersøkelser av effekter på individuelle fisk til undersøkelser av bestandseffekter.

Lakselus spiser vertsfiskens slim, skinn og vev og forårsaker sår og vevsskader. Laboratorie- og feltundersøkelser har vist at lakselus kan forårsake ubalanse i fiskens osmoregulering (dvs. saltbalanse), fysiologisk stress, anemi, redusert appetitt og vekst, økt sårbarhet for sekundære infeksjoner, redusert sykdomsmotstand og økt risiko for dødelighet hos individer av sjøørret.

Sjøørret i oppdrettsfrie områder har generelt lave nivå av lakselus. I oppdrettsintensive områder varierer nivået betydelig mellom ulike undersøkelser og områder, fra lave nivå sammenlignbart med oppdrettsfrie områder til så høye nivå at de innebærer en risiko for betydelig økt dødelighet forårsaket av lakselus. Flere undersøkelser har vist høyere lakselusnivå på vill sjøørret nær oppdrettsanlegg sammenlignet med lenger unna. Dette er spesielt fremtredende i områder nærmere oppdrettsanlegg enn 30 km. Blant laksefisk er sjøørret særlig sårbar for lakselus fordi de oppholder seg nær kysten under hele sjøoppholdet, i samme type områder som oppdrettsanleggene gjerne er lokalisert.

Basert på undersøkelsene som er gjennomgått kan det konkluderes at lakseoppdrett medfører økt mengde lakselus i sjøen, og at til tross for tiltak som rutinemessig gjennomføres av fiskeoppdrettsindustrien så har ville sjøørretbestander i intensive oppdrettsområder blitt negativt påvirket av lakselus ved redusert vekst og økt dødelighet i sjøen. Reduksjonen i ville sjøørretbestander på grunn av lakselus kan i de fleste tilfeller ikke tallfestes på grunn av mangel på omfattende feltdata og undersøkelser av bestandseffekter.

Bestandseffekter av lakselus har blitt kvantifisert hos laks ved å sammenligne vekst og overlevelse i sjøen hos grupper av utsatt fisk som har blitt kjemisk beskyttet mot lakselus med ubeskyttede kontrollfisk. Det finnes få slike undersøkelser hos sjøørret, men resultatene for laks tyder på at i gjennomsnitt 12-44 % færre gytefisk er potensielle nivå av ekstra dødelighet som et resultat av lakselus i oppdrettsintensive områder. Undersøkelser hos laks representerer trolig minimumsestimat for dødelighet hos sjøørret ved de samme lokalitetene, fordi laksesmolt vandrer raskt gjennom kystnære områder på vei til oppvekstområdene i havet, mens sjøørreten forblir i de kystnære områdene under hele sjøoppholdet.

Lakselus medfører ikke økt fare for at ørret skal utryddes som art, men lusa kan endre livshistoriestrategien hos sjøørreten. Siden bare en del av ørreten vandrer til sjøen, vil redusert vekst og overlevelse minke fordeler ved sjøvandring, og kan dermed resultere i seleksjon mot sjøvandring i områder med høye lusenivå. I ekstreme tilfeller kan slik seleksjon medføre at livshistoriestrategien med sjøvandring forsvinner lokalt. Bestander som utnytter små bekker og elver med ustabile miljøforhold i deler av året, og som dermed er avhengi-

ge av å være i sjøen for å overleve gjennom slike perioder, er spesielt sårbare. For større vassdrag med stabile forhold for ørret gjennom hele året er det en mindre risiko for tap av ørreten. En betydelig reduksjon eller tap av sjøvandrende individer kan imidlertid medføre (1) redusert framtidig rekruttering, og (2) redusert eller tapt høstbart overskudd av ørret for fiske.

Tap av vekstmuligheter for ørret i sjøen og redusert rekruttering til gyting kan totalt sett medføre redusert produksjon av ørret, og at det blir færre storvokste individ som gjerne er målet for fiskere. Slike individer bidrar i tillegg med store bidrag til eggdeponering i bestanden. Effekter av lakselus kan også medføre endret genetisk sammensetning og diversitet blant sjøørret, samt at sjøørretbestander kan endres til å bli mer ferskvannsstasjonære. Overvåking av ville bestander tyder på at slike endringer allerede har skjedd i noen vassdrag i oppdrettsintensive områder. Mangel på omfattende langtidsovervåking av sjøørretbestander og undersøkelser av bestandseffekter av lakselus medfører imidlertid at det ofte er vanskelig å trekke slike konkrete konklusjoner.

Tema for denne rapporten er effekter av lakselus på sjøørret, men sjøørretbestander påvirkes også av andre menneskeskapte påvirkninger. Det er lokal og regional variasjon i betydningen av ulike påvirkningsfaktorer, og status for sjøørreten varierer innen utbredelsesområdet. Andre menneskeskapte påvirkningsfaktorer inkluderer klimaeffekter, forurensing, overfiske, og sykdommer forårsaket av virus, bakterier, sopp og andre parasitter. Noen av disse påvirkningene kan knyttes til økt oppdrettsaktivitet, vannkraftproduksjon og andre elvereguleringer, vandringshindre og habitatendringer. Effekter av samspill mellom to eller flere slike påvirkningsfaktorer kan være komplekse og uforutsigbare. For sjøørretbestander som er utsatt for negative menneskeskapte påvirkninger både i ferskvann og sjøen, er det behov for koordinerte tiltak.

Det er et godt kunnskapsgrunnlag om effekter av lakselus på individuelle sjøørret, og de viktigste kunnskapsbehovene er knyttet til effekter på bestandsnivå. Tallfesting av reduksjon av ville sjøørretbestander på grunn av økt dødelighet og redusert vekst (og dermed fekunditet) bør være et prioritert forskningsområde. For bedre å forstå bestandseffekter, er det behov for mer detaljert og omfattende kunnskap om sjøørretens vandringsatferd i sjøen, hvilke områder i sjøen de benytter og sårbarhet for lakselusinfestasjon. Sammenlignet med laks er sjøørretbestander relativt dårlig undersøkt, overvåket og kartlagt. Dermed er status for sjøørreten og basiskunnskap om hvilke menneskeskapte faktorer som påvirker dem for mange vassdrag ikke godt nok kjent.

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UTVIDET SAMMENDRAG

(Extended summary in Norwegian)

Her gis det et sammendrag av rapporten kapittel for kapittel.

Introduksjon

Lakselus (*Lepeophtheirus salmonis*) er en ekstern parasitt på laksefisk i sjøen. Oppdrettslaks kan også være verter for lakselus, og åpne merder med oppdrettslaks (*Salmo salar*) bidrar dermed til økt produksjon av lakselus i kystområdene. Oppdrettsaktivitet har ikke utvidet utbredelsesområdet for lakselus, men effektene av lakselus på ville laksefisk er potensielt problematiske i områder med intensiv lakseoppdrett i Irland, Norge, Skottland og andre land. Formålet med denne rapporten er å oppsummere eksisterende kunnskap om effekter av lakselus på sjøørret (*Salmo trutta*) basert på gjennomgang av internasjonale vitenskapelige publikasjoner i journaler og bøker med fagfellevurdering (peer-review).

Lakselus klekkes som naupliuslarver fra eggstrengene til voksne hunnlus. De har to planktoniske og frittsvømmende naupliusstadier. Ved det tredje skallskiftet omdannes de til kopepoditter, som er det infektive stadiet der de må finne en vertsfisk for å overleve. Etter at de har festet seg til en vertsfisk, omdannes kopepoditten til det første av to fastsittende chalimusstadier, som etterfølges at ytterligere to skallskifter til preadult og voksent stadium. Lakselus bruker raspende munndeler til å spise av vertsfiskens slim, skinn og vev, og kan forårsake sår og vevsskader.

Ørret gyter i ferskvann, og det finnes både ferskvannsstasjonære og anadrome (sjøvandrende) bestander. Anadrom ørret kalles sjøørret. I anadrome bestander foretar en del av, eller alle, individene vandringer til sjøen for å spise. Innen bestander er det liten genetisk forskjell mellom de sjøvandrende og ferskvannsstasjonære individene, og det kan være betydelig krysning mellom dem. Den anadrome livshistoriestrategien er et trekk som styres av flere gener og miljøpåvirkninger.

Livshistoriestrategier for sjøørret i sjøfasen

Kunnskap om hvor og når sjøørreten er i sjøen er nødvendig for å kunne evaluere sårbarheten for lakselusinfestasjoner, utvikle, forbedre og tolke overvåkingsmetoder, samt utvikle og evaluere tiltak for å redusere effekten av lakselus på ville bestander. Å forstå hvordan lakselus påvirker livshistorietrekk, som sjøvandring, er også viktig for å forstå effekter av lakselus på bestandsnivå.

Det er betydelig variasjon i livshistoriestrategier hos sjøørret, særlig knyttet til tidspunkt og varighet av sjøvandringer. En større andel av sjøørreten er hunner enn hanner, trolig fordi hunner har større fordel av å oppnå stor kroppsstørrelse ved at de får økt eggantall.

Sjøørretsmolten forlater vanligvis elvene og kommer til sjøen for første gang om våren eller forsommeren, mellom februar og juni. Smolten er vanligvis 1-8 år gamle og 10-25 cm lange, og dette varierer med breddegrad og innen og mellom bestander. Sjøørret kan også vandre til sjøen for første gang på andre tider av året. Postsmolt av sjøørret kan oppholde seg i sjøen kun noen måneder om sommeren og deretter returnere til ferskvann for å overvintre, og deretter regelmessig vandre til sjøen og sommeren og tilbake til ferskvann om vinteren. De kan gyte etter første sommer i sjøen, men det er kanskje vanligere at de gyter i andre eller tredje året etter smoltifisering.

Sjøørreten returnerer ikke nødvendigvis til ferskvann etter første sommer i sjøen, men de kan bli værende kontinuerlig i sjøen gjennom sommer og vinter inntil de kjønnsmodnes og returnerer til ferskvann for gyting påfølgende år eller senere. Sjøørret forekommer vanlig i sjøen om vinteren, både i sørlige og nordlige deler av utbredelsesområdet. Varigheten og tidspunktet for sjøvandringer er trolig et resultat av en balanse mellom gevinst i form av vekstmuligheter og kostnader i form av økt dødelighetsrisiko i de ulike leveområdene, og den overordnet mest gunstige strategien kan variere både mellom individer og bestander. Strategien med å bli værende i sjøen om vinteren er trolig vanligere i bestander fra små vassdrag med ustabile og ugunstige forhold for sjøørreten om vinteren. Sjøørret fra små bekker og kystvassdrag med lite vann og perioder med tørke kan oppholde seg i ferskvann bare en liten periode etter klekking og deretter leve i sjøen resten av livet unntatt korte turer til ferskvann for å gyte.

Sjøørreten lever i kystområdene og foretar ikke lange vandringer til åpne havområder. De kan imidlertid vandre ut i åpent kystvann som i Østersjøen og Nordsjøen. Sjøørreten oppholder seg vanligvis innen 80 km eller mindre fra hjemelva si, men noen individer kan foreta lengre vandringer. Det er eksempler på gjenfangster av sjøørret mer enn 500 km fra elva hvor de ble merket. De fleste sjøørretene i sjøen oppholder seg trolig kun opp til noen kilometer fra hjemelva si.

Sjøørreten kan oppholde seg både i brakkvann, estuarier og i fullt sjøvann. Postsmolten kan ha en tendens til å oppholde seg nær elvemunninger og nær land, særlig i de første ukene og månedene av sjøoppholdet. Sjøørreten oppholder seg hovedsakelig nær vannoverflaten når de er i sjøen, i de øverste 1-5 m av vannmassene, men med dykk ned til nesten 30 m dybde. Dødelighet i sjøen synes hovedsakelig å være påvirket av tetthetsuavhengige og ikke tetthetsavhengige faktorer.

Sjøørreten er blant de minst undersøkte laksefiskene i sjøfasen. Kun få sjøørretbestander har blitt langtidsovervåket. Det finnes lite informasjon om status for sjøørretbestander i mange områder på de britiske øyer og i Skandinavia. Det finnes også lite informasjon om naturlig variasjon i sjøoverlevelse, om hovedårsaker til dødelighet, og hvordan og hvorfor sjøoverlevelse varierer over tid og mellom områder.

Andre menneskeskapte påvirkningsfaktorer på sjøørret enn lakselus

Tilstanden for sjøørretbestander og fiske etter sjøørret varierer med påvirkninger av lokale og regionale faktorer gjennom utbredelsesområdet. Menneskeskapte faktorer som kan påvirke sjøørret i ferskvann er forsuring, annen forurensing (f.eks. fra landbruk, veier og bergverk), kraftregulering, andre reguleringer av vannføring, vandringshindre og habitatendringer. I sjøen, i tillegg til lakselus, kan mulige påvirkningsfaktorer være konstruksjoner som havner, moloer, bruer, oppdrettsanlegg og annen industri. Det finnes imidlertid lite kunnskap om hvordan slike strukturer og tilknyttet aktivitet kan påvirke sjøørreten. Klimaendring, overbeskatning i fiske, samt økt risiko for sykdommer forårsaket av økt mengde eller introduksjoner av nye virus, bakterier, sopp og parasitter knyttet til fiskeoppdrett, er også faktorer som kan påvirke sjøørreten både i ferskvann og i sjøen. Det er lokal og regional variasjon i hvilke menneskeskapte påvirkningsfaktorer som har størst betydning.

Flere menneskeskapte faktorer kan virke samtidig på sjøørretbestander, og det er ofte vanskelig å isolere og analysere effektene av enkeltfaktorer for ville bestander. Resultater av samvirkninger mellom ulike faktorer kan være komplekse, ikke-lineære og uforutsigbare.

Klimaendring er en faktor som vil ha betydning for effekten av mange andre menneskeskapte påvirkninger, inkludert effekter av lakselus. Negative effekter av lakselus kan bli mer alvorlig over større geografiske områder som et resultat av klimaendring, og nordlige sjøørretbestander kan i økende grad bli negativt påvirket. Sjøørretbestander med redusert bestandsstørrelse og genetisk variasjon, samt med redusert variasjon i livshistoriestrategier på grunn av andre påvirkninger, vil være mindre robuste til å tilpasse seg raske klimaendringer.

Historisk tilbakeblikk på undersøkelser av lakselus

I oppdrett forekom de første observerte lakselusutbruddene i norske oppdrettsanlegg på 1960-tallet, like etter at lakseoppdrett i sjøen startet. Lignende utbrudd forekom i skotske lakseoppdrettsanlegg fra midten av 1970-tallet. I Irland ble for første gang vill sjøørret med store mengder lakselus og i dårlig fysisk tilstand registrert å returnere prematurt til ferskvann i 1989-1991. Det samme fenomenet ble dokumentert i Norge fra tidlig på 1990-tallet. Siden da har et stort antall fysiologiske og økologiske undersøkelser blitt gjennomført, og disse utgjør grunnlaget for denne rapporten. Undersøkelsene omfatter effekter av lakselus på individuelle fisk i laboratorier, feltundersøkelser og analyser av bestandseffekter.

Evaluering av innsamlings- og overvåkingsmetoder

Innsamling av presise og representative data om lakselusnivå for vill sjøørret er utfordrende på grunn av variasjonen i livshistorie, atferd og interaksjoner både hos verten og parasitten. Som for mange andre parasitter, er lakselus ofte skjevt fordelt mellom individer av vertsfisken. Dette medfører at noen få individer av vertsfisken har veldig store antall lakselus. En av de grunnleggende utfordringene ved innsamling av fisk er at sannsynligheten for å fange individuelle fisk trolig er avhengig av deres lusenivå. For eksempel kan tungt infiserte fisk ha returnert til ferskvann eller allerede dødd i sjøen på grunn av effektene av lakselus, og det er derfor fare for å ekskludere fiskene med de høyeste lusenivåene fra innsamlingen. Undersøkelser basert på innsamling av sjøørret i eller nær elvemunninger kan derimot medføre overestimat av lusenivåene hvis det er hovedsakelig prematurt tilbakevandret sjøørret til ferskvann som samles inn. Men elvemunninger brukes også av fisk som nettopp har kommet ut i sjøen og som ikke er smittet med lakselus enda, og innsamling av mye slik fisk kan medføre et underestimat av lusenivå. Denne naturlige variasjonen og kompleksiteten i utbredelse stiller krav til datainnsamling og analyser, og det er behov for en stor mengde data for å beskrive statistiske sammenhenger mellom parasittmengde og forekomst av lakselus på den ville fisken. I tillegg er det flere metodiske utfordringer knyttet til praktisk datainnsamling, som fangstredskap, telling av lus og analysemetoder, som må tas hensyn til under planlegging og gjennomføring av datainnsamlingen og overvåkingen.

Effekter av lakselus på individuelle sjøørret i laboratorieundersøkelser

Laboratorieundersøkelser har vist at lakselus kan forårsake ubalanse i osmoregulering (dvs. saltbalansen), fysiologisk stress, anemi, redusert appetitt og vekst, økt sårbarhet for sekundære infeksjoner, redusert sykdomsmotstand og dødelighet hos individer av sjøørret. Problemer med saltbalansen er trolig forårsaket både av den mekaniske skaden på skinn og vev, samt en mer generell fysiologisk stressrespons. Mekanisk skade på barrieren mellom fiskekroppen og sjøvannet medfører økt lekkasje av vann fra fisken, og påvirker dermed fiskens saltbalanse.

Et stort antall chalimuslarver på finnene kan forårsake stor vevsskade, men det er de såkalte mobile preadulte og voksne stadiene av lakselus som forårsaker de aller mest alvorlige vevsskadene. Fysiologiske stressresponser kan forårsakes av chalimuslarver, særlig for fisk med et stort antall larver. Stressresponser er mer alvorlige når lakselus har utviklet seg til mobile stadier. Dødelighet av sjøørret på grunn av lakselus begynner å skje 10-20 dager etter at fisken har blitt eksponert for kopepoditter i laboratorieundersøkelser, det vil si når lusene har utviklet seg til preadulte og voksne stadier.

Effekter av lakselus på individuelle sjøørret i feltundersøkelser

Det er samsvar mellom resultater fra laboratorie- og feltundersøkelser når det gjelder hvordan lakselus medfører mekanisk skade på vertsfisken, fysiologiske responser, og redusert vekst og overlevelse. Feltundersøkelser har bekreftet laboratorieundersøkelser som viser at lakselus kan forårsake problemer med saltbalansen, fysiologiske stressresponser, anemi, redusert vekst, økt sårbarhet for sekundære infeksjoner og økt dødelighet. Feltundersøkelser har også bekreftet at problemer med saltbalansen oppstår allerede ved moderate nivå av lakselus. Vertsfiskens stressrespons øker med økende lakselusnivå. Chalimuslarver kan forårsake betydelig vevsødeleggelse hos vertsfisken når de forekommer i store antall.

Prematur tilbakevandring av sjøørret med store mengder lakselus til ferskvann har blitt dokumentert både i Irland, Skottland og Norge. Prematur tilbakevandring tolkes som en adaptiv respons hos vertsfisken på problemer med saltbalansen forårsaket av lakselus. Retur til ferskvann kan på kort sikt medføre at fisken gjenvinner saltbalansen og overlever. Retur til ferskvann medfører også at fisken etter hvert mister lakselusene, fordi lakselus har lav ferskvannstoleranse. På lang sikt blir imidlertid veksten og framtidig fekunditet for individer betydelig redusert når sjøvandringen blir forkortet på grunn av lakselus.

Lakselusnivå hos vill sjøørret
Lakselus på sjøørret i områder uten oppdrettsaktivitet, eller i områder undersøkt før etablering av oppdrettsanlegg, forekommer generelt i lave antall (dvs. med lave intensiteter, som er beregning av antall lus per fisk basert kun på de individene som har lus), selv om andel fisk med lus (dvs. prevalens) kan være høy mot slutten av sommeren. Naturlig nivå av lakselus på sjøørret i oppdrettsfrie områder kan være så lavt som 0-3 lus per fisk, med en prevalens på 0-20 % sent på vinteren og våren. Dette kan øke til en topp opp mot 4-8 lus per fisk og høyere prevalens på sensommeren og høsten. Selv i oppdrettsfrie områder kan noen få sjøørret ha lakselusnivå som er så høye at de kan ha negative effekter på vekst og overlevelse hos vertsfisken.

Det er ingen publiserte registreringer av lakselusepidemier på vill sjøørret i oppdrettsfrie områder. Det finnes imidlertid registreringer av lakselusepidemier på andre ville laksefisk i Canada fra årene 1939-1940. Lakselusepidemier ser ikke ut til å ha vært et vanlig fenomen i ville sjøørretbestander eller hos andre laksefisk i oppdrettsfrie områder.

Lakselusnivå for sjøørret i oppdrettsintensive områder varierer betydelig mellom undersøkelser, fra lave nivåer sammenlignbart med oppdrettsfrie områder til så høye nivå at det er en betydelig risiko for dødelighet forårsaket av lakselus. I områder der sjøørreten har høye lusenivå er det sjelden at det registreres voksne lus på fisken, og chalimusstadier dominerer. Dette kan skyldes høye nivå av luselarver i området. Det kan også skyldes at fisk med preadulte og voksne stadier med lus ikke blir effektivt fanget fordi de allerede har dødd, eller de kan ha returnert til ferskvann før lusene utviklet seg til mobile stadier.

Storskala feltundersøkelser i Irland, Skottland og Norge har vist økt risiko for dødelighet hos sjøørret på grunn av lakselus i områder med høye lusenivå. På grunn av usikkerhet om hvor representative innsamlet fisk er for hele bestander, er det vanskelig å utlede disse dataene til tallfestede estimat av bestandseffekter i oppdrettsintensive områder.

Sammenheng mellom oppdrettsaktivitet og lakselusnivå på sjøørret i kystområder
Flere feltundersøkelser har vist en sammenheng mellom oppdrettsanlegg for laks og lakselusnivå hos vill sjøørret, med økte lusenivå for sjøørret nær oppdrettsanlegg. Flere undersøkelser har vist økte lusenivå hos sjøørret særlig innenfor 30 km fra de nærmeste oppdrettsanleggene. Økte lusenivå kan også registreres lengre unna oppdrettsanlegg enn dette, og modeller har vist at planktonstadiet av lakselus kan spres lengre enn 100 km. Hvor langt og i hvilken retning spredningen skjer kommer an på mange faktorer, som lusenes utviklingshastighet, vanntemperatur, vannstrømmer og saltholdighet. Flere undersøkelser har også vist sammenhenger mellom lusenivå på vill sjøørret og hvilket stadium av produksjonssyklusen fisken i nærliggende oppdrettsanlegg er i. Det er også vist økte lakselusnivå med økt biomasse av oppdrettsfisk i nærliggende anlegg.

Bestandseffekter av lakselus

Storskala feltundersøkelser av vekst og overlevelse i sjøen hos grupper av utsatt fisk kjemisk beskyttet mot lakselus sammenlignet med ubehandlede kontrollgrupper har bidratt til å kunne kvantifisere bestandseffekter av lakselus. Det er gjort få slike undersøkelser av sjøørret, men det er gjort flere relevante undersøkelser av laks. Som forventet er det stor variasjon i effekter av lakselus mellom år og elver, med det er generelt færre ubeskyttede fisk som returnerer til elvene etter sjøoppholdet enn blant dem som er kjemisk beskyttet mot lus (relativ risiko fra 1.14:1-1.41:1). Resultatene viser at lakselus potensielt har en betydelig negativ effekt på sjøoverlevelsen hos laks. Metaanalyser og langtidsundersøkelser, og like resultater fra et økende antall undersøkelser i Irland og Norge, støtter at dette er nivåene av ekstra dødelighet (dvs. 12-44 % færre gytefisk) som kan forventes for laks på grunn av lakselus i oppdrettsintensive områder. En omfattende metaanalyse av alle publiserte data viste at kjemisk behandling mot lakselus hadde en betydelig positiv effekt på overlevelse fra utsetting som smolt til de returnerte som voksne, med estimert relativ risiko mellom behandlet og ubehandlet fisk på 1.29:1. Dette tilsvarer et potensielt tap på 39 % av voksne gytefisk av laks.

Luseindusert dødelighet fra undersøkelser av laks, som beskrevet i avsnittet over, kan betraktes som minimumsestimat for dødelighet hos sjøørret på samme lokaliteter. Det finnes kun én lignende undersøkelse for sjøørret, der overlevelse for behandlet fisk var 3,4 % og for ubehandlet fisk 1,8 %. Selv om disse overlevelsesnivåene er lave så er de signifikant forskjellige mellom behandlet og ubehandlet sjøørret. Resultatene tyder på at det kan være en betydelig effekt av lakselus i form av redusert mengde voksen gytefisk i noen bestander, i dette tilfellet en halvering.

Økt dødelighet i sjøen, som dødelighet på grunn av lakselus, resulterer generelt i en proporsjonal reduksjon i antall voksne gytefisk. Siden sjøørreten i større grad er hunner enn hanner vil enhver reduksjon i sjøoverlevelse kunne medføre redusert eggdeponering og dermed redusert rekruttering i større grad enn om andelen sjøvandrende individer var lik mellom kjønnene.

Den store forekomsten og geografiske utbredelsen av ferskvannsstasjonær ørret medfører at en marin påvirkningsfaktor som lakselus ikke kan øke faren for at ørreten utryddes som art. Siden ørreten er en delvis anadrom art, vil imidlertid redusert vekst og økt dødelighet i sjøen redusere fordelen med sjøvandring for individer i anadrome bestander, og dette kan føre til seleksjon mot anadromi i områder med høye lusenivå.

Reduksjon, og i noen tilfeller kollaps av sjøørretbestander, har blitt knyttet til økt lakselusproduksjon fra oppdrettslaks i flere oppdrettsintensive områder i Irland, Skottland og Norge. Denne reduksjonen av ville sjøørretbestander på grunn av luseindusert dødelighet og redusert vekst kan imidlertid i de fleste tilfeller ikke kvantifiseres på grunn av mangel på overvåkingsdata og undersøkelser av effekter på bestandsnivå. I tillegg kan det også være stor variasjon i størrelse på gytebestander mellom år av andre årsaker enn effekter av lakselus fra oppdrettsanlegg. Selv om det er vist at effekter av lakselusinfestasjoner på sjøørretbestander kan være betydelige, er effekter vanskelig å isolere fra andre potensielle påvirkninger.

Bruk av sjøørret som indikator på lakselusnivå hos laks

Innsamling og analyser av sjøørret frambringer data på lakselusnivå mellom ulike områder og over tid som også er relevante og verdifulle for vurdering av risiko for effekter av lakselus på laks. Forskjeller i vandringsatferd og habitatbruk i sjøen mellom sjøørret og laks kan imidlertid medføre at artene har ulik risiko for å få lakselus.

For å bruke sjøørreten som en indikator for infeksjonsrisiko og kvantitative konklusjoner om lusenivå hos laks, bør kunnskap om lokale miljøforhold benyttes for å vurdere (1) hvordan kroppsstørrelse hos sjøørreten som fanges for overvåking kan påvirke lusenivået sammenlignet med mindre postsmolt av laks, (2) om utvandringen fra ferskvann til sjøen hos de to artene skjer til samme tid, (3) varigheten på eksponering for lakselus, (4) hvilke områder sjøørreten har vandret gjennom og oppholdt seg i før de ble fanget, (5) hvordan ferskvannslag, brakkvann og fiskens vertikale vandringer i området kan ha påvirket lusenivåene, og (6) om sjøørreten som fanges kan ha oppholdt seg i lengre tid i ferskvannspåvirkede områder nær elvene.

For å øke presisjonen ved bruk av sjøørreten som indikator på lusenivå hos laks, er det behov for å analysere data separat for postsmolt og større sjøørret, og også analysere de ulike lusestadiene hver for seg. Sjøørreten kan ikke brukes i overvåking alene for å vurdere lusenivå hos postsmolt laks, men sjøørreten kan brukes sammen med andre metoder for å analysere de generelle lusenivåene.

Konklusjoner

Undersøkelsene som er vurdert i denne rapporten viser at lakseoppdrett øker mengden lus i sjøen, og at lakselus i intensive oppdrettsområder har påvirket sjøørretbestander negativt. Effektene av lakselus på sjøørret kommer til uttrykk som økt dødelighet og redusert vekst i sjøen. Disse konklusjonene baseres på omfattende undersøkelser av effekter av lakselus og inkluderer:

1) Undersøkelser av individuelle sjøørret i laboratorie- og feltundersøkelser som dokumenterer (i) vevsødeleggelse, (ii) problemer med osmoregulering og andre fysiologiske stressresponser, (iii) redusert vekst, og (iv) økt sårbarhet for sekundære infeksjoner og redusert sykdomsmotstand.
2) Undersøkelser som dokumenterer prematur tilbakevandring til ferskvann av sjøørret med høye nivå av lakselus. Prematur tilbakevandring kan medføre økt overlevelse og redusert lusenivå for individer, men reduserer deres potensial for vekst og dermed potensiell framtidig fekunditet fordi tiden de oppholder seg i sjøen blir redusert. Sjøørret med betydelige skader i skinnet kan også være mer sårbare for sopp og bakterieinfeksjoner i ferskvann enn uskadd fisk.
3) Undersøkelser basert på fangststatistikk og rutinemessig bestandsovervåking ved bruk av fiskefeller som har vist endringer i bestandsstørrelser og endrede livshistoriekarakteristikker knyttet til lakselus.
4) Overvåking av lusenivå hos vill fisk.
5) Sammenligning av lusenivå i oppdrettsintensive og mindre oppdrettsintensive områder.
6) Indikasjoner på bestandseffekter hos sjøørret basert på overvåking av lakselusnivå i feltundersøkelser sett i sammenheng med terskelnivå for fysiologisk stress og dødelighet hos individuelle fisk fastsatt ut fra eksperimentelle undersøkelser.

Kombinert kunnskap fra undersøkelsene som er gjennomgått i denne rapporten viser at lakselus har hatt en generell negativ effekt på sjøørret i intensivt oppdrettede områder i Irland, Skottland og Norge. Prematur tilbakevandring til ferskvann, redusert vekst og økt dødelighet i sjøen på grunn av økte lakselusnivå innebærer (1) reduksjon i antall og kroppsstørrelse for sjøørret som vandrer tilbake til ferskvann for gyting, og (2) et redusert eller eliminert høstbart overskudd for sportsfiske og kommersielt fiske.

I ekstreme tilfeller kan redusert vekst og økt dødelighet i sjøen resultere i tap av lokale sjøørretbestander, særlig i vassdrag som har ugunstige forhold i ferskvann for ørret i enkelte perioder av året. For større vassdrag med brukbare forhold for sjøørret gjennom hele året er det trolig ikke en stor risiko for totalt tap av ørretbestander, men en betydelig reduksjon eller tap av anadrom livshistoriestrategi (dvs. sjøvandring) kan resultere i endret genetisk sammensetning av bestanden, etablering av bestander karakterisert av ferskvannsstasjonæritet og kanskje redusert genetisk diversitet og mindre variasjon i livshistoriekarakteristikker. Tapet av gode vekstmuligheter i sjøen kan også medføre lavere total forekomst av ørret, redusert rekruttering og tap av de store individene som er populære blant fiskere. De store gytefiskene bidrar også uforholdsmessig mye til eggdeponering, og bør derfor kanskje være sentrale for bevaringsstrategier. Noen økologiske endringer kan ha skjedd allerede for sjøørretbestander og vassdrag i oppdrettsintensive områder, som noen overvåkingsundersøkelser tyder på. En generell mangel på langtidsovervåking av sjøørretbestander og undersøkelser av bestandseffekter medfører at det generelt er vanskelig å vurdere dette.

Kunnskapsbehov
Status for sjøørretbestander og forståelse av menneskeskapte påvirkningsfaktorer som potensielt kan påvirke dem er for mange vassdrag ikke godt nok kjent. Sammenlignet med laks har sjøørretbestander blitt lite undersøkt, overvåket og kartlagt. Spesielt når det gjelder atferd og overlevelse under sjøoppholdet finnes det lite kunnskap om sjøørreten sammenlignet med mange andre arter laksefisk. Det er behov for mer kunnskap om sjøvandringer og hvilke områder de bruker, sett i sammenheng med marin akvakultur.

Effekter av lakselus på sjøørret er et relativt godt undersøkt tema, med et stort antall publiserte undersøkelser, som vist i denne rapporten. Effektene av lakselus på individer av sjøørret er godt dokumentert, både gjennom laboratorie- og feltundersøkelser, mens de viktigste kunnskapsbehovene er knyttet til effekter på bestandsnivå og til å kunne kvantifisere reduksjonen av ville bestander på grunn av økt dødelighet og redusert vekst for individuelle fisk på grunn av lakselus. For å kunne evaluere effekter av lakselus på sjøørretbestander er det behov for flere felteksperiment med sammenligning av overlevelse og vekst under sjøoppholdet mellom fisk behandlet kjemisk mot lakselus og ubehandlede kontrollgrupper.

Foreword

The aim of this project was to summarize available knowledge on effects of salmon lice on sea trout to provide the aquaculture industry, wild fishery managers and researchers with a comprehensive and updated knowledge status. Knowledge gaps are also identified. The literature review is based primarily on international publications in peer-reviewed journals or books. In order to establish a solid and justifiable knowledge base on the effects of salmon lice on sea trout, the main focus is on international publications in scientific journals and books that have undergone independent peer-review evaluation and are available through conventional channels such as literature search bases and libraries. Where they are especially relevant, observations and data published in technical reports also have been referred to.

The authors of the report constitute an international group of scientists, from several institutions in Ireland, Norway and Scotland. A reference group was established to serve as advisors for the authors of the report. Members of the reference group were Morten A. Bergan (NINA), Jan G. Davidsen (Norwegian University of Science and Technology, NTNU), Geir Magne Knutsen (Bremnes Seashore AS) and Ketil Rykhus (Norwegian Seafood Federation, FHL).

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Bengt Finstad
Project leader

1 Introduction

Salmon lice (*Lepeophtheirus salmonis*) are external parasites on salmonids in the marine environment (**box 1**). They occur naturally on wild salmonids in the North Atlantic and North Pacific Oceans. Aquaculture activities have not extended the natural geographic distribution range of salmon lice, but because farmed salmonids also act as hosts for salmon lice, open net cage farms can increase the production of infective salmon lice larvae in coastal areas. The effects of salmon lice on wild salmonid populations are potentially problematic in areas with intensive Atlantic salmon (*Salmo salar*) aquaculture in Ireland, Norway, Scotland and other countries (Finstad et al. 2011). Amongst salmonids in the northern Hemisphere, sea trout − the anadromous form of brown trout (*Salmo trutta*) (**box 2**) − are perhaps especially vulnerable to salmon lice infestation because they typically remain feeding and growing in coastal waters where salmon farms are situated. By contrast, juvenile Atlantic salmon typically leave coastal waters quickly and migrate to offshore or oceanic feeding areas. Never the less, Atlantic salmon smolts in some locations, such as the extensive fjords of western Norway, may have an extended migration of >100km before gaining access to offshore waters.

Brown trout have been one of the most popular and highly prized fish species for European anglers for centuries, and are pursued for their fighting abilities and value as food. For these reasons, this species has been introduced to many countries outside their natural distribution range, and has now a world-wide distribution (Klemetsen et al. 2003). Sea trout have an especially high social and economic importance as a resource for recreational angling in both freshwater and seawater (Harris & Milner 2006, Butler et al. 2009). However, since the late 1980s and early 1990s, some sea trout populations in western European countries including Norway, Scotland and Ireland have suffered severe stock declines. Such population declines have been linked to the development of open net cage salmon farming in coastal waters and with resultant salmon lice infestation on local wild sea trout stocks (Tully & Whelan 1993, Gargan et al. 2003, 2006a,b, Butler & Walker 2006, Skaala et al. 2014b).

The aim of this report is to summarize and review existing knowledge on the effects of salmon lice on sea trout. The work is based on a thorough literature review of international publications in peer-reviewed journals and books. We are aware that there is a large body of so-called “grey literature” on this issue. Grey literature includes informally published material such as technical reports that are not widely accessible and difficult to trace through conventional channels. Grey literature usually does not have an independent peer review quality control, or may have a quality control system that is difficult to assess. In order to establish a solid and justifiable knowledge base on the effects of salmon lice on sea trout, we have focused primarily on international publications in scientific journals and books that have undergone independent peer-review evaluation before publication, and that are available through conventional channels such as literature search bases and libraries. Observations and data published in technical reports have been referred to in a few cases. When references are made to grey literature, this is made clear in the text by stating that the reference is a technical report. We would like to stress the importance of publishing important data through quality controlled channels, and thereby make results available to a wider scientific audience. Using such publication channels also means scientific work is made available to criticism by other scientists after publication. This is not only an appeal to other scientists, but also to funding agencies and other clients to provide sufficient funding to enable scientists to publish their work in international scientific journals in addition to inclusion in technical reports.

Literature searches for this report were made through the Thomson Reuters Web of Science database and ProQuest Biological Sciences database with different combinations of the key words “sea trout”, “brown trout”, “*Salmo trutta”*, “salmon lice”, “sea lice”, “*Lepeophtheirus salmonis”* and “marine migration”. In addition, several authors of this report have undertaken research on salmon lice and sea trout for many years, and their collections of scientific literature were used, as well as searching through reference lists of previous publications. The aim was to cover publications on effects of salmon lice on sea trout as extensively as possible.

There are several previous reviews on the effects of sea lice on salmonids published in international journals or books (e.g. Pike & Wadsworth 1999, Todd 2007, Ford & Myers 2008, Costello 2009, Finstad et al. 2011, Finstad & Bjørn 2011, Torrissen et al. 2013). The present review differs from these in that it covers specifically and thoroughly the effects of salmon lice on sea trout. Previous reviews have to a larger extent embraced salmonids in a wider context, with much focus on Atlantic salmon and sea lice in general, including effects of the sea louse *Caligus elongatus*. Here, the focus is primarily, but not exclusively, on sea trout and salmon lice. Thus, for example, in chapter 10 there is necessarily some discussion of the results of recent papers reporting on large-scale experimental releases of Atlantic salmon smolts treated with anti-parasiticides.

Specifically, the objectives of this report are to:

- Provide the aquaculture industry, wild fishery managers and researchers with a comprehensive and updated overview of documented knowledge on the effects of salmon lice on sea trout. This includes physiological and pathological effects on individual sea trout in laboratory studies, verification of effects from field studies and impacts on sea trout populations (chapter 6-10).
- Provide a historical outline of documentation of salmon lice infestations and effects of salmon lice on sea trout (chapter 4).
- Evaluate sampling methods for wild sea trout and the methodology and analysis for monitoring salmon lice levels in wild populations (chapter 5).
- Evaluate the use of results from sea trout as a proxy for the estimation of salmon lice levels on migrating Atlantic salmon smolts (chapter 11).
- Review knowledge on habitat use and migration patterns of sea trout in the marine environment relevant to their potential exposure to, and effects of, salmon lice (chapter 2).
- Discuss the effects of salmon lice *versus* other influences on wild sea trout populations (chapter 3, 10 and 12).
- Identify knowledge gaps and research needs (end of each chapter and chapter 13).

Box 1 Salmon lice and their life cycle

Salmon lice, with the scientific name *Lepeophtheirus salmonis*, are marine parasitic copepods and belong to the family Caligidae. They occur mainly on salmonids in the North Atlantic Ocean, but also in the North Pacific Ocean (Pike & Wadsworth 1999). Salmon lice in the Atlantic and Pacific oceans are regarded as two different sub-species (Skern-Mauritzen et al. 2014). Salmon lice are planktonic and free-living in the sea during the first, post-hatching, larval life-stages, before they attach externally to the surface of the host fish.

The life cycle of salmon lice comprises five phases, namely the nauplius, copepodid, chalimus, preadult and adult phases, which are further described below (Johnson & Albright 1991b, Pike and Wadsworth 1999, Boxaspen 2006, Costello 2006, Hayward et al. 2009, **figure 1**). Each phase comprises one or two life stages, and the life cycle has a total of eight life stages. Each life stage is separated from the preceding stage by a moult, which involves shedding of the outer cuticle, exposing a new cuticle underneath. The life cycle was previously divided into ten stages, but it has been suggested recently (Hamre et al. 2013) that there are in fact only two chalimus stages, and not four as previously reported.

The first phase of the life cycle (**figure 1**) is the free-swimming, planktonic **nauplius phase** (two stages). Nauplius I larvae are released to the water column from female egg strings at hatching. Following the first moult to nauplius II, the larva then moults to the still free-swimming **copepodid phase** (one stage), which is the infective stage when the salmon louse must find a host fish to survive. Once the copepodid has attached to a host fish by a frontal filament it moults into the **chalimus phase** (two stages, separated by a moult). The sessile chalimus larvae remain attached with the frontal filament and feeding is restricted to the host skin around the attachment point. This phase is followed by the immature **preadult phase** (two stages/moults) and finally the **adult phase** (one stage). The louse becomes mobile from the first preadult moult and can move over the body surface of the host fish. Preadults and adults also can swim in the water column for short periods and perhaps successfully infest other fish. Both the nauplius I and II stages, and the copepodid stage prior to attachment to the host fish, are non-feeding and the larva subsists on reserves provided by the female within the egg. Attached copepodids, chalimus larvae, preadults and adults feed on host mucus, skin and underlying tissue including blood (Brandal et al. 1976, Costello 2006).

Salmon lice use rasping mouthparts to graze the host and remove mucus, skin and tissue. It is usually the mobile preadult and adult stages that cause the most severe lesions, although chalimus larvae may cause severe erosion of the skin, fins and dermal musculature when occurring in large numbers. As skin damage and lesions develop and extend, host fish may be vulnerable to osmoregulatory dysfunction, physiological stress, secondary microbial infections and ultimately mortality (see chapter 6 and 7).

Adult salmon lice typically are light to dark brown in colour, and the sexes can be distinguished by morphology and body size (females 10-18 mm, males 5-7 mm, Pike & Wadsworth 1999, Hayward et al. 2011). Females undergo internal fertilisation of eggs prior to their extrusion into a pair of external egg sacs, or egg strings, which are up to 2 cm long. Each of the two egg sacs can contain up to 500 eggs (Pike & Wadsworth 1999). Each female may extrude up to 11 pairs of sacs with fertilised eggs (Pike & Wadsworth 1999) over a period of months. Hence, a large number of offspring may be produced over the life time of each female, but the maximum longevity of salmon lice on wild fish remains unknown.

The planktonic stages may last up to 1-2 months (Heuch et al. 2005). This means that in areas with strong currents, the free-swimming and infective stages may be widely dispersed from the source (perhaps up to 100 km or more; Asplin et al. 2011, 2014). Salmon lice are absent from sites with low salinity (Pike and Wadsworth 1999, Bricknell et al. 2006) and are shed by the host fish after a few days or weeks if that fish re-enters freshwater (McLean et al. 1990, Finstad et al. 1995) (see also **box 3**).

A lower prevalence of salmon lice on sea trout in late winter may be due to a decline in reproduction and survival during winter, followed by growth of salmon lice populations under warmer water conditions (Boxaspen 2006). However, salmon lice can develop into the infectious stage during winter, even though biological processes slow down with low temperatures. A water temperature of 4°C or higher is probably required for salmon lice to complete their life cycle. The effects of high temperature on salmon lice is poorly documented, but Boxaspen (2006) observed that salmon lice were absent from salmon farms when water temperatures exceeded 18°C.

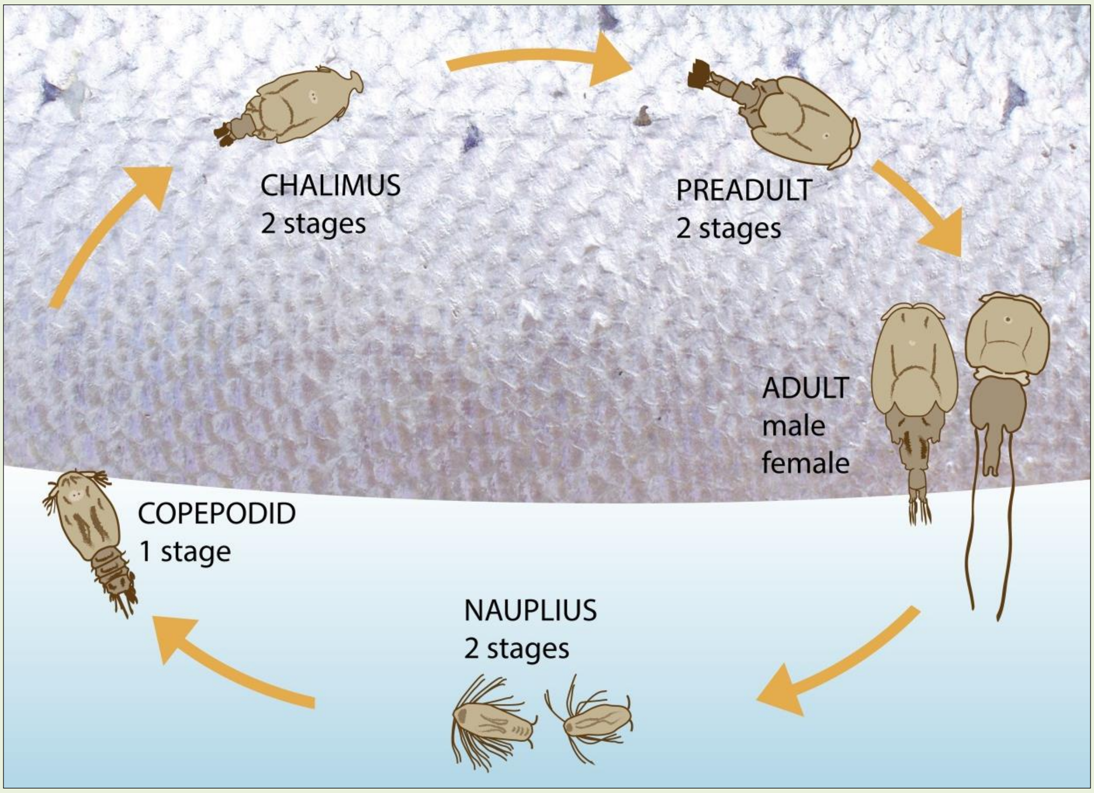


Figure 1. *Life cycle of salmon lice.*

Box 2 Brown trout / sea trout

The brown trout, with the scientific name *Salmo trutta*, belongs to the family Salmonidae. The species is indigenous to Europe, North Africa and western Asia, but has been widely introduced to other parts of the world (Klemetsen et al. 2003). Brown trout are found in a wide range of habitats, from small streams to large rivers, lakes and coastal marine areas. They spawn only in freshwater. Anadromous brown trout that migrate to marine habitats for feeding are termed sea trout and are the main focus in this report.

Migrate to sea or not?
Brown trout occur both as freshwater resident and anadromous populations, and is a partially migrating species (Klemetsen et al. 2003, Solomon 2006, Jonsson & Jonsson 2011). Individuals of freshwater resident populations may undertake migrations between different freshwater habitats, such as between rivers and lakes. In anadromous populations, some or all individuals undertake feeding migrations to marine habitats, often repeatedly during their life time (so-called veteran migrants). Anadromous and freshwater resident individuals are difficult to identify and distinguish between by external appearance (Koksvik & Steinnes 2005).

Within populations, there is little genetic differentiation between anadromous and resident individuals, and there is significant interbreeding between the two types (Jonsson & Jonsson 2006a,b). Migrant and resident brown trout within rivers can spawn separately, or they can spawn together successfully, and may be freely interbreeding fractions of a single spawning stock (Jonsson & Jonsson 2006a,b). Freshwater residents can have sea trout mothers and *vice versa* (e.g. Limburg et al. 2001). Anadromy is a quantitative trait that is controlled both by multiple genes and environmental influences (Ferguson 2006). In individual water systems, the balance of costs and benefits associated with freshwater residency and anadromy may result in evolution of different life-history strategies coexisting within the same water system, likely as a result of frequency-dependent selection (Ferguson 2006, Solomon 2006).

Sea trout populations are well studied in only a few catchments (e.g. Pemberton 1976b, Pratten & Shearer 1983a,b, Berg & Berg 1987a,b, 1989, Elliott 1993b, Byrne et al. 2004, Jonsson & Jonsson 2009a, Jensen et al. 2012a). However, there probably are several thousand rivers and streams that contain sea trout populations, although the populations are poorly mapped and incompletely studied. There is little information on the total number of populations, and quantitative information on the proportion and number of anadromous *versus* resident individuals and other life history traits in the different populations is largely lacking.

Why migrate to sea?
For anadromous fishes, the migration between freshwater and the marine environment is seen as a life-history strategy of adaptive value, with individuals utilizing the optimal habitat during different stages of the life cycle in order to increase individual fitness (Gross et al. 1988, Lucas & Baras 2001). The advantages of marine migrations for sea trout include the opportunities to access more productive feeding conditions to enhance growth, fecundity and thereby evolutionary fitness. Often there is a greater tendency for female brown trout to undertake marine migrations (see chapter 2). Females may have a greater advantage compared to males by increasing their body size, and hence egg production. Conversely males can adopt either a strategy of becoming large and dominate the spawning ground, or choose the alternative tactic of maturing at a very small size and undertaking ‘sneaking’ matings as precocious males during spawning, and therefore attain significant reproductive success without the costs of migration (Jonsson & Jonsson 2011). The costs of migrating to sea may be related to the physiological demands of the smoltification process, an increased risk of predation and the energetic investment necessary during migration itself.

The particular life history strategy adopted, and mixture of residency and anadromy reflected within a population, is likely that which over the long term maximises reproductive potential under the prevailing conditions for individuals of that population. There seems to be stability in such patterns, but stocks also can change their migratory habits and the tendency for marine migration *versus* residency, especially when introduced to new areas or when a major environmental factor changes (Solomon 2006). If marine mortality rates are high and/or feeding conditions in the marine environment are relatively poor, then freshwater residency may be favoured as the optimal life-history strategy over anadromy (Solomon 2006).

Sea trout from Ireland. Photo: William Roche

Sea trout life cycle

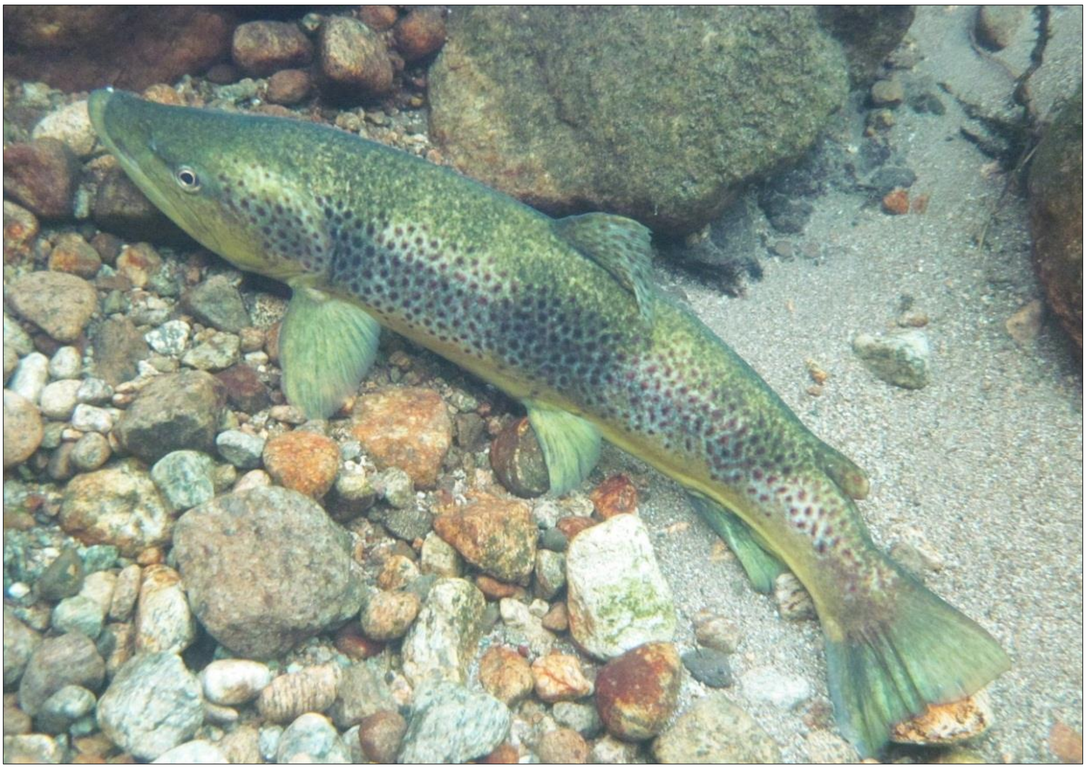
Brown trout spawn in freshwater rivers and streams in the autumn and the eggs hatch the following spring. Spawning in lakes may also occur. Sea trout remain in rivers or lakes for 1-8 years (most commonly 2-4 years) before they undertake their first marine migration. They are then usually 11-25 cm long, but this varies among populations. They may remain in fjords and coastal areas until summer or autumn before returning to freshwater, or they may stay at sea for one to two years or more before returning to freshwater. Long-distance migrations to the open ocean are not common. Many sea trout populations include individual fish which may undertake repeated marine migrations during their life-time, and they may repeatedly spawn in multiple years. Sea trout are known to home to their natal stream for spawning.

Life history strategies and marine migrations of sea trout are described in more detail in chapter 2.

2 Life history strategies of sea trout at sea

Knowledge of when and where sea trout are located at sea is required to evaluate their vulnerability to salmon lice infestations, to develop and improve monitoring methods, to interpret salmon lice monitoring results and to develop and evaluate mitigation measures to reduce impacts of salmon lice on wild populations. Understanding how salmon lice affect life history traits, such as partial migration, also is important in order for fishery managers to fully comprehend the potential effects of salmon lice impacts at the population level.

This chapter provides a review of life history strategies, behaviour and habitat use of sea trout in the marine environment, including their timing and duration of marine migration, the distance of migrations, feeding, growth, survival and homing. This chapter therefore provides background ecological information on sea trout which is used as a basis for discussions in later chapters of the report.



Sea trout from Espedalselva, Norway. Photo: Ulrich Pulg

2.1 Life history strategies and duration of marine migration

The brown trout is a remarkably adaptable species showing considerable life-history variation within and among populations (Klemetsen et al. 2003). Brown trout, including sea trout, spawn in freshwater and remain in freshwater during the juvenile phase. After 1-8 years in freshwater, sea trout undergo smoltification (L'Abée-Lund et al. 1989, Jonsson & L'Abée-Lund 1993) and undertake either brief or prolonged feeding migrations to the marine environment over the remainder of their life. Some sea trout remain largely at sea, excepting brief spawning migrations to freshwater (e.g. Pemberton 1976a, Borgstrøm & Heggenes 1988, Järvi et al. 1996). The proportion of female brown trout undertaking marine migration(s) typically is the greater (Jensen 1968, Pemberton 1976b, Pratten & Shearer 1983a, Euzenat 1999, Knutsen et al. 2004, Olsen et al. 2006, Solomon 2006, Jensen et al. 2012a), but equal sex ratios among migrants also have been reported (Elliott 1993a). Sea trout mostly are at sea and feeding there during the summer months, but considerable variation is shown among individuals and populations, to the extent that some may remain at sea also during the winter months .

Sea trout display marked variation in the timing and duration of their marine migration. They may spawn after just the one summer at sea, but others may delay first reproduction until having spent two, three or more summers at sea (e.g. Järvi 1040, Went 1962, Jensen 1968, Fahy 1978, L'Abée-Lund et al. 1989, Jonsson & L'Abée-Lund 1993, Euzenat 1999, Skaala et al. 2014a). Sea age at first maturity typically increases with latitude (L'Abée-Lund et al. 1989, Jonsson & L'Abée-Lund 1993) and is dependent not on in-river growth rate, but on growth rate at sea (L'Abée-Lund 1994). A higher freshwater age at smoltification may reduce age at maturity (L'Abée-Lund et al. 1989, L'Abée-Lund 1994). Males usually attain maturity at a younger age than do females (22 of 31 studied populations; L'Abée-Lund et al. 1989).

The sea trout is an iteroparous species, which means that individuals may spawn two or more times during their lifetime. According to several authors, sea trout spawn annually after their first spawning (Jensen 1968, Pemberton 1976b, Jonsson & Jonsson 2009b, L'Abée-Lund 1994). They can spawn at least five times according to Went (1962) and at least seven times according to Euzenat (1999), and a sea age up to 13 years has been recorded (L'Abée-Lund et al. 1989). The sea age of 50% maturity was 0.5 years in the south and 3 years on the north for European populations ranging between 54 and 70°N (Jonsson & L'Abée-Lund 1993).

The typical pattern is for sea trout to migrate down rivers and enter the sea for the first time (as smolts) in spring or early summer (Jensen 1968, Gargan et al. 2006a, Jonsson & Jonsson 2009b). Some fish return to freshwater in the autumn, following a few months at sea, and they are variously known as finnock, harvesters, whitling, juniors or post-smolts (Went 1962, Jensen 1968, Fahy 1978, Pratten & Shearer 1983a, Euzenat 1999, Gargan et al. 2006a). These fish may regularly spend their summers at sea and winters in freshwater, as described by Berg & Berg (1989) and Skaala et al. (2014a). In a north Norwegian river, sea trout were observed to repeat the annual feeding migration to the sea for about two months every summer, irrespective of their sexual maturity status (Berg & Berg 1989, Berg & Jonsson 1989, 1990). Marine residence time averaged 68 days during the summer months, with yearly means ranging from 54 to 88 days (Berg & Berg 1989): fish that descended first typically undertook the longest stay at sea, the duration of which increased with sea temperatures (Berg & Berg 1989). When autumn river levels were low, the upstream migration was delayed and the duration of marine migration was accordingly extended (Berg & Berg 1989). Both in that river, and another river in western Norway (Jensen 1968), males were recorded as staying at sea for a shorter period than did females.

Sea trout are frequently recorded in the sea during the winter months in many geographic areas (Svärdson & Fagerström 1968, Pemberton 1976b, Knutsen et al. 2004, Olsen et al. 2006, Jensen & Rikardsen 2008, 2012). Therefore, and by contrast to the foregoing, sea trout in certain locations and regions may remain at sea continuously for a year or more, until they mature and return to freshwater to spawn (see also Järvi 1940). These trout are termed maidens, and are known in Ireland and Great Britain to be an important component of the spawning stock (Went 1962, Fahy 1978, Pratten & Shearer 1983a, Gargan et al. 2006a). The large variation among individual sea trout in their timing and duration of marine migration also is apparent from long-term studies in a south Norwegian river where the sea trout population has been monitored since 1976 (Jonsson & Jonsson 2002, 2009b). Jonsson & Jonsson (2002) report a run of first-time migrants to sea both in spring and autumn. The mean annual duration of the marine migration there was 6-9 months for first-time migrants moving to sea between January and June, and 8-18 months for those migrating to sea between July and December (Jonsson & Jonsson 2009b). Mean duration of the marine migration was longer for first-time migrants than for veterans and individual variation in time at sea ranged from 1 month to 3 years (Jonsson & Jonsson 2009b). Hence, one component of the population remained over winter in the river while another overwintered either in the estuary or at sea (Jonsson & Jonsson 2002).

Some sea trout have adopted life history strategies apparently intermediate to freshwater residency or anadromy, with some fish migrating only to estuarine areas, or undertaking repeated and relatively brief movements between freshwater and the sea (Pratten & Shearer 1983b, Chernitsky et al. 1995, Koksvik & Steinnes 2005). For example, sea trout captured in a large Scottish freshwater loch during winter had carbon stable-isotope values indicating either a repeated movement between freshwater and marine environments, or estuarine residency (Etheridge et al. 2008). One third of the muscle tissue in winter was derived from marine resources (Etheridge et al. 2008). Frequent movements between freshwater, estuary and sea during winter were also recorded for individually tagged sea trout in a north Norwegian river (Jensen & Rikardsen 2012). Most (91%) of those sea trout were recorded in the estuary and at sea during the winter months, but there was marked individual variation both in habitat use and behaviour. The shortest stay in saltwater was only a few hours, and the longest continuous stay was 39 days. Individuals made, on average, 23 habitat shifts between freshwater, estuary and the sea during the winter. The mean total number of days spent in the estuary during the winter was 34 days whilst the at-sea mean was 50 days. Euzenat (1999) reported that sea trout from two French rivers in winter could have short visits to estuaries and lower parts of rivers other than their river of origin. In a Russian Barents Sea river, part of the sea trout population seems to feed only in the brackish estuary, whereas another part of the same population has more distant coastal migrations (Chernitsky et al. 1995). Those sea trout feeding in the estuary move up and down the estuary twice daily with the tides, and thereby always remain in fresh or brackish water (Chernitsky et al. 1995). The advantage of sea trout remaining in estuaries may relate to the productivity of that habitat and the attendant feeding opportunities for brown trout, but there may be other benefits with a shorter migration − including the avoidance of some marine predators − and salinity is lower such that fish may not necessarily be required to adapt physiologically to full-salinity sea water. However, the physical and biological characteristics of estuaries show considerable variation and it is therefore difficult to generalize.

The specific life-history strategy adopted by a sea trout, the duration of its marine migration, and whether or not an individual resides in the sea, estuary or freshwater during winter, is likely governed by trade-offs between the costs and benefits associated with those different habitats and strategies. The most advantageous strategy may vary both among individuals within populations, as well as among populations, and depends ultimately on the habitat-related differences in survival rates and growth opportunities. The most beneficial strategy also may depend on the particular status (e.g. gender, size, age, energetic stores) of the individual fish, as has been shown for Atlantic salmon (Halttunen et al. 2013). Furthermore, Jonsson & Jonsson (2009b) have suggested that sea trout may choose the winter habitat as a consequence of a density-dependent mechanism which balances mortality risk against metabolic costs. They suggested that if this is correct, the proportion of sea trout spending the winter in freshwater should be greater in large rivers than in small streams.

The strategy of remaining at sea during winter may be more frequent amongst populations utilizing small catchments. Smaller catchments may provide unstable or relatively poor winter conditions for sea trout, whereas larger rivers offer more stable water flow, large pools and perhaps even lakes where the sea trout can remain during winter (Knutsen et al. 2004, Olsen et al. 2006, Östergren & Rivinoja 2008, Jensen & Rikardsen 2012). Low water discharge, and potentially also ice build-up in more northern areas, may confer adverse environmental winter conditions for salmonids due to a restriction of over-wintering possibilities. Low water levels also may increase their vulnerability to bird and mammal predators. Jensen & Rikardsen (2008, 2012) suggested that sea trout may exploit different strategies in rivers with and without lakes, and that the tendency to reside in marine areas over the winter is greater for rivers lacking integral lakes. A significant proportion of Irish sea trout populations overwinter in lakes (Gargan pers. obs.). Östergren & Rivinoja (2008) found that sea trout spawning both in tributaries and the main stem of a large Swedish river over-wintered in the main stem of the river under ice cover in deep, slow-flowing sections where water depth was ≥2 m.

Other studies have shown that the spawning migration to freshwater was of very short duration, and likely constrained by low and unstable discharge and drought periods in the relevant rivers and streams (Pemberton 1976b, Borgstrøm & Heggenes 1988, Järvi et al. 1996). Knutsen et al. (2004) and Olsen et al. (2006) all have suggested that the sea trout captured at sea in their studies originating from brooks and small coastal streams with poor over-wintering conditions, and that following smoltification these fish remained in freshwater for only short periods to spawn. Because sea growth in terms of increased body length was rapid in the summer, but did not continue during autumn and winter, this extended stay in marine areas during autumn and winter may not have been linked to the potential for growth, but rather to increased survival and reduced migratory costs (Olsen et al. 2006). Increased levels of stored lipids during the winter months (November-April) never the less indicated that marine feeding during winter may represent a valuable and important source of food acquisition in order for individual fish to maintain or increase their body condition (Rikardsen et al. 2006).

Some coastal streams exploited by sea trout can be very small, and commonly typified by low and variable water discharge, which in some periods may result in their running dry (Titus & Mosegaard 1989, Järvi et al. 1996, Landergren & Vallin 1998, Limburg et al. 2001). The dependency on the marine habitat throughout the lifetime of individuals therefore will be much greater for such streams compared to large, stable rivers, and the coastal zone may provide an important refuge and/or nursery habitat especially during early life (Järvi et al. 1996, Limburg et al. 2001). Out-migration at a small size and young age is thought to comprise a response to low and unreliable water discharge in small streams (Borgstrøm & Heggenes 1988, Titus & Mosegaard 1989, Järvi et al. 1996). From such streams draining to the Baltic Sea, it has even been observed that young-of-the-year parr may emigrate from freshwater and enter the coastal zone (Limburg et al. 2001, Landergren 2004). In one study, the smallest parr were those that migrated downstream, and these individuals might otherwise have been out-competed by larger territory-holders in the stream (Landergren 2004). In another study, there was no difference in body size between fry migrating to sea and those remaining in the stream (Järvi et al. 1996). Laboratory experiments showed that high initial fry density, and fluctuating or decreasing water depth, increased the number of out-migrating parr (Landergren 2004). Hence, out-migration of parr in these small streams seems to be generated by competition for food and space following emergence from the redd, and may be promoted by variable hydrological conditions (Landergren 2004). Laboratory data show that growth and survival of young-of-the-year parr are not negatively affected by transfer to brackish water of salinity as high as 6.7 (Landergren 2001). It has been speculated that sea trout may even spawn in brackish water in the Baltic, but egg development is inhibited at salinities exceeding 4.0, so spawning at higher salinities is likely not to lead to successful development (Landergren & Vallin

1998). However, in stream outlets where the salinity is lower than 4.0, such spawnings can contribute to the recruitment (Limburg et al. 2001).

2.2 Timing of seaward migration

Sea trout migrating to sea include both first-time migrants and veterans that may be sexually immature or mature. First-time migrants generally are termed smolts at the time they emigrate from freshwater, and post-smolts once they enter the marine environment. Smolts usually are 1-8 years old and 10-25 cm in length. Smoltification is a process of physiological, morphological and behavioural changes preparing juveniles for life in saltwater (Høgåsen 1998). However, sea trout may move from freshwater to brackish water without having undergone smoltification (Tanguy et al. 1994, Landergren 2001, Limburg et al. 2001). Hence, although first-time sea migrant sea trout may not necessarily always be characterized as true smolts, they are consistently referred to as such in the scientific literature and the present report.

2.2.1 Smolt age

Sea trout typically undergo smoltification and migrate to sea for the first time when between 1 and 8 years old (Went 1962, Fahy 1978, L'Abée-Lund et al. 1989, Jonsson & L'Abée-Lund 1993). In a study including 102 European populations (54-70°N), mean smolt age increased from 2.1 years in the south to 4.5 years in the north (Jonsson & L'Abée-Lund 1993). More specifically, along the Norwegian coast between 58 and 70°N, mean smolt age for populations varied between 1.5 and 5.6 years, with mean smolt age tending to decrease with increased river and adjacent sea temperatures (L'Abée-Lund et al. 1989). British Isles sea trout show a similar smolt age range of 1 to 6 years, and smolt age also was found to increase there with latitude although 5 and 6 year old fish are rare (Fahy 1978). For Irish sea trout, again smolt ages of 1-6 years have been recorded, with 2 and 3 year old fish being the most common (Went 1962, Poole et al. 1996). By contrast, in a study from the Netherlands, 75% of the sea trout captured at sea had reared for only the one year in freshwater before migrating to sea, with 20% first migrating at two and 5% at three years of age (de Leeuw et al. 2007). Similarly, in French rivers, smolt age was typically 1 or 2 years, and 3-year old smolts were the exception (Euzenat 1999). One complication, that cannot be accounted for in cases where emigrant smolts are monitored as an entire population at or near to the outfall of the river catchment, are within-river spatial variations in smolt age structure. Thus, for example, L'Abée-Lund (1994) have shown that sea trout juveniles from the upper stretches of a river tended to undergo smoltification at an older river age compared with those rearing in the lower reaches.

2.2.2 Smolt size

Mean sizes of sea trout smolts varied between 10.7 cm and 25.2 cm among the 102 European populations assessed by Jonsson & L'Abée-Lund (1993), but no correlation was apparent between smolt size and latitude. However, within more restricted geographic areas, such as along the Norwegian coast, mean smolt size was noted to increase with latitude but decrease with increasing adjacent sea temperature (L'Abée-Lund et al. 1989). Individual smolt sizes within Norway varied between 6 and 32 cm, with population means of between 10.7 and 22.6 cm (L'Abée-Lund et al. 1989). British Isles sea trout have smolt sizes commonly ranging between 15 and 23 cm (Fahy 1978, Pratten & Shearer 1983a), and in Irish rivers, smolt size was similarly reported as averaging 17-25 cm (Went 1962). Mean smolt size in some French rivers was 20 cm and 90 g, with body lengths ranging from 11 to 33 cm.

Within populations, smolt age tends to depend on freshwater growth rate, with faster-growing parr typically undergoing smoltification at a younger age and smaller size than slow-growing parr (Økland et al. 1993). Hence, there appears to be no simple threshold size that regulates the age at smolting. Rather there is a complex interaction between size, age and growth rate that might be viewed as comprising a trade-off between expected benefits and costs imposed by differences in individual growth rate (Økland et al. 1993).

2.2.3 Timing of seaward migration for first-time migrants

Sea trout smolts typically migrate downriver to the sea in spring or early summer, and generally from end of February to June (Pratten & Shearer 1983a, Byrne et al. 2004, Carlsen et al. 2004, Gargan et al. 2006a, Bohlin et al. 1993, Euzenat 1999, Jonsson & Jonsson 2009b, Jensen et al. 2012a). For Atlantic salmon, the timing of the migration has an important role in determining smolt survival in the marine environment, and it is believed that Atlantic salmon smolts are adapted to use environmental cues in rivers that may predict favourable ocean conditions and for them to initiate downstream migration (Thorstad et al. 2012). Preference for specific ocean temperatures could be explained by increased smolt mortality due to low salinity tolerance at low sea temperatures (Thorstad et al. 2012). Increased survival at higher sea temperatures also may be linked to match-mismatch hypotheses, and in that context specifically to prey availability and which may be expressed as growth-mediated survival. The importance of temperature may also be manifest in increased swimming performance that may enhance predator avoidance at higher temperatures. Hence, from a range of standpoints, it could be argued that the timing of the Atlantic salmon smolt run is locally adapted to meet the most optimal environmental conditions in the sea (Thorstad et al. 2012).

Similar mechanisms and ecological challenges may apply to the timing of sea trout smolt migration, but there are few appropriate studies of sea trout at this particular life stage. As discussed below, the tendency for sea trout smolts from southern populations to migrate earlier than smolts from more northern populations may be explicable by sea temperatures reaching preferable or optimal levels later in the season further north. However, there are indications that sea trout also may be adapted to migrate to sea with timing perhaps to match the most favourable marine conditions. Thus, for example, Kallio-Nyberg et al. (2007) found that for hatchery-reared sea trout smolts released to the Baltic Sea, recapture rates indicative of survival were improved for fish released at warmer (4-16°C) temperatures than was recorded from releases at lower water temperatures. Furthermore, they found that recapture rates were greater for fish released in May than in April or June. Kallio-Nyberg et al. (2006, 2007) have, however, suggested that this phenomenon might ultimately be an expression of prey availability and not necessarily sea temperature *per se*. In conclusion, it is apparent that sea trout, like Atlantic salmon, are adapted to respond to in-river environmental cues to initiate downstream migration such that may encounter favourable ocean conditions. The duration of the main smolt emigration run in sea trout may last for one or two months. The migration period seems generally longer, and occurs in less discrete and well-defined periods, than has been inferred for Atlantic salmon (Thorstad et al. 2011, 2012).

The onset of the physiological smolt transformation is triggered by daylength, whereas water temperature regulates the rate and duration of the smoltification process itself (Høgåsen 1998, Byrne et al. 2004). Once fish have smoltified, and are physiologically capable of migration to saltwater, a proximate stimulus initiates the migration (Høgåsen 1998, Byrne et al. 2004, Nielsen et al. 2006). The stimulus for downstream migration of sea trout smolts may include environmental influences such as water temperature and water flow in the spring (Bohlin et al. 1993, Hembre et al. 2001, Aarestrup et al. 2002, Byrne et al. 2004, Carlsen et al. 2004, Jonsson & Jonsson 2009b, Jensen et al. 2012a).

In a river in southern Sweden, the number of degree-days (sum of average temperature for all days >4°C from March 1), and changes in water level/flow and water temperature, all increased the number of smolts migrating (Bohlin et al. 1993). By contrast, for a river in southern Norway, increased water temperature – but not water flow – influenced the timing of the seaward migration of smolts, but not of older/veteran migrants in springtime (Jonsson & Jonsson 2002). The colder the river temperature in February-March, the later in the spring did the smolts move to sea (Jonsson & Jonsson 2009b). For autumn-migrating fish, an increase in water discharge stimulated downstream migration, especially for smolts (Jonsson & Jonsson 2002). Sea trout smolts from a river in central Norway migrated to sea within a one-month period, with the majority of individuals migrating within only a 1-2 week period (Hembre et al. 2001). Few smolts descended when the river discharge was <50 m^3s^{-1} and water temperature <4°C. The relative importance of high water discharge and temperature as triggers or initiators of smolt migration has been shown to vary among years (Hembre et al. 2001). Smolt migration has been monitored for 22 years in a river in northern Norway, and water flow and temperature – as well as changes or interaction between both factors – could explain day-to-day variation in the smolt migration (Jensen et al. 2012a). The main migration period – as defined by the days between the first and third quartiles of the total smolts migrating – extended over an average of only 28 days (Jensen et al. 2012a). In that particular river, smolt migration occurred at water temperatures as low as 0°C, but there were few migrants noted at temperatures <3°C (Carlsen et al. 2004).

In an Irish river where smolt migration was monitored over an extended period (1971-2000), the absolute water level, followed by change in water level, water temperature and photoperiod, all affected day-to-day variation in the number of migrating smolts (Byrne et al. 2004). Mean duration of the entire smolt run (from start to finish – cf. the quartile metric of Jensen et al. 2012a) was 118 days, whereas the mean duration of the middle 50% of the smolt run (first to third quartiles) was 69 days. The smolt run shifted from discrete and well-defined periods during the 1970s to more dispersed and less distinct runs during the 1990s. Thus, for example, 50% of the run occurred within 57 days during the 1970s and over as much as 73 days during the 1990s (Byrne et al. 2004). The smolt migration occurred at river temperatures ranging between 5 and 13°C (Byrne et al. 2004) but river temperature alone could not account for the observed inter-annual, and longer term, changes and shifts in smolt migration behaviour and timing.

Other studies, which were temporally more restricted, have shown that, for example in a river in southern Sweden, smolt migration occurred mainly between 3 May and 6 June, but with a few individuals starting as early as late March and the last migrants being recorded in early July (Svärdson & Fagerström 1982). In another river in southern Sweden, 90% of the smolts migrated over a period of 29 days, with the median date ranging from 26 April to 17 May (Bohlin et al. 1993).

In early quantitative sampling studies of western Scottish sea lochs, the first post-smolts were recorded in marine catches from mid-May onwards (Pemberton 1976b). In one particular study year, the smolt migration was one month later than normal, and likely due to freshwater drought (Pemberton 1976b). Annual smolt runs recorded in various Scottish rivers (rather than sea lochs) have been reported as occurring from the end of March to mid-May, but with variation in timing of the peak of the run among years ranging from as early as April to as late as the first half of May (Pemberton 1976b). On the basis of the aforementioned Norwegian and Irish studies, it is likely that this variation was related primarily to prevailing environmental conditions, with heavy rain during March and April in the earliest year, and a 7-week drought period during the latest year being especially influential (Pemberton 1976b). In contrast to the west Scotland data presented by Pemberton 1976b), for a Scottish east coast river, the peak smolt migration has been reported occurring in May-June, but with the first migrants noted in April and the last as late as August (Pratten & Shearer 1983a).

Sea trout smolts in a central Norwegian river have been shown to typically migrate to sea during the middle period, or the second half, of May (Hembre et al. 2001), and in a northern Norwegian river, the median migration date has been noted as late as 4 July (Jensen et al. 2012a), albeit with substantial annual variation, and 30 days between the earliest and latest median date for migration (Jensen et al. 2012a). Of some interest was the observation that sea trout smolts migrated to sea approximately two weeks later than did Atlantic salmon smolts in the same river (Carlsen et al. 2004), suggesting that the proximate triggers and initiators of migration are not necessarily the same for these two species. In an additional northern Norwegian river, the main month of sea trout entering the sea was shown to be June, but with some downstream migration also noted in May (Berg & Berg 1989).

Larger sea trout smolts tended to migrate earlier in the season in a Swedish river and in French rivers (Bohlin et al. 1993, 1996 Euzenat 1999). A similar pattern was found for a northern Norwegian river, whereby smolt length increased during the main migration period, but decreased again later in the summer (Jensen et al. 2012a). Svärdson & Fagerström (1982) recorded that the earliest migrants were among the youngest smolts. In a west coast Irish river, larger smolts predominated in the earlier portion of the smolt run each year, with a general tendency towards smaller smolt sizes as the migration progressed (Gargan et al. 2006a).

In some rivers there is an additional autumn run of first-time migrants to sea (Pemberton 1976b, Poole et al. 1996, Jonsson & Jonsson 2002, 2009b), and these typically are smaller than the smolts migrating in the spring of that year. A migration of new recruits (10-17 cm long) from freshwater to Scottish sea lochs also was noted to occur in the autumn, between September and November (Pemberton 1976b). These latter fish were smaller, younger and showed a greater proportion of males in comparison to the spring-migrating smolts (Pemberton 1976b). In a river in southern Norway, the autumn-migrating smolts left the river at the time when the larger sea trout re-entered, and Jonsson & Jonsson (2002) deduced that it may be advantageous for the juveniles to leave the river before the more aggressive adults gather on the spawning grounds. It is not known, however, whether these fish migrated only to the estuary and remained there over the winter, or whether they migrated further out along coastal waters. Poole et al. (1996) regarded these autumn migrants as unsmoltified trout based on their unsilvered coloration, and their river age ranged from 0+ to 3+ years. Survival of these autumn migrants was low, and total return of tagged fish was only 1.7%.

2.2.4 Timing of seaward migration for veteran migrants

So-called veteran migrants include those sea trout that have undertaken previous marine migrations. They may include either immature individuals, or mature individuals that have spawned in freshwater (kelts).

Kelts remain in-river for varying periods of time and after spawning, with variations seen both within and among individuals in a population and between catchments. In some catchments, all or most sea trout may remain in freshwater over the winter (e.g. Jensen 1968, Berg & Berg 1989, Östergren & Rivinoja 2008). In other watersheds, there may be considerable individual variation, with some individuals returning to sea almost immediately following spawning and yet others remaining in freshwater for weeks or months before returning to sea (Aarestrup & Jepsen 1998, Euzenat 1999, Jensen & Rikardsen 2008). Aarestrup & Jepsen (1998) recorded that individually tagged sea trout spent an average 70 days (range, 2-163 days) in freshwater in association with spawning in a Danish river, but the extent of their variable residence was not correlated either with fish size or age. Jensen & Rikardsen (2008) found that most of their tagged sea trout in a northern Norwegian river re-entered the sea almost immediately after spawning in late September to early October, although a small proportion remained in-river until February. In a Scottish river, kelts were recorded migrated downstream over an extended period from November (immediately following spawning) to as late as May in the subsequent calendar year (Pratten & Shearer 1983a). River size and flow discharge may well be important determinants of post-spawning residence in freshwater and, for example, in small streams with low and unstable water flow, most kelts may leave the stream soon after spawning (Pemberton 1976b, Borgstrøm & Heggenes 1988).

Fish trap in River Imsa, Norway (left) and Burrishoole, Ireland (right), where wild sea trout populations are monitored. Photos: Eva B. Thorstad

The optimal duration of the post-spawning freshwater residence may depend not only on flow regime and its stability, but ice conditions, relative food availability (compared to the marine environment) and relative predation risk all might also be relevant. Furthermore, the relative water temperature difference between the two habitats also may influence the optimal duration of freshwater residence, because of the temperature dependence of metabolic costs (Jobling 1994). Finally, because the energy reserves of post-spawners typically are generally very low (Jonsson & Jonsson 1998), individual and gender-related variation in post-spawning energy reserves also may affect the length of freshwater stay. For example, stable over-wintering conditions in freshwater may confer a more benign habitat for sea trout, with fewer potential predators than in coastal waters. And even though food availability in autumn/winter may be low in the river, in northern areas subject low river temperatures or even freezing, the metabolic costs also are very low until water temperatures increase in the following spring. For example, for Atlantic salmon it was found that the timing of kelt migration to sea was dependent on individual energy reserves (Halttunen et al. 2013). Individual salmon with low energy reserves tended to migrate early to the more hazardous, but more productive, marine habitat whereas individuals with greater energy reserves remained in-river until their energetic costs related to water temperature increased to a level that demanded outward migration (Halttunen et al. 2013). There may, therefore, be marked variations among catchments and watersheds in the typical local winter conditions which may affect whether or not sea trout kelts tend to remain in-river for an extended period during the winter. Individual migration timing may, in addition, be the proximate outcome of an adaptive state-dependent use of habitat, related both to individual and sexual differences in energy allocation during spawning. In this context, it is pertinent perhaps that male sea trout kelts migrated to sea earlier than females (Jensen 1968, Östergren & Rivinoja 2008), similar to that observed for Atlantic salmon (Halttunen et al. 2013). This may reflect a lower bioenergetic status of males, attributable to their differential allocation of energy and resources during spawning.

During spring, larger and older veteran sea trout often descend to sea earlier than do the smolts (Pemberton 1976b, Berg & Jonsson 1989, Jonsson & Jonsson 2002). Water flow seems not to influence the timing of this seaward migration of veteran migrants in spring (Jonsson & Jonsson 2002, Östergren & Rivinoja 2008), and this may reflect a lesser vulnerability of larger sea trout to environmental variations and perturbations that may influence their success in adapting to marine conditions.

In conclusion, kelts may migrate to sea immediately after spawning, or may remain in freshwater for a few further months; or perhaps they can even delay migration to sea again until the following spring or early summer. For this specific behavioural pattern there is both individual variation (which may depend upon, for example, bioenergetic status) and variation among catchments (which may be linked to the comparative quality of the winter freshwater and marine habitats).

2.3 Timing of return from sea to freshwater

Sea trout returning from the sea to freshwater include both immature fish returning for winter residency, and mature individuals undergoing the spawning migration. In a river in southern Norway, where sea trout migrations were monitored since 1976, sea trout ascended the rivers in all months over the period April to December, but with the main upstream migration (72%, Jonsson & Jonsson 2002) occurring between August and October. There was no difference between small and large trout in their timing of upstream migration and, for veteran migrants, the timing of return in the autumn was independent of the timing of their previous seaward migration (Jonsson & Jonsson 2009b). Early in the migration season, when water discharge generally was higher (Jonsson & Jonsson 2002), increased water discharge stimulated upstream migration. In a river in western Norway, upstream migration commenced in July and continued until November (Jensen 1968). Males tended to enter the river earlier than did females (Jensen 1968). The opposite was found in French rivers, where a larger proportion of males entered the rivers late in the season (Euzenat 1999). In those rivers, the upstream migration extended from May to January, and occurred in two distinct runs, with fewest upstream migrants in August-September (Euzenat 1999). The relative importance of the two runs varied among the studied rivers, with the autumn run being the more important in the river with irregular and low summer flow (Euzenat 1999). In a Scottish river, first-time migrants (so-called finnock) returned to the river in July of the same calendar year that they migrated to sea; return continued until March of the following year, with most migrating upstream in August-October (Pratten & Shearer 1983a). Older sea trout returned to the river over the period May-October.

As for Atlantic salmon, sea trout spawning occurs in the autumn months, but the timing varies among populations. In rivers in northern Norway and Sweden, spawning is reported to occur in September and October (Berg & Jonsson 1990, Östergren & Rivinoja 2008, Jensen & Rikardsen 2012), whereas in Scotland spawning extended from early November to the first week of December (Campbell 1977). In the Norwegian river where spawning occurred in October, the attendant return migration was between July and September (Berg & Berg 1989, Berg & Jonsson 1990), whereas observations from a study in Scottish sea lochs indicated that upstream migration occurred only shortly before spawning and that spawners in freshwater remained as briefly as possible, perhaps in response to unstable flow-rates in those rivers (Pemberton 1976b).

Wild large-grown sea trout from River Vefsna in Northern Norway.
Photo: Eva B. Thorstad

2.4 Distance of marine migration

Sea trout at sea typically remain in near-coastal areas and do not commonly undertake long-distance migrations to the open ocean (e.g. Jensen 1968, Pemberton 1976b, Pratten & Shearer 1983b, Berg & Berg 1987a, Berg & Jonsson 1989, Davidsen et al. 2014, Jensen et al. 2014). However, in Norwegian waters, sea trout may feed offshore in the outer regions of fjords or in nearby open-coast areas. For example, sea trout have been sampled in pelagic waters and at distances up to 5 km offshore (Rikardsen & Amundsen 2005). Rikardsen & Amundsen (2005) refer to a personal communication from J.C. Holst (Institute of Marine Research, Norway) in stating that during years of research trawling for Atlantic salmon post-smolts in the Atlantic Ocean several miles offshore from the coast, no sea trout have been captured. Examples of individuals showing longer-distance marine migrations have, however, been reported in the literature. From a large tagging programme in a river on the east coast of Scotland, one smolt crossed the North Sea and was recaptured in southern Norway; others were recaptured in Sweden, Denmark, and even from a river on the Scottish west coast (Pratten & Shearer 1983b). These four recaptures all were made >500 km distant from the river where they were tagged. For the Baltic Sea, Gulf of Bothnia and Gulf of Finland, long-distance open water migrations of sea trout also have been recorded (Svärdson & Fagerström 1982, Kallio-Nyberg 2002). Pratten & Shearer (1983b) suggested that open ocean migrations may therefore actually be rather more common than is generally indicated from recapture programmes, perhaps owing to a lack of suitable fisheries to enable tag recaptures in the areas to which trout are migrating.

Sea trout tagged in a northern Norwegian river remained primarily within 40-80 km of the river mouth, with only 0.3% of recaptures >80 km distant and 53% made within only three km of the river mouth (Berg & Berg 1987a, Berg & Jonsson 1989). A few individuals were noted to migrate further, and of 2628 recaptured fish, three (two in the sea and one in a river) were recaptured >400 km away. There was no correlation between fish size and migration distance (Berg & Berg 1987a, Berg & Jonsson 1989). Those sea trout migrating a longer distance apparently followed the coastal current in a northward direction (Berg & Berg 1987a). Groups of hatchery-reared smolts were released in a fjord in southern Norway, and recaptures were made at a mean distance of 21-72 km away from the release site (Jonsson et al. 1995), and from tagging studies in a river in western Norway, all recaptures were made within 70 km of the release river, with most made within 10-15 km (Jensen 1968). Similarly, and from a large tagging programme on the east coast of Scotland, numerous recaptures were made >100 km away from the river where they were tagged and released (Pratten & Shearer 1983b). Of hatchery-reared fish released in the Gulf of Finland, 83-89% of all recaptures were within the Gulf itself and the remainder of the tags were retrieved from the main basin of the Baltic, or in the Gulf of Bothnia (Kallio-Nyberg

2002). Recaptures in the latter study typically were made within 200 km of the release site, although 2.5-6% were retrieved at distances exceeding 200 km from the release site. The most distant recaptures were >800 km from the release site (Kallio-Nyberg 2002). There are, however, indications of age-related variations in migration distances. Thus, for example, Svärdson & Fagerström (1982) found that sea trout in the fourth year following their first sea migration were recaptured closer to their home river than were younger fish, and they concluded that these older trout may typically make significantly shorter marine migrations than do younger trout.

In addition to migrations being influenced by local environmental conditions, there may also be a partial genetic control of migration distance (Svärdson & Fagerström 1982, Jonsson et al. 1995, Kallio-Nyberg et al. 2002), as indicated by the distance between the release site and that of recapture differing between stocks of sea trout (Jonsson et al. 1995). Certainly, differences between stocks were found for hatchery-reared sea trout released to the Baltic Sea in Finland (Kallio-Nyberg et al. 2002), and the likelihood is that this may well extend to natural stocks and populations.

2.5 Habitat use in coastal areas

2.5.1 Habitat use

Sea trout in coastal areas exploit a range of habitats, and may reside in estuaries, at sea in full-salinity seawater, or may move repeatedly between estuaries and adjacent marine areas (e.g. Finstad et al. 2005, Pemberton 1976b, Middlemas et al. 2009, Jensen & Rikardsen 2012, Davidsen et al. 2014, Jensen et al. 2014). Seasonal variation in habitat use may also occur; sea-trout seemed to move out of Scottish sea lochs in spring and early summer into fully marine conditions and to return to sea lochs and embayments in late summer and autumn (Pemberton 1976b). A seasonal difference in habitat use also was observed in the Baltic Sea, where hatchery-reared smolts were recaptured more frequently in near-shore coastal waters than in the sea during the autumn (September-November, Kallio-Nyberg et al. 2002). There are, however, only few studies that have followed sea trout in the same area throughout the year, and these typically have been undertaken either in summer or winter, and seldom over suitably extended periods. Marine habitat use also may be stock-specific. Kallio-Nyberg et al. (2002), for example, found differences between stocks of hatchery-released sea trout in their tendency to stay near the coastline as opposed to migrating further offshore.

Studies of post-smolts tagged with acoustic transmitters have shown that sea trout in western Scotland tend to stay close to their natal rivers for the first two weeks after entering the sea, move further away thereafter, and ultimately display considerable individual variation in habitat use (Middlemas et al. 2009). However, it has also been shown that individual post-smolts in Norway may move >3 km away from the river mouth within the day of entering the marine environment (Thorstad et al. 2004). Other Norwegian, hatchery-reared sea trout post-smolts that were tagged with acoustic transmitters and released in a river mouth remained largely within the inner 9 km of the fjord system during the first three months at sea, but 27% of the fish were recorded as far as 48 km from the release site (Finstad et al. 2005). Within fjords, post-smolts seem to exert a preference to remain close to shore rather than exploiting open waters within the mid-fjord areas (Thorstad et al. 2004, 2007). Mean distance to shore for post-smolts immediately following their entry to the marine environment was 125 m (Thorstad et al. 2004). Similarly, sea trout in Scottish sea lochs were captured largely within 200 m of the shore (Pemberton 1976b).

In a study in northern Norway, results indicated sea trout to reside primarily within the inner (and warmer) parts of the fjord during the summer months, in contrast to Arctic char

(*Salvelinus alpinus*) that moved to the colder outer areas (Rikardsen et al. 2007, Jensen et al. 2014). Sea trout with attached sensor tags have been shown to variously remain at sea, reside in estuarine waters, or undertake frequent movements between the freshwater and marine habitats (Jensen & Rikardsen 2012), and in winter these fish have been shown to experience water temperatures in the sea as low as 2°C.

For French sea trout from Normandie/Picardy, Euzenat (1999) described that post-smolts during the first months following sea entry migrated northwards, and possibly made excursion into the lower parts of other rivers. Their feeding areas were situated in the English Channel and the North Sea, with the most distant recaptures made from the west coast of Denmark.

2.5.2 Saltwater tolerance

Sea trout parr may survive transfer from freshwater to brackish water without undergoing the physiological process of actual smoltification (Parry 1960, Tanguy et al. 1994, Landergren 2001), and, perhaps surprisingly, alevins may be more saltwater tolerant than are parr (Parry 1960). The saltwater tolerance of parr themselves may increase with increasing body size, but in order to be able to survive in full-strength seawater, sea trout juveniles need to be physiologically prepared by the smoltification process (Parry 1960).

Migratory sea trout smolts apparently display well-developed hypo-osmoregulatory capacity and seawater tolerance whilst still in freshwater and prior to entering the marine environment (Hogstrand & Haux 1985, Tanguy et al. 1994, Lysfjord & Staurnes 1998, Ugedal et al. 1998, Nielsen et al. 2006). This is in accordance with results from behavioural studies; individual sea trout smolts monitored with acoustic transmitters apparently required no prior acclimation when moving from fresh to salt water (Moore & Potter 1994, Moore et al. 1998). Similarly, migrations from freshwater to full-salinity seawater within a few hours were recorded for individual sea trout tagged with sensor tags (Jensen & Rikardsen 2012). Individuals remaining in estuarine waters for extended periods did not attempt to remain at intermediate salinities, but often resided at water depths where they experienced large salinity shifts within the tidal cycle (Jensen & Rikardsen 2012).

Sea water tolerance may improve with increased body size (Tanguy et al. 1994). For hatchery-reared smolts, Ugedal et al. (1998) found that half of the variation in seawater tolerance was explained by fish size. Size effects may be attributable to a lesser surface area-to-volume ratio of larger fish, and/or a gradually increasing osmo- and ionregulatory capacity with body size. However, no size effects were found in downstream-migrating wild sea trout smolts (Ugedal et al. 1998), or for hatchery-reared smolts of body size 46-131 g (Hogstrand & Haux 1985).

Some authors (e.g. Larsen et al. 2008) have suggested that the combination of high salinity and low marine temperatures may be physiologically stressful for sea trout. However, sea trout may reside throughout the winter in full strength sea water (salinity 30-32) at water temperatures as low as 1-2°C (Rikardsen 2004, Jensen & Rikardsen 2012), which shows that sea trout may be able to adapt to harsh winter conditions in the marine environment. However, saltwater tolerance may vary among sea trout populations. For example, Larsen et al. (2008) documented that there may be intra-specific differences in expression of important stress-related and osmoregulatory genes, most likely reflecting adaptive differences between trout populations on a regional scale, and strongly suggesting local adaptations to saltwater tolerance driven by the local marine environment.

Sea trout may be rather less saltwater tolerant than are Atlantic salmon (Parry 1960, Lysfjord & Staurnes 1998). Tanguy et al. (1994) concluded that smolting was not as well developed in brown trout as in Atlantic salmon, but do reiterate that smoltification, *per se*, is not necessary for seawater adaptation in brown trout.

2.5.3 Swimming depths

Sea trout have been recorded as remaining primarily in the upper 1-3 m (Lyse et al. 1998, Rikardsen et al. 2007) or upper 5 m (Sturlaugsson & Johannsson 1996, Gjelland et al. 2014) of the water column, but short dives in fjords and down to depths of 26-28 m have been recorded for large sea trout (37-65 cm body length, Sturlaugsson & Johannsson 1996, Rikardsen et al. 2007). However, there are few studies of the depth use of sea trout in the marine environment, and those available include only the summer period (Sturlaugsson & Johannsson 1996, Lyse et al. 1998, Rikardsen et al. 2007, Gjelland et al. 2014). Sturlaugsson & Johannsson (1996) is a technical report.

In one of the few studies of depth use, sea trout with depth recording tags spent more than half of their time at depths between only 1 and 2 m of the water surface, and >90% of their time at depths shallower than 3 m (sea trout body length 37-59 cm, Rikardsen et al. 2007). Mean depth during the entire sea journey during the summer months was 1.8 m. Sea trout did, however, remain at shallow depths during their first five days at sea, during which they spent 46% of the time between 0 and 1 m depth. They showed a slight tendency to be deeper during the day, and made frequent dives especially towards the end of the sea migration. These dives (down to 28 m) usually lasted 10-20 minutes. Rikardsen et al. (2007) suggested that the fish used these deep dives (below the thermocline) for orientational purposes in relation to the homing behaviour (Rikardsen et al. 2007). Sturlaugsson & Johannsson (1996) undertook a similar study, and observed sea trout (body length 39-65 cm) to stay slightly deeper, and frequently to exploit depths down to 5 m. Some individuals in that study showed a diurnal pattern of behaviour, staying closer to the surface at night.

2.5.4 Progression rates, swim speeds and diurnal activity

Sea trout smolts have been shown to display slower horizontal progression rates following entry to the marine environment in comparison to in-river progression rates (Aarestrup et al. 2014). Progression rates in the marine environment shortly after leaving the river showed a mean of 3.2 km day^{-1}, or 0.02 body lengths s^{-1} (Aarestrup et al. 2014). Overall, sea trout post-smolts with acoustic transmitters spent on average 21 days migrating down a 17 km river stretch and subsequently 29 km through a Danish marine fjord (Aarestrup et al. 2014). The movement activity was primarily nocturnal, but some individuals moved also during the day (Aarestrup et al. 2014). The results of Moore & Potter (1994) and Koed et al. (2006) also showed that smolt movements through an estuary were primarily nocturnal but, in contrast, Moore et al. (1998) recorded estuarine movements of smolts during both the day and night.

In a Norwegian fjord, sea trout post-smolts tagged with acoustic transmitters were recorded 9 km from the river mouth release site within an average of 18 days after release, corresponding to a progression rate of 0.07 km h^{-1}, or 0.11 body lengths s^{-1} (Finstad et al. 2005). In a subsequent study in the same area, the average progression rate over the first 9 km of the fjordic migration was 0.03 km h^{-1}, or 0.06 body lengths s^{-1} (Thorstad et al. 2007). Although average values indicate slow overall progression rates, the movement of some individuals can be much faster. Based on tagging observations of sea trout during their seaward migration, and their subsequent recapture, the mean distances of daily travel away from the river for the four fastest individuals were 20, 8, 8 and 6 km per day for post-smolts, and 6, 6, 5 and 5 km per day for older and larger sea trout (Berg & Berg 1987a).

Studies of migration of wild sea trout tagged with acoustic transmitters implanted in the body cavity (upper photos) in Middle Norway. Tagged fish were recorded when passing fixed station receivers deployed at different marine sites (lower photos). Photos: Eva B. Thorstad

The progression rates referred to above are based on movements registered between fixed station receivers recording the signals from identifiable sea trout with acoustic transmitters, or on tagging and recapture of individual fish. Of course, the fish may have moved a longer distance than the shortest route between receiver stations or points of tagging and recapture, which is the assumption in these progression rate estimates. The fish may therefore show much higher swim speeds over shorter distances. Swimming speeds of post-smolts with acoustic transmitters have been recorded on a finer time-scale by Lyse et al. (1998) and Thorstad et al. (2004). Average ground swimming speed of continuously tracked post-smolts varied between 0.4 and 5.7 cm s^{-1} (Lyse et al. 1998). The fastest ground speeds over 30-minute periods varied among individuals from 5.7 to 55.5 cm s^{-1} (Lyse et al. 1998). Ground speeds are not corrected for the speed and direction of the water current and, without so doing, the true swimming capabilities of the fish cannot be known. Thorstad et al. (2004) therefore simultaneously recorded swim speeds of post-smolts (181-245 mm total length) and water currents over 10-minute periods. Mean observed migration speed over the ground was 0.56 body lengths s^{-1} (individual means from 0.33 to 0.88 body lengths s^{-1}). When corrected for the speed and direction of the water current, actual swim speed was 0.68 body lengths s^{-1} (individual means from 0.48-1.11 body lengths s^{-1}). The fish were released in the river mouth and subsequently followed during their marine migration for an average of 8.6 hours. During this period, the fish did not follow a straight line route along the fjord. The most seaward position during tracking was, on average, 1687 m from the release site (individuals ranging from 113 to 3702 m). This corresponds to a mean net rate of seaward movement of 4.7 km day^{-1}. Neither the observed movement directions over the ground, nor the actual swimming directions when corrected for the movement of the water, depended on the direction of the water current.

2.6 Feeding and growth

The energy requirements for downstream-migrating sea trout smolts and veteran migrants may be high (Jonsson & Jonsson 1998), and therefore it is most likely important for these fish to be able to initiate feeding and growth as soon as they enter saltwater.

2.6.1 Diet

Sea trout are generalist and opportunistic predators at sea. They feed upon a variety of fish species, crustaceans (shrimps, amphipods and krill), surface terrestrial insects and polychaete worms (Pemberton 1976b, Grønvik & Klemetsen 1987, Chernitsky et al. 1995, Lyse et al. 1998, Knutsen et al. 2001, 2004, Rikardsen et al. 2006, 2007). Sea trout seem to be a more generalist than are Atlantic salmon, in taking a wider range both of prey types and sizes (Grønvik & Klemetsen 1987). Geographical and seasonal variations in feeding rate and prey choice probably reflects spatial and temporal differences in prey abundance (Pemberton 1996a, Haluch & Skóra 1997, Rikardsen et al. 2006), and the prey taken by sea trout varies with their body size, season and habitat occupied (Pemberton 1976a, Knutsen et al. 2001, 2004, Rikardsen & Amundsen 2005, Rikardsen et al. 2006).

Fish often comprise the dominant prey (Grønvik & Klemetsen 1987, Haluch & Skóra 1997, Knutsen et al. 2001, 2004, Rikardsen & Amundsen 2005, Rikardsen et al. 2007), especially for larger sea trout (>25 cm, Rikardsen et al. 2007). Pelagic fishes such as herring (*Clupea harengus*) were dominant in stomachs of sea trout captured in northern Norway, but also sand eels (*Ammodytes* sp.) were frequently taken (Grønvik & Klemetsen 1987, Rikardsen & Amundsen 2005, Rikardsen et al. 2004, 2007). Herring may be a preferred dietary item in areas and years when they are abundant (Rikardsen et al. 2004, 2007). Also in coastal waters along the Norwegian Skagerrak coast, the main prey categories noted in gut content analyses were fishes of the families Clupeidae and Gobiidae (Knutsen et al. 2001, 2004). Herring seemed also important for hatchery-reared sea trout in the Baltic Sea, because cohort survival was positively correlated with the local abundance of 0+ herring (Kallio-Nyberg 2006, 2007). In the Gulf of Gdansk, sea trout of body length ≥40 cm were recorded as preying primarily on fish, with herring and European sprat (*Sprattus sprattus*) as the main component, but also sand eels being important (Haluch & Skóra 1997). Fish were important food items for sea trout also in west coast Scottish sea lochs, with Clupeidae (including herring) and sand eels being the most frequently taken items (Pemberton 1976a).

A larger body size for a marine predator facilitates piscivory and/or the taking of larger prey items. For example, Pemberton (1976a) found that there was a shift in apparent dietary preference at ~21 cm body length, with smaller sea trout feeding mainly on crustaceans and insects and larger sea trout mainly taking fish. On the other hand, Knutsen et al. (2001) found insects most frequently in gut content analyses of young sea trout, whereas polychaetes were most commonly recorded in older trout. For fishes and crustaceans, Knutsen et al. (2001) found no difference in their frequency of occurrence in stomach contents between different age-groups of sea trout.

The season also affects food availability. The food of sea trout was shown to vary with season in a study from northern Norway (Rikardsen et al. 2006), with sea trout feeding mainly on crustaceans during winter and fish during late spring, summer and autumn (Rikardsen et al. 2006). Food consumption rates were lowest during late autumn and early winter (October-December) and highest from April-September. These patterns matched the seasonal variation in condition and lipid content of the fish (Rikardsen et al. 2006). The highest lipid levels were noted in July/August for mature fish and in September for immature fish. Thereafter, lipid levels were noted to decrease until November/December and to increase again by March/April. Despite low sea temperatures and high salinity in the sampling area, sea trout fed actively during the entire winter (Rikardsen et al. 2006). In southern Norway, sea trout fed most intensively in spring and early summer, but feeding declined from a high in May-June to a low in July (Knutsen et al. 2001). Sea trout in this area frequently had food items in their stomachs during winter (Knutsen et al. 2004).

In Scottish sea lochs, benthic feeding (on crustaceans and annelid worms) was more pronounced in winter, whereas mid-water and surface-occurring organisms such young fish and wind-blown insects seemed preferred in summer (Pemberton 1976a). Benthic feeding seemed predominant during the day whilst the extent of mid-water and surface feeding increased between sunset and sunrise during 24-h surveys in June and September (Pemberton 1976a). The frequency of empty stomachs was lowest in spring and early summer and highest in November and December. Maximum food intake was recorded in early summer and in mid-winter (Pemberton 1976a).

The habitat exploited by the sea trout also is likely to affect the available prey composition. Sea trout may exploit multiple different habitats, such as estuaries, shallow near-shore areas, or more pelagic open waters (Knutsen et al. 2001, Rikardsen & Amundsen 2005). In a Russian estuary, the amphipod (*Gammarus oceanicus*) and sand eels were the main components of the diet. Sea trout captured 500-5000 m away from shore over water depths of 50-450 m in Northern Norway had almost exclusively a piscivorous diet (Rikardsen & Amundsen 2005).

2.6.2 Growth

For sea trout, the growth rate at sea typically is considerably greater than that in the river (L'Abée-Lund et al. 1989). Growth seems to be positively correlated with duration of the marine migration, to vary among years and to be greater in years with generally higher sea temperatures (Berg & Berg 1987b, Berg & Jonsson 1990). In a large European study covering 102 populations, post-smolts were observed to grow on average 12.5 cm during the first year at sea (variance, 8.0 to 21.8 cm; Jonsson & L'Abée-Lund 1993).

In a river in southern Norway, the specific growth rate (cm cm^{-1} day^{-1}) at sea during the two first years after smolting was higher for those fish spending the entire period at sea compared to those returning for over-wintering in freshwater (Jonsson & Jonsson 2009b). This was related to the cost of spawning, because many of those fish returning to freshwater spawned after only the one summer at sea. For example, first-time migrants that returned from the sea in the same year as they emigrated from the river increased in average size from 19 cm and 67 g to 30 cm and 297 g (Jonsson & Jonsson 2009b). First-time migrants that remained at sea for 1-2 years averaged 38 cm and 588 g, whilst those that remained in marine waters for 3 years averaged 43 cm and 834 g in size. The timing of river descent is important also; specific growth in the first season at sea was lower for post-smolts descending during spring compared to those emigrating in autumn. The advantage of autumn migration appeared here to confer enhanced growth during the subsequent year. The marine growth for those returning to the river after one growth season at sea was higher than that for (larger) veteran migrants (Jonsson & Jonsson 2009b). In a river in western Norway, the sea trout returning in the autumn after having spent the first summer at sea were 20-35 cm long (Skaala et al. 2014a). In a river in southern Sweden, first-time migrants increased from 14-19 cm body length at their outward migration in May, to 25-45 cm (average 38 cm) at return to the river in the autumn (Svärdson & Fagerström 1982). Those fish not returning to the river in the first autumn after emigration, but returning as spawners during the second autumn, showed body lengths of ~50-55 cm. Those that were still immature at this time, and which remained at sea, showed mean body lengths of ~60 cm. Similarly, those returning for spawning in the third autumn had body lengths of ~65-70 cm (Svärdson & Fagerström 1982). British Isles maiden sea trout were commonly between 30 and 34 cm at the end of the winter of their first year of migration (Fahy 1978), but there are considerable differences among stocks, with length increases ranging between 40 and 93% during this period at sea (Fahy 1978).

In Norway, the length increment attained during the first year at sea was shown to not depend on latitude (Jonsson & L'Abée-Lund 1993). However, in a previous study of sea trout populations along the Norwegian coast (58-70°N), annual length increment of sea trout during the first year after smolting did decrease towards the north, and increased with sea temperature (L'Abée-Lund et al. 1989). Nevertheless, differences in sea growth were small between southern and northern populations. Further south, in the Netherlands, growth during the first year at sea was shown to attain increments of 21-26 cm (de Leeuw et al. 2007). Sea trout increased in length from an average 24 cm as post-smolts in May-June to 41 cm by October-November, representing an overall summer growth of 3.4 cm mo^{-1} during the first summer at sea. Fish captured after the first winter at sea averaged 51 cm in length. Such rapid growth at southern latitudes compared to the rates observed further north does indicate that the growth capacity is higher in a warmer climate with a prolonged growth season and the possibly attendant richer feeding opportunities (Jonsson & Jonsson 2009b).

Sea growth varies throughout the annual season, and may be particularly rapid in the early summer months (Berg & Berg 1987b, Knutsen et al. 2001, 2004, Olsen et al. 2006). Sea growth for first-time migrants in northern Norway was fastest in late June (Berg & Berg 1987b). Growth increased gradually from the time that fish first entered the sea and until June and then decreased again. For southern Norwegian sea trout remaining the entire year at sea, growth in length was rapid during summer (May-September), but there was no evidence for continued growth during autumn and winter (Olsen et al. 2006). However, not all individuals followed the general pattern of seasonal growth (Olsen et al. 2006).

2.7 Survival

Sea trout are heavily preyed upon in the sea by a host of different predators, and the risk of mortality is greatest during the first sea migration. Post-smolts are most vulnerable soon after entering the sea (Dieperink et al. 2001, Koed et al. 2006, Middlemas et al. 2009, Aarestrup et al. 2014). Of 78 smolts tagged with radio-transmitters in a Danish stream, 65% were taken by cormorants (*Phalacrocorax carbo* L.) and herons (*Ardea cinera* L.) during the first four weeks after entering the sea (Dieperink et al. 2001). Predation was particularly severe during the first few days, with a daily predation rate during the first two days at sea as high as 25-30%. Predation rates were highest among smaller smolts (Dieperink et al. 2001). In another Danish study, 12% of tagged sea trout smolts were taken by cormorants in the estuary (Koed et al. 2006). In a further Danish study, mortality for outward-migrating post-smolts swimming through a fjord was 0.63-0.92% km^{-1} of the migration, and overall survival for sea trout with acoustic transmitters was only 79% during a 21-day migration though a 17 km river stretch and 29 km through a marine fjord (Aarestrup et al. 2014). In a Scottish study, sea trout post-smolts tended to stay close to their natal rivers for the first 14 days after entering the sea, during which time approximately half the fish were lost (Middlemas et al. 2009). It should be noted that all the studies referred to here were based on fish tagged with acoustic transmitters, and the mortalities should therefore be regarded as maximum mortalities because the consequences of the tagging process, and presence of a tag itself, may potentially have increased the predation risk.

In a river in northern Norway (1956-1963 and 1967-1970), sea survival during the first summer at sea was observed to be minimally 37% during an average period of 70 days (Berg & Jonsson 1990). The survival rate for relatively small-sized males was higher than for the females. Survival for repeat-migrant fish was 56-68% (Berg & Jonsson 1990). The return rates for adult sea trout after one summer at sea in another study in Northern Norway was 85% in one study year and 79% in the following study year (different individuals tagged in the two study years, Jensen et al. 2014). In a river in central Norway, Jensen (1968) estimated that survival to autumn for sea trout tagged during their downstream migration in the spring was 56% (confidence interval 51-69%). In French rivers, a high survival is recorded after spawning, whereby 30-50% of individuals tagged as kelts subsequently returned (Euzenat 1999). By contrast, in one river, only 14.4-20% of sea trout tagged as smolts successfully returned to the river (Euzenat 1999).

The timing of sea entry typically has an effect on survival of individual sea trout. Thus, in a river in southern Norway, marine survival of smolts descending to sea in the spring was higher than that of first-time migrants descending in the autumn (Jonsson & Jonsson 2009b). The survival was highest for those emigrating in May, with 15% of the tagged fish subsequently returning to the river to spawn. As mentioned above, that percentage result must, however, be regarded as a minimum survival estimate because it is based on externally visible Carlin tags which tend to increase the mortality risk for the fish because of the tag itself (Jonsson & Jonsson 2009b). For veteran migrants, mean sea survival was 33%, and survival was not dependent on the specific month in which the fish emigrated to sea (Jonsson & Jonsson 2009b).

As is to be expected, the rates and levels of mortality at sea can vary also among years. For example, in a Norwegian study during the period 1976-2005, the highest survival was recorded for those fish leaving the river as smolts in 1979 and 2003, with the lowest in 1980. The sea survival of most cohorts between 1993 and 2002 also was low (Jonsson & Jonsson 2009b).

Long term data on sea trout marine survival are available from the Burrishoole fishery in western Ireland, prior to the onset on marine salmon farming. Over the period 1970-1987, the percentage of sea trout smolts that survived to return as 0+ sea age finnock in the same calendar year ranged from 11 to 32% with a historical mean of 21% (Poole et al. 2006). Gargan et al. (2006b) recorded sea trout finnock marine survival of 19% in another west of Ireland sea trout fishery in the absence of salmon farm production.

Even though there is no evidence of density-dependent mortality of sea trout at sea (Elliott 1993b, Jonsson & Jonsson et al. 2009b), the survival of spring-migrating sea trout increased with increasing numbers of Atlantic salmon moving to sea in the same year (Jonsson & Jonsson 2009b). This may be related to predation during actual sea entry, and that reduced vulnerability of individuals to predation was a functional response of a high abundance of alternative prey. By emigrating synchronously with large numbers of smaller Atlantic salmon smolts, sea trout smolts may be exposed to reduced predation risk as a result of potential predators becoming satiated by feeding on the more abundant (and perhaps more easily captured) salmon smolts. On this particular river, sea trout smolts typically are twice the weight, but half as numerous, as salmon (Jonsson & Jonsson 2009b).

2.8 Straying and homing

Return-migrant sea trout can stray further from their natal rivers than do Atlantic salmon. For example, in northern Norway, 16% of recaptures of tagged sea trout smolts originated from a different river (Berg & Berg 1987a, Berg & Jonsson 1989). However, it is not known if the apparently straying sea trout would have returned ultimately to the river where they were tagged for actual spawning. In this particular context, it is notable from an extensive tagging programme in a river on the east coast of Scotland, that a larger number of recaptures was made in the neighbouring river (South Esk) than in the North Esk river where they were tagged (Pratten & Shearer 1983b).

Genetic differences among brown trout populations in different catchments (Hansen et al. 2002, Hovgaard et al. 2006) indicate that effective straying and gene flow among catchments is limited. Known straying rates for sea trout approximate to 1-3% (i.e. the proportion of individuals in a river that originate from other rivers and which successfully breed and contribute to succeeding generations in the new river; Ferguson 2006, Jonsson & Jonsson 2006b). If effective straying rates were higher than a few individuals per generation, the genetic differences that are documented among populations would not exist (Ferguson 2006). Hence, a larger number of individuals may stray between rivers, but all straying does not necessarily result in successful spawning and genetic introgression.

2.9 Concluding statements

- There is considerable variation in sea trout life history strategies, particularly in relation to the timing and duration of the marine migrations, both among individuals and populations.
- Females tend to adopt the anadromous life history strategy more than do males.
- Sea trout smolts typically leave rivers and enter the sea for the first time in spring or early summer, between February and June. Sea trout also may enter the sea for the first time at other times of the year.
- Sea trout post-smolts may remain at sea only for a few months during the summer and return to the river to over-winter, and thereafter they may regularly spend their summers at sea and winters in freshwater. Sea trout need not return to freshwater after the first summer at sea, but can remain continuously at sea during the summer and winter until they mature and return to freshwater for spawning.
- Sea trout are frequently recorded at sea during winter, both in southern and northern areas of their distribution.
- Some sea trout have adopted an “intermediate” life history strategy exemplified by migrating only to the estuary, or by undertaking repeated, relatively short-term, movements between the freshwater, estuarine and marine habitats.
- The duration and timing of marine migration within the adopted life-history strategy is likely governed by trade-offs between growth opportunities and survival risk associated with the different habitats.
- The strategy of remaining at sea during winter is likely more common in populations from small catchments with unstable and poor freshwater winter conditions, including low water discharge and perhaps ice build-up in northern areas. Sea trout from small coastal streams with little water flow and periods of droughts may reside in freshwater only for a brief parr stage and then remain in the sea the rest of their life, excepting short returns to freshwater for spawning.
- Due to considerable individual variation, sea trout in a given watershed may enter and leave the catchment at any time of the year. However, the greatest outmigration generally is in spring and early summer, when both juvenile smolts and adult kelts may migrate to sea. The time of the year when most sea trout return to the freshwater seems to be in summer and autumn, when adults return to spawn and immature fish re-enter freshwater to be resident over the winter months.
- Sea trout typically remain in coastal areas, and do not undertake long-distance migrations to open ocean areas. However, they may feed offshore in pelagic waters in outer coastal areas and in the Baltic and North Seas.
- Sea trout usually remain within 80 km or less of their river of origin, but a few individuals may undertake longer distance migrations. Examples of recaptures of wild

sea trout >500 km from the river where they were tagged are recorded. The largest numbers of sea trout in the sea are likely to be found within a few kilometres of their river of origin.

- Sea trout may reside in a variety of marine habitats, and are found both in estuaries and full salinity sea water and can frequently move between habitats. Post-smolts may tend to remain closer to river mouths and nearer to shore, especially during their first few weeks to months at sea.
- Sea trout parr are, to some extent, saltwater tolerant and can survive transfer from freshwater to brackish water without undergoing a physiological smolting process. They are increasingly saltwater tolerant with increasing body size. However, to survive long-term in full-strength seawater they need to be physiologically prepared by the actual smoltification process.
- Sea trout smolts and adults can tolerate rapid and frequent shifts between freshwater and seawater, and can move from freshwater to seawater without apparent periods of acclimation.
- Some authors have reported that the combination of high salinity and low water temperature may be physiologically stressful for sea trout. However, sea trout are, in some locations, regularly observed to reside throughout the winter, in full salinity seawater (salinity 30-32) and at water temperatures as low as 1-2°C, in more northern areas.
- There are indications that there are genetic differences between sea trout population with respect to their saltwater tolerance.
- Sea trout remain primarily in the upper 1-3 m, or upper 5 m, of the water column whilst at sea. Short dives to 26-28 m depth have been recorded.
- Average horizontal progression rates of individually tagged post-smolts in the marine environment vary from 0.7 to 3.2 km day^{-1}, or from 0.02 to 0.11 body lengths s^{-1}. However, the fastest individuals may migrate much more quickly, and progression rates of up to 20 km day^{-1} have been recorded for post-smolts. Between recordings, the fish may have moved a longer distance than the shortest route, and the fish may therefore have much higher swim speeds over shorter distances.
- Sea trout are generalist and opportunistic predators at sea and feed on a variety of fish species, of differing sizes, crustaceans (shrimps, amphipods and krill), surface insects and polychaete worms.
- Fish are often found in gut content analyses to be the most important food item, especially for sea trout >21-25 cm body length. Fishes of the family Clupeidae (e.g. herring) and the genus *Ammodytes* (sand eels) are often found to be important food items for sea trout, and herring may be especially preferred in areas and years when they are locally abundant.
- Prey taken by sea trout varies with their body size, season and habitat. Geographical and seasonal variations in feeding rate and prey choice probably reflect differences in prey abundance both on spatial and temporal scales.
- Growth rates of sea trout are greater at sea than in freshwater.
- Marine mortality seems largely influenced by density-independent factors and not by density-dependent factors.
- The movement from freshwater to the marine environment as first-time migrants (smolts) is a critical phase in the life cycle of sea trout, and high mortality rates have been reported for fish in the estuary and during their first few days at sea. The smolts are especially vulnerable to predators (including birds and other fish species) during this phase.
- Reported sea survival during the first summer at sea is up to 37%. One reported average from long-term monitoring in a river in southern Norway was 15% for Carlin-tagged smolts leaving the river in May, but with variation among cohorts. From long-term monitoring in Ireland in 1970-1987, the percentage of sea trout smolts

that survived to return as 0+ sea age finnock in the same calendar year ranged from 11 to 32% with a historical mean of 21%. Survival to return to freshwater following the marine migration for veteran migrants is reported to be as high as 33-68%.

- Genetic differences among brown trout populations indicate that effective straying and gene flow among watersheds is limited. Known straying rates for sea trout (i.e. the proportion of individuals in a river that originate from other rivers and which successfully breed and contribute to succeeding generations in the new river) approximate to 1-3%. Larger numbers of individuals may stray between rivers, but all straying does not result in successful spawning and genetic introgression.

2.10 Knowledge gaps

- Marine behaviour and survival has frequently been studied for Atlantic salmon and various species of Pacific salmonids including Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*) and sockeye salmon (*O. nerka*). By contrast, sea trout are among the lesser studied salmonids in the marine environment (Drenner et al. 2012).
- The variation in migration pattern and life-history strategies displayed by sea trout has been studied for only a few watersheds. There is little information on the proportion of individuals and populations showing the various life history strategy options regarding the timing, duration and distance of marine migrations, and how anadromy may be under genetic control. Studies are needed on how large a proportion of sea trout may overwinter at sea amongst differing locations, geographical regions and populations.
- Sea trout populations have been monitored over the long-term for only a very few catchments. There is little information in many areas on the status of the sea trout populations. There also is little information on natural variation in marine survival, the major sources of risk and mortality for sea trout, and how and why sea survival may change in space and time.
- Detailed information on marine habitat exploitation, migration routes, migration distance and depth use of sea trout in the marine environment over the course of the year is needed. Specifically, information on how differences and changes in water temperature and salinity may interact to affect sea trout feeding, growth, behaviour and migration is also needed. Information on how salmon lice infestation may affect the marine behaviour of sea trout also is needed to facilitate the effective sampling and monitoring of populations.

3 Anthropogenic impacts other than salmon lice on sea trout populations

Small sea trout from River Imsa in southern Norway. Photo: Eva B. Thorstad

In this chapter, anthropogenic impact factors other than salmon lice that might exert negative influences on sea trout populations are outlined and reviewed.

One of the main conclusions from the First International Sea Trout Symposium, held in Cardiff, UK (Harris & Milner 2006) was that "*Sea trout stocks are apparently healthy in some regions, but in others there have been major collapses*". It was further concluded that the status of sea trout stocks and fisheries varies across the distribution range, according to the influence of local and regional factors (Milner et al. 2006). Although this is a rather general and non-specific statement, salmon lice were specifically identified as an important negative impact factor that has caused marked declines of sea trout populations in the western British Isles, and over-exploitation has occurred in coastal fisheries in the northern Baltic region. Moreover a combination of uncontrolled illegal fishing in coastal waters and environmental problems in freshwater was identified in the Black Sea region (Milner et al. 2006). They stated that elsewhere sea trout stocks appear to be in a more healthy condition. Additional significant detrimental environmental factors reported by speakers from most countries included physical barriers to migration, reduced river flows, siltation of spawning gravels, nutrient enrichment as a consequence of intensive agriculture, river habitat destruction and increased predation (Milner et al. 2006).

In Norway, there has been generally little monitoring and research on sea trout populations, and few studies published regarding these various potential impact factors. Because Norway was not specifically considered in that summary of the conference, it can be added here that healthy stocks of sea trout is not the case throughout Norway. A technical report dating from 2009 (Jonsson et al. 2009), and official catch statistics updated through 2013, show that catches have more than halved in western and central Norway since the turn of the century. In northern Norway, catches increased during the 1990s, but have decreased since 2005. For southern Norway, along the Skagerrak coast, catches have been relatively stable and show no clear temporal trend since early 1990s. Jonsson et al. (2009) commented that the recent declines are likely linked to salmon lice but perhaps also to yet other marine impact factors including climate change and fish diseases. Anthropogenic impact factors in freshwater such as pollution, acidification, hydropower flow regulation and other habitat alterations probably have reduced sea trout populations in many catchments, but these factors either have been stable, or have had a reduced negative impact, in recent years and are therefore likely not responsible for the declines seen in some regions (Jonsson et al. 2009).

3.1 Impact factors in freshwater

Human impact factors that may act on sea trout in freshwater include acidification, other pollution (e.g. from agriculture, roads and mining), hydropower development, other regulation of river flow, migration obstacles and habitat alterations.

Freshwater acidification arising from industrial emissions of sulphur dioxide and nitrogen oxides to the atmosphere, and consequent acid precipitation, has caused the loss or reduction of several fish populations, particularly in some areas in southern Norway. Emissions have been reduced, but many rivers still are affected by chronic or episodic acid water (e.g. Kroglund et al. 2008, Rosseland & Kroglund 2011). Increased fish mortality during acidification may be related both to elevated H^+ levels (reduced pH) and high concentrations of toxic inorganic aluminium (Rosseland & Kroglund 2011). In running waters, there has been particular concern about their effects on salmonids, with the primary focus on impacts on Atlantic salmon populations (Hesthagen & Hansen 1991, Hesthagen et al. 2011). The acidification-driven decline in Atlantic salmon stocks probably started as early as the 19th century, and by 1970 many stocks in the affected area were lost (Hesthagen & Hansen 1991). Atlantic salmon populations were eliminated or reduced in more than 50 rivers as a result of acidification (Hesthagen et al. 2011). Since the 1980s, large-scale liming programmes have been applied to restore Atlantic salmon and brown trout populations in formerly acidified rivers in Norway (Hesthagen et al. 2011). Because brown trout are less vulnerable to acidification than are Atlantic salmon (Henrikson & Brodin 1995), it is likely that any liming strategy adopted specifically for Atlantic salmon may well also restore water to a quality suitable for sea trout. However, liming strategies can still be optimised to improve conditions for sea trout in tributaries and small streams that presently are still not included in a given liming programme for the main stem of a river.

In addition to acidification, a wide range of freshwater contaminants derived from intensive agriculture, afforestation, mining and other industries can have a significant impact on sea trout populations, both as a consequence of direct effects in the freshwater phase, but also by perturbation of the parr-smolt transformation, and influences on run-timing and survival of smolts once they enter the marine environment (Rosseland & Kroglund 2011, McCormick et al. 1998). Many contaminants, in addition to acid precipitation and its associated metal-binding, can severely damage fish gills and thereby compromise smolt osmoregulatory capacity (McCormick et al. 1998, Kroglund et al. 2007). Sublethal exposure to contaminants during smoltification may therefore have implications for subsequent marine survival. Research has, to a larger extent, been undertaken preferentially on Atlantic salmon rather than brown trout, and few references to brown trout and the effects of contaminants are to be found through literature searches (Thomson Reuters Web of Science database). Jonsson et al. (2011) studied the effects of land-use and water chemistry in streams in the Skagerrak area in southern Norway. They found that there was a balance between agricultural land use in the catchment and sea trout production in the streams. Agricultural activity enhanced fish production, probably because of increased nutrient enrichment, but only up to a threshold at 20% cultivated area in the catchment. When agriculture covered a larger proportion of the catchment, fish production declined. They suggested that the decline may be explained by agricultural chemicals causing environmental stress, augmented suspended sediments and/or chemical oxygen demand. Jonsson et al. (2011) also emphasised that afforestation along the river banks may have a positive effect on fish production. They did, however, highlight also that the effects of land-use on fish production may be less pronounced in large rivers than for the smaller streams covered by their study.

Road and railroad activities also may contribute to freshwater pollution, but there is little specific available information in this regard for sea trout. Meland et al. (2010) suggested that traffic-related contaminants, especially those emanating from contaminated tunnel wash water, caused reduced growth in sea trout juveniles in their study stream. Building of roads, railroads, bridges and other installations also may incur migration barriers for sea trout. In some cases, migrations may be completely blocked, whereas in others, culverts or other constructions may not be sufficiently well-designed to enable or facilitate fish passage. Studies that include the documentation or mapping of such impacts on sea trout are not available in the scientific peer-reviewed literature. One study (Cocchiglia et al. 2012) did raise questions as to whether or not the construction of culverts might affect brown trout egg survival as a result of elevated sediment levels. Fine sediment was shown to have a negative effect on egg survival in the laboratory, but in the field no significant difference was detected in egg survival between the upstream control sites and test sites downstream of culverts.

Regulation of water flow for hydropower production may cause altered river discharges, changes in temperature regime and variation in water quality. Power stations, dams and weirs all may comprise major obstacles to migrating fish and cause marked alteration of riverine habitats. River flows are regulated not only for hydropower production, but also for other purposes, including irrigation, freshwater fish hatcheries, channel modification to facilitate boat traffic (e.g. locks) and the building of infrastructure along the rivers; all of these may pose challenges to migratory fish similar to that from hydropower regulation. In addition to the direct abstraction of river water, the result of such interventions can include a loss of channel connectivity, and significant alteration of overall environmental conditions. The specific effects of river regulation will vary among rivers, and associated impacts will range from minor to major for given sea trout populations. There is a large body of internationally published literature in peer-reviewed journals on the effects of hydropower development and other river regulation on salmonids, and many of the studies of other salmonid species are relevant also for sea trout. Furthermore, there also are a number of studies specific to brown trout concerning the restoration of spawning habitats, changes in overwintering environmental conditions, fish strandings due to rapid flow decreases, migration barriers, turbine mortality and the effects of flow and temperature regimes on juvenile growth, behaviour and recruitment (e.g. Saltveit et al. 2001, Aarestrup & Koed 2003, Halleraker et al. 2003, Flodmark et al. 2004, 2006, Alonso-Gonzales et al. 2008, Barlaup et al. 2008, Östergren & Rivinoja 2008, Erkinaro et al. 2011, Pulg et al. 2013). Because sea trout are potentially iteroparous, and therefore may spawn repeatedly, and in the knowledge that individuals of this species show considerable variation in habitat use and migration timing over their life time, there has been increasing awareness that conservation strategies require a broader perspective at adequate temporal and spatial scales to maintain and restore connectivity among the various habitats exploited by populations (Calles & Greenberg 2009, Kraabøl et al. 2009). There is a need not only for the construction of fishways and other measures to facilitate upstream migration, but also a requirement to reduce selective and delayed transit of individuals, both upstream and downstream, through artificial barriers at all relevant times of the year (Calles & Greenberg 2009, Kraabøl et al. 2009).

3.2 Impact factors in marine habitats

Human-derived impact factors that may act on sea trout in the marine environment include salmon lice but extend also to the construction and deployment of fish farm structures, offshore wind turbines, harbours, piers, bridges and other industrial developments.

A possible effect of fish farming in coastal areas may be attributable to sea trout being attracted to, and behaviourally delayed by, fish farm installations. However, no published studies are available on this topic. In Norway, it has been shown that large numbers of marine fish are indeed attracted to Atlantic salmon farms and they do feed on waste pellets. Saithe (*Pollachius virens*) and Atlantic cod (*Gadus morhua*) are among the species most commonly associated with farms (Dempster et al. 2009). Both species may prey on out-migrating post-smolts, but salmonids were not found in stomach content analyses of over 300 saithe and 200 Atlantic cod caught during the summer months (June-August) at nine Atlantic salmon farms along the Norwegian coast (Dempster et al. 2009). Whether or not attraction of marine predators to coastal fish farms represents an increased predation pressure on wild salmonids is thus unknown, but it is reasonable to expect increased predation when fish farms are located close to river mouths. By the same token, it may be possible that fish farms actually reduce smolt predation pressure, because potential smolt predators that aggregate at farms appear to switch from a fish diet to pellets from farms.

Other than the widely documented effects of salmon lice, there is little published information relating to how anthropogenic factors and an increased human development activity in coastal areas could be, or actually are, impacting sea trout survival and movements. It is not known how harbours, piers, bridges, fish farm structures, industrial developments and deposits from mining activity might affect sea trout in the marine habitat. Tidal power turbines also are being developed and their spinning blades could have direct physical impacts upon fishes. An increasing portion of the ocean is also now being illuminated at night. This stems from the construction of port facilities with piers or tethering systems that can extend far offshore, as necessitated by the increasing size of ocean-going vessels. It is not known how such facilities may impact sea trout.

3.3 Impact factors that may occur both in freshwater and marine habitats

Fish farming may affect sea trout populations by introducing, or increasing the occurrence of, new infectious diseases caused by viruses, bacteria, fungi and parasites other than salmon lice. Such diseases may affect both the freshwater and marine stages of the sea trout life cycle. There is generally very little knowledge and monitoring of such effects of fish farming on wild salmonid populations (Bakke & Harris 1998).

The possible effects of climate change on sea trout populations have been extensively reviewed by Jonsson & Jonsson (2009a) and Elliott & Elliott (2010). The expected climate change in the Atlantic region is for milder and wetter winters, with more precipitation falling as rain and less as snow, a decrease in ice-covered periods and more frequent periods of extreme weather. Overall, Jonsson & Jonsson (2009a) predicted a northward movement of the distributional range of sea trout, with decreased production and population extinction in the southern regions and invasion of new spawning and nursery rivers and feeding areas in the north. Other predicted climate effects from the review by Jonsson & Jonsson (2009a) included: (1) Increased threats from parasites and contagious fish diseases due to increased transmission rates, faster development and increased virulence of the infectious agents. (2) Increased winter mortality of parr in northern and southern parts of the distribution range. (3) Delayed timing of spawning in the autumn and advancement of egg hatching and alevin emergence in spring. The length of the growing season probably will increase, and growth rates also will increase if temperatures are below the optimum for growth. (4) Increased annual body size increment and reduced age at smoltification, especially in the northern and intermediate parts of the distribution range. (5) Advanced timing of smolt migrations in spring and increased early post-smolt mortality in the sea because of higher temperature increases in rivers than in marine habitats. (6) Advanced timing of spawning migrations. Extreme flow conditions can delay upstream spawning migration and reduce spawning stocks. (7) Decreased post-smolt growth, survival, age at sexual maturity, and recruitment. The effect would probably be strongest in the intermediate and southern parts of the distribution range. Precocious maturation of parr could perhaps increase in frequency. Freshwater resident individuals could be selectively favoured in populations including a mix of anadromous and freshwater resident individuals. (8) A large part of these changes could present a relatively rapid phenotypic response to the altered climate. In the longer term, however, genetic changes in traits such as age at smoltification, age at maturity and disease resistance also can be expected (Jonsson & Jonsson 2009a).

Sea trout are exploited through fishing both in the freshwater and marine habitats. Overexploitation, i.e., when a population is exploited to the extent that the optimal recruitment cannot be maintained due to a lack of spawners and thereby insufficient egg deposition, can lead to marked population declines over time. Because sea trout potentially are serial spawners, the impact of exploitation tends to be cumulative on older and larger fish (Solomon & Czerwinski 2006). The fishing regulations and traditions vary across the distribution range of sea trout, and generalisations about exploitation levels and the degree of overexploitation are difficult to draw. Catch statistics, as well as information on catch per unit effort and catch rates, are important for monitoring of sea trout populations and assessment of the levels of their exploitation. The quality of catch statistics for sea trout is adequate in some fisheries and countries, but needs improvement in others (Milner et al. 2006). The extent of illegal fishing for sea trout is generally not known.

3.4 Interactions among impact factors

Often, several anthropogenic factors can impact sea trout populations simultaneously, but studies of the interactive effects of anthropogenic disturbances on fish populations often are complicated and expensive to conduct, and very few such studies on any species exist in the literature. This is one reason why it is difficult to isolate and analyse the effects of single factors for any wild population. In addition, the interactive effects of two or more impact factors may be complex, non-linear and unpredictable, and certainly not apparent from combining knowledge of the effects of single factors studied in isolation. Two examples include the reports of Finstad et al. (2007, 2012), wherein the interactive effects of salmon lice and acidification on Atlantic salmon post-smolt survival were studied. These studies showed that smolts exposed to freshwater acidification were subsequently more vulnerable to salmon lice than were control groups held in good quality fresh water. Vulnerability to salmon lice was, however, reduced if there was a recovery period following the acidification episode and prior to exposure to salmon lice. Hence, results of these studies point to year-on-year variation in interactive effects of these particular impact factors in relation to the relative timing and intensity both of acidification and the risk of salmon lice infestation.

Climate change can affect all stages of the sea trout life cycle, and is inevitably an impact that will interact with yet other anthropogenic influences. Thus, for example, even the effects of salmon lice will show complex interaction with climate change. The abundance of salmon lice in coastal areas has been shown to increase with temperature throughout the summer (Heuch et al. 2002). Climate change is predicted to lead to elevated ocean temperatures, which may increase the abundance of salmon lice as a result of reduced life cycle periods and thereby an increased number of salmon lice generations per year (Johnson & Albright 1991a, Boxaspen & Næss 2000). Hence, negative effects of salmon lice might become more severe over larger geographical areas as a result of climate change, and northern populations will likely be increasingly impacted. If smolt size is reduced due to increased in-river growth rates and a lower river age at smoltification (see reference to Jonsson & Jonsson 2009a in chapter 3.3), tolerance levels for the number of salmon lice per smolt will also be reduced. The effects of the highest sea temperatures on salmon lice are poorly documented, and whether sea temperatures above 18 °C may have any negative effects on salmon lice production should be further examined (Boxaspen 2006). Climate change in coastal waters might also result in temperature-related shifts in the geographic distribution of other caligid parasites, such as the host-generalist *Caligus elongatus*, and their impacts on more northern populations of sea trout. *C. elongatus* has long been a pest species to salmon aquaculture in Scotland (e.g. Revie et al. 2002a), and this parasite might well extend further north in Scandinavia as Atlantic climate change progresses.

The ability of sea trout populations to adapt to rapid environmental shifts due to climate change is likely to be reduced if they suffer reduced genetic variation and population sizes due to other impact factors. Hence, stocks of reduced population size and genetic variability, and less variation in life history traits attributable to other impacts, are expected to be less robust in adapting to climate change.

3.5 Concluding statements

- There is local and regional variation of the impact factors that influence sea trout populations and which of those impact factors are the most important.
- The status of sea trout stocks and fisheries varies across the distribution range according to the influence of local and regional factors.
- Impact factors that may act on sea trout in freshwater include acidification, other aquatic pollution (e.g. from agriculture, roads and mining), hydropower development, other river flow regulation, migration obstacles and habitat alterations.
- Human-derived impact factors that may act on sea trout in the marine environment include salmon lice but extend also to the construction and deployment of harbours, piers, bridges, fish farm structures, and other industrial developments. However, there is little information on how such structures and their associated activity may impact on sea trout.
- Climate change is an important impact factor that can act on sea trout populations both in the freshwater and marine habitats.
- Overexploitation in recreational and commercial fisheries, and diseases caused by viruses, bacteria, fungi and parasites due to fish farming, are also impact factors that may affect sea trout both in the freshwater and marine habitats.
- Often, several anthropogenic factors can impact sea trout populations simultaneously. Studies of the interactive effects of anthropogenic disturbances on fish populations are often complicated and expensive to conduct, and very few such studies on any species exist in the literature. This is one reason why it is difficult to isolate and analyse the effects of single factors in any wild population. The interactive effects of two or more impact factors may be complex, non-linear and unpredictable, and certainly not apparent from combining knowledge of the effects of single factors studied in isolation.
- Climate change inevitably is an impact factor that interacts with other anthropogenic influences. The effects of salmon lice will also interact with climate change. Negative effects of salmon lice might become more severe over larger geographical areas as a result of climate change, and more northerly populations will likely be increasingly impacted.
- Sea trout populations of reduced population size and genetic variability, and less variation in life history traits attributable to other impacts, are expected to be less robust to adapt to climate change.

3.6 Knowledge gaps

- The effects of different impact factors, and their interaction, are generally not well studied in sea trout. Effects of hydropower development and other causes of river flow regulation are better studied than are other impact factors, and a number of studies on other salmonids can also be used to infer impacts on sea trout. The effects of climate change on sea trout have been recently reviewed, but the effects of contaminants and pathogens from farmed fish, potentially causing fatalities in wild fish, seem to be among the least studied impact factors for sea trout.

- Studies of interactive effects of multiple impact factors are largely lacking.

4 Historical outline of salmon lice studies in sea trout

Wild sea trout in areas lacking salmon farming have generally low intensities of salmon lice, and salmon lice epizootics seem not to be a common phenomenon for sea trout and other wild salmonids in farm-free areas, or prior to the commencement of farming (see chapter 8). In the case of farmed salmon, the first outbreaks of salmon lice infestation occurred on Norwegian Atlantic salmon farms during the 1960s, soon after cage culture began (Pike & Wadsworth 1999). Similar outbreaks occurred in Scottish Atlantic salmon farms from the mid-1970s (Pike & Wadsworth 1999).

In Ireland between 1989 and 1991, heavily salmon lice-infested wild sea trout in poor physical condition were for the first time recorded to show premature migratory return to freshwater (Whelan 1991, Tully et al. 1993b). Based on the observations from Ireland, field studies were initiated in Norway in 1992. The phenomenon of sea trout returning to freshwater prematurely in poor physical condition and with heavy salmon lice infestations was documented also in Norway (Birkeland 1996, Birkeland & Jakobsen 1997). Preliminary investigations in Norway in the early 1990s indicated that larval lice infestations also occurred on wild Atlantic salmon post-smolts (Finstad et al. 2011).

These early observations of epizootics initially stimulated research into salmon lice biology and their control. The majority of research papers concern the salmon louse, *Lepeophtheirus salmonis*. This species is a specialist parasite on salmonid hosts, is the most frequent on salmon and causes the greatest damage both to cage-cultured and wild populations (Pike & Wadsworth 1999). Another sea louse species, *Caligus elongatus* − which is a host generalist, but also a frequently recorded parasite of farmed salmonids in Scotland and Ireland − occurs in conjunction with salmon lice and can cause significant pathology if abundant (Wootten et al. 1982). However, the present review is concentrated on the salmon louse *L. salmonis* and not *C. elongatus*.

In the early 1990s, knowledge of the physiological effects of salmon lice on salmonids was generally limited (Wootten et al. 1982), and few field studies of salmon lice on wild salmonids existed (Finstad et al. 2011). The physiological and ecological consequences of the observed infestation, and the possible causal relationship between fish farming and salmon lice infestation of wild salmonids, had not been ascertained. Clearly, the further clarification of the phenomenon of premature migratory return of wild sea trout, and more information on the physiological effects of salmon lice in salmonids, both were needed.

The first phase of research focused on testing the physiological effects of salmon lice on artificially infested sea trout, Atlantic salmon and Arctic char post-smolts (Finstad et al. 2011). Further information on the ontological development of salmon lice on artificially infested post-smolts, their development and survival rate, distribution on the host body surface and their pathogenicity also was described. This was achieved by undertaking controlled laboratory experiments on artificially infested salmonids and by studying the physiological and pathological consequences of the salmon lice for the host fish (see chapter 6). The second phase of research focused on analysing causal connections between the salmon lice epizootics in wild salmonids and the rapidly expanding salmon farming industry, and to ascertain the fraction of wild salmonid populations infested with salmon lice levels assumed to have negative physiological or even lethal effects. This was investigated through extensive field studies involving the capture of sub-populations of sea trout, Atlantic salmon and Arctic char both in intensively fish farmed areas, and in control areas, and by quantifying the salmon lice level on these fish (see chapter 7, 8 and 9). The third phase of research centred on the effects of annual salmon lice epizootics on populations or cohorts of wild salmonids, especially of sea trout and Atlantic salmon post-smolts, in intensively farmed coastal areas (see chapter 10). The experimental protocol involved protecting individually Carlin-tagged salmon and sea trout smolts by means of a prophylactic chemical treatment against salmon lice, and thereafter releasing them (together with control groups of untreated fish) in the vicinity of their native river. This treatment protects the fish against salmon lice for several weeks, and provided it does not interfere with the fish in other ways, these experiments permit the calculation of estimates of population effects of lice on the host species (chapter 10). Finally, this avenue of research has developed to include larger study areas, with a view to evaluating the establishment of farm-free areas in Norway (see chapter 7, 9 and 10).

5 Evaluation of sampling and monitoring methods

In this chapter, sampling and monitoring methods applied in assessing salmon lice levels on wild sea trout are discussed and evaluated. In order to assess the salmon lice levels on sea trout populations, there is a need to obtain representative samples both of sea trout and the salmon lice on those fish. In practice, the acquisition of accurate and representative data is challenging because of the variation in the life history, behaviour and interactions of both the host and the parasite. As is well known for many other parasites, salmon lice typically are aggregated on their hosts. Often, this leads to a skewed distribution where a few individual hosts can have very high numbers of lice (see **box 3** and chapter 8). This natural variability and complex distribution imposes requirements on data sampling and data analysis; large amounts of data are needed in order to confidently describe the statistical relationships between the parasite larval pool and salmon lice levels on the wild fish. In addition, there are several methodological issues about the practicalities involved – including, for example, aspects of the sampling gear, sampling strategy, counting and analysis methods − that require careful consideration when planning and conducting field studies.

5.1 Sampling for sea trout

The sampling strategy for sea trout depends naturally upon the research question being posed. Irrespective of this, one of the main challenges in quantifying the host-parasite relationship for an entire sea trout population in a given locality is to sample effectively all the host life-stages. Here, the choice of sampling gear to be deployed, and the locations and timing of placement of that gear, all have implications for the obtaining of suitably comprehensive and representative data. Thus, one has to consider the sampling strategy carefully. Regardless of the sampling methods utilised, one of the fundamental problems in sampling is that the likelihood of capturing fish is most likely dependent on the levels of salmon lice. For example, infested sea trout may have returned to freshwater or died at sea due to physiological stress caused by the infestation (see chapter 7) and may therefore never be sampled in the sea. This means that there might be an inherent bias in sampling methods targeting fish at sea, perhaps to the extent that there is a risk of excluding observations of the highest intensity infestation levels (Lester et al. 1984). This can lead to a general underestimation of salmon lice levels. In addition, there is a general lack of quality control of methods. There exist few methodological studies that compare different sampling methods and gears, and no consensus has been attempted on standardized sampling procedures.

During their period of growth and feeding after leaving the river (see chapter 2), sea trout may be found in marine and brackish waters, and some may prematurely return to freshwater again if lice levels are high. All of these habitats should be sampled if the objective is to fully document the effect of salmon lice on sea trout populations (Bjørn et al. 2001). The survey design and placement of the sampling gear in certain habitats might lead to biased sampling of the population. For example, if sampling is concentrated only in a fjord then fewer small and heavily infested fish are likely to be caught (Bjørn et al. 2001), whereas sampling only in the estuary and freshwater might include only those most heavily infested and partially de-loused fish (Bjørn et al. 2001). Heavily infested trout can either to return to freshwater or the estuary for extended periods (see chapter 7). Therefore, studies based on sampling sea trout in, or close to, river mouths might lead to an overestimation of the local salmon lice levels. Conversely, river outfalls also are used by fish that only recently entered the sea and are yet to be infested, and data from these fish may in some periods lead to underestimation of salmon lice levels. Also, salmon lice die in fresh water and the number of salmon lice on returned trout will therefore decrease with time following river reentry.

Box 3 Prevalence, abundance and intensity of salmon lice

Parasitologists conventionally apply three distinct terms to define the frequency of parasites of host individuals by a given parasite species, and the abundance of that parasite species among individual hosts (Bush et al. 1997). Thus, “Prevalence” is defined as the proportion, or percentage, of infested hosts in a sample. “Abundance” refers to the mean number of parasites per host sampled, and “Intensity” is the mean number of parasites per infested host. Abundance and intensity also may be expressed as the median, rather than the mean, value for the population sampled (e.g. Rikardsen 2004). Quantitative biologists commonly wish to summarize variation amongst individual organisms with a simple measure of the central tendency of that variable, and perhaps to compare that measure among samples or populations. Typically, one would measure the variable for multiple individuals from a sample and then compute the mean (average) or median (mid-point) as the descriptive measure of central tendency. The use of the arithmetic mean as a descriptor of the central tendency is, however, not appropriate if the variable shows a distinctly non-normal frequency distribution. Shaw & Dobson (1995) and Shaw et al. (1998) reviewed and analysed an extensive series of data for 49 host-macroparasite associations, and showed that parasite burdens amongst individual hosts almost invariably show a non-random pattern: that is, the variance of abundance typically exceeds the mean abundance and the data can be mathematically described by the negative binomial distribution. Aggregation – or statistical over-dispersion – of parasites amongst host individuals typically is reflected by a small proportion of the host population being parasite-free, most individuals showing a low abundance and a few individuals carrying very high burdens. Statistically, this pattern is referred to as being right skewed, and the arithmetic mean of such a frequency distribution will over-estimate the central tendency (the “average” abundance of the parasite on the host). Under such circumstances, a more appropriate indicator of mean parasite abundance would be to utilise only the median values (e.g. Rikardsen 2004), or perhaps to log-transform the data (e.g. Todd et al. 2006), prior to further analysis.

This latter issue is perhaps of specific relevance to comparative assessments of salmon lice on sea trout because within samples there commonly is a high degree of over-dispersion. This may be especially important for samples of post-smolt juvenile sea trout with the early chalimus stages of salmon lice: a few individual sea trout within a sample may be exceptional or atypical in carrying several hundred chalimi, and the computation of the arithmetic mean can therefore over-estimate the central tendency of parasite abundance amongst those individual post-smolts. For example, the intensity of salmon lice of sea trout both in Scotland (e.g. MacKenzie et al. 1998) and Norway (Bjørn et al. 2001) has been reported to exceed 200 parasites per fish, whilst the mean/median intensity was one or two orders of magnitude lower.

At sea, the most commonly used sampling gears to capture host fish include gill nets, trawls and traps. Each of these methods has advantages and biases. Gill nets are effective and easy to use, but mesh size will be size-selective of the host fish caught and might under-sample the smallest and/or largest fish. This can be important for sea trout sampling because the smallest fish most likely to succumb to infestations, and are at times heavily infested (Bjørn et al. 2001). Gill nets deployed in coastal marine waters might under-sample highly infested, less mobile trout because they are less likely to actively swim into the net, and trout that have prematurely returned to freshwater are, by definition, not available for capture at sea (Bjørn et al. 2001, Gjelland et al. 2014). Trawling can be effective in catching the smallest (post-smolt) fish that otherwise might escape gill nets. However, trawling for post-smolts at sea can be inefficient (Bjørn et al. 2007), costly, and the data might overestimate the abundance of heavily-infested post-smolts because the burden of motile salmon lice can affect the swimming capacity (and hence catchability) of trout (see chapter 6). This latter problem is, however, seldom applicable to post-smolts owing to these young fish typically being infested by copepodid and chalimus larval stages (Finstad et al. 2000, Bjørn et al. 2007). Furthermore, because trawling is likely to be undertaken over a wide area it is likely to provide data for multiple or mixed stocks of fish if there are several rivers in the sampling locality. By contrast, gill nets can be set close to particular rivers of interest, and therefore provide more localized or specific data (Bjørn et al. 2007). Traps with small mesh sizes, and which retain fish free-swimming, are less size-selective than are gill nets and offer the additional advantage that the fish are caught alive with a minimum of damage or mechanical abrasion (Barlaup et al. 2013). Because sea trout stocks are critically low in many areas, understandably there is considerable pressure to use non-destructive capture methods for sampling fish, and to release at least the largest captured individuals. Consequently, these constraints all have resulted in relatively more data being available for smaller sea trout in monitoring programmes (Serra-Llinnares et al. 2014). None the less, salmon lice levels on small, immature sea trout are acknowledged to be indicative of local sources because these hosts often use nearshore coastal waters for feeding (see chapter 2).

In fresh water and estuaries, the most common sampling methods to catch prematurely returned host fish are by electrofishing and purse seine nets. Electrofishing has been criticized for being ineffective in brackish water (>500-800 µS/cm), where in many cases the host fish are found. Thus, using electrical fishing equipment might provide an indication of lice levels if fish with large numbers of lice are caught, but one cannot infer low lice levels if no infested fish are caught, because the infested fish might occur out of reach and closer to the river outlet. Purse seine nets are preferred methods of catching the fish in estuaries, but are more time consuming to use. As mentioned above, sampling prematurely returned fish might overestimate salmon lice levels as a result of biased sampling of the smallest, most heavily infested fish (Bjørn et al. 2001). However, when used to compare among years and regions (Skaala et al. 2014), or in combination with other methods (Bjørn et al. 2001), this approach might still provide an efficient and low cost method of assessing local salmon lice levels. Permanent freshwater traps have also been used in sampling sea trout, and data from these sources can provide valuable population information for selected watercourses. Such traps can be implemented only in few rivers because of their expense in construction and maintenance and, by definition, they are not moveable between locations. In addition, if they are placed in the middle reaches of the river, they may have little relevance for sampling prematurely returning host fish which perhaps remain in the lower stretches.

The survey design must also consider the timing of the sampling to be undertaken, because sea trout normally enter sea water in spring and early summer (see chapter 2 for details). A standard longitudinal sampling design often is an advantage because the timeline of the salmon lice levels can be followed (Anderson & May 1982), and detailed studies can then be conducted at multiple time points and perhaps with several sampling methods (Bjørn et al. 2001). More geographically dispersed studies can concentrate on the one standardized sampling method, and perhaps include two or more critical time periods. An example of the latter is given by Serra-Llinnares et al. (2014) in comparing salmon lice levels on sea trout in Norwegian national salmon fjords throughout the Norwegian coastline: the first sampling period was undertaken a few weeks after most of the salmonid smolts had entered seawater, and the second period was approximately one month later with the specific aim of investigating the acquired salmon lice levels on sea trout halfway through their marine migration.

In summary, the design of the sampling protocol should encompass a specific strategy; if possible, several sampling or capture methods should be used in concert not only to sample all the life-stages of the host fish, but also to enable the acquisition of statistically meaningful sample sizes (Bjørn et al. 2001, Serra-Llinnares et al. 2014). The latter are crucial for data analysis when the aim is to draw inferences for the whole population (see chapter 5.5 for more on analysis). However, in view of the complexity and plasticity of sea trout behaviour and life history, as well as logistical considerations, this always will be challenging.

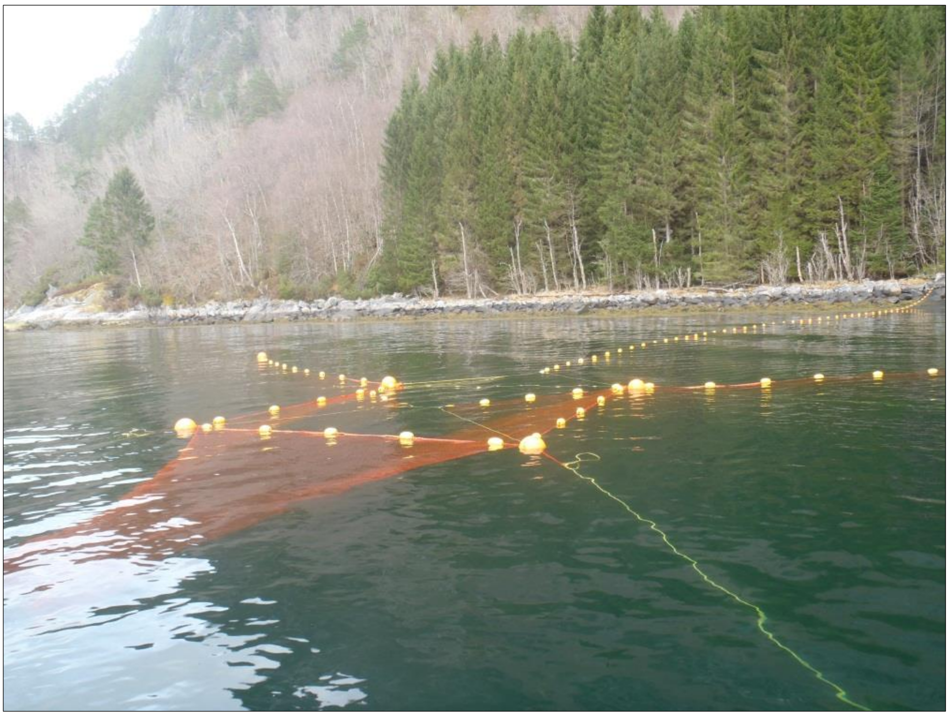
5.2 Enumeration and quantification of salmon lice on sea trout

The main challenge in quantifying salmon lice on sea trout is for the sampling process to permit retention of the parasites on the captured fish, and for recorder personnel to recognize and distinguish all the sea louse life stages. The key issues are the use of a sampling method that will best represent the true number of salmon lice on the fish, and a counting method that is comparable between studies.

The sampling gear can affect the lice count on sampled sea trout in several ways. Sampling gear can physically remove or abrade the lice when the fish is caught. The gear also may kill the fish and induce mobile salmon lice to detach from the host, or lice might transfer between sampled fish. Gill nets have been widely used in assessment programmes for salmon lice, but can both physically remove the lice and kill the fish. However, both problems are reduced with reduced soak (= deployment) time of the gill net (Bjørn et al. 2001, Serra-Llinnares et al. 2014). Traditional trawling also potentially removes the lice and kills the fish. Holst et al. (2000) developed the FISH-LIFT trawl, which sorts small post-smolts into a closed aquarium, connected to the trawl cod-end, such that it allows large numbers of fish to continue to swim unharmed in the aquarium once caught. The sea trout net trap reported by Barlaup et al. (2013) is anchored to the seabed and catches all size classes of sea trout unharmed and, because there is no large-mesh gear in which the fish might become entangled, it also yields the most reliable assessments of salmon lice levels on individual fish (Barlaup et al. 2013). By comparing catches and counts between their fixed trap and anchored conventional gill nets, Barlaup et al. (2013) were able to show that the abundance of adult salmon lice on trout caught in the trap was significantly higher than those taken in gill nets. There was, however, no significant difference between the two designs of gear for the attached larval lice stages. It is important to note, however, that Barlaup et al. (2013) deployed gill nets overnight; such extended soak times would not generally be used due to the high expected loss of mobile salmon lice on dead fish (Bjørn et al. 2001, Bjørn & Finstad 2002, Bjørn et al. 2007, 2011, Serra-Llinnares et al. 2014). Another methodological challenge in using traps (or any other method that keeps the individual fish alive and close together) is the possibility of lice switching hosts, leading to an overestimation of prevalence in the sampled population. However, using traps in freshwater can also lead to underestimation of lice loads due to lice mortality.

The recognition, distinction and/or enumeration of the various louse life stages has varied considerably amongst published studies and monitoring programmes. This variability in the available data makes it difficult to draw meaningful comparisons amongst studies, because the quality of the biological information is dependent on the counting resolution. In response to this, the Norwegian government has implemented a mandatory reporting of lice for the salmon farming industry; the usual practice is to provide separate counts of the sessile stages (chalimus), motile stages (pre-adults and adults), and adult females from a subsample of fish under anaesthesia, and to report average numbers for the three groupings (Revie et al. 2009, Jansen et al. 2012). The scientific community has not developed a standard procedure of enumeration because the counting method in a given study has, to some extent, depended on the research question at hand. In general, however, it is advisable to count all life stages of salmon lice separately when this is possible, and to pool data only at the completion of enumeration. In the Norwegian salmon lice monitoring programmes (see chapter 5.4) lice are grouped into their sessile or motile stages, although sometimes these data can be more detailed (e.g. Bjørn et al. 2001), and they include the total number of lice as well as other parameters (Bjørn et al. 2001, Serra-Llinares et al. 2014). Previously (Bjørn et al. 2001), counting of salmon lice with a stereomicroscope in the laboratory or field for frozen and thawed trout was the common procedure. Subsequently, the counting of lice on freshly-caught sea trout in the field, and by using a hand-held stereoscope (Serra-Llinnares et al. 2014), has become the recommended ideal standard method. For prematurely returned sea trout captured in freshwater by electrofishing, the enumeration of salmon lice on the live fish in a shallow water tank has been the preferred method (Skaala et al. 2014). Together with a light sedation, this counting technique is also preferred in purse seine net captured sea trout (Barlaup et al. 2013, Serra-Llinnares et al. 2014).

The different approaches to enumerating salmon lice can provide different biological information. For example, relating salmon lice levels on sea trout to estimates of pelagic salmon lice exposure is likely to be more closely correlated when applied to data for the early life stages of salmon lice, as there is considerable variation in the development time between individual salmon lice (Stien et al. 2005). In addition, the different counting methods incur various statistical analysis constraints due to the differences in the distribution of the data (see chapter 5.5. for more on analysis).



Modified bag net used to collect wild sea trout for monitoring of salmon lice in Middle Norway. Photo: Marius Berg

5.3 Quantifying the potential salmon lice levels on sea trout

Direct quantification of salmon lice levels on sea trout requires the availability of a sufficient number of fish to be sampled within a given geographical area. This is not always the case. In addition, the fact that high levels of salmon lice can affect the behaviour of individual trout (as exemplified by, for example, premature migratory return: Birkeland & Jakobsen 1997, Bjørn et al. 2001, Gjelland et al. 2014), makes it important for the observer to be able to quantify the local salmon lice levels independently of the presence of fish, i.e. with indirect methods. As discussed above, directly quantifying salmon lice on sea trout may be potentially biased, and is also logistically demanding. A review is provided here of the primary methods used in indirectly quantifying the potential salmon lice levels on sea trout in a given locality or area.

Salmon lice levels recorded as the number of infective copepodid stages of salmon lice in the water column at a given locality, has proven difficult to assess. The primary reason for this is that the concentration of salmon lice relative to other planktonic stages of zooplankton typically is low (and hence lice larvae are difficult to enumerate in a general plankton sample), and that the copepodids are patchily distributed in the ocean (Penston et al. 2004, 2008b).

At present, there are different methods for assessing the concentration of the planktonic nauplius and copepodid stages in the water column. For example, horizontally towed plankton nets have been successfully used to assess the along-shore and open water concentrations of salmon lice in Scottish sea lochs (Penston & Davies 2009, McKibben & Hay 2004, Penston et al. 2008a). These data have been correlated with the fallowing regimes applied by adjacent salmon farms and have shown that the salmon lice levels in bays and sea lochs with salmon farms is heavily dependent on the production cycle of farmed fish (Penston & Davies 2009). In addition, they have demonstrated that copepodids tend to concentrate along-shore and below the halocline at the outlets of rivers (McKibben & Hay 2004). Light traps (Flamarique et al. 2009) and plankton pumps (Kilburn et al. 2010) also have been tested and applied to the collection of the free-living planktonic stages of salmon lice; but these have not, to our knowledge, been used in surveys targeted at documenting the local salmon lice levels. A feature that is common to these methods is that the identification of larval salmon lice in plankton samples is extremely labour intensive. Detecting and enumerating particular life stages or species in a plankton sample has traditionally been a time-consuming task that is further complicated by difficulties in reliably assigning the species.

With the emerging methodologies of molecular biology alternative methods to allow accurate species assignment has been used for several zooplankton species (Lindeque et al. 1999). This advance in methodology has also been extended to detecting salmon lice from environmental samples using molecular methods such as quantitative polymerase chain reaction (QPCR) (McBeath et al. 2006, Penston et al. 2011), and similar approaches have been used for other crustaceans (Jensen et al. 2012b). QPCR uses specific primers to accurately determine the relative amount of DNA from a target species relative to a standard sample. Despite the ability of the approach to give relative abundances using the appropriate calibrations, the methodological approach has not gained widespread use. Reasons for this include variability in assay stability under various conditions which compromise estimate precision, and variability in the “DNA target sequence:specimen” ratio that will invariably be found in specimens that grow and increase in cell numbers. One message however is clear: even miniscule target amounts of DNA can be qualitatively detected using PCR-based methods (Skern-Mauritzen et al. 2014). Although this approach may be too laborious for routine surveillance, it may without problems be applied to a limited number of samples as required to, for example, parameterise and validate hydrographic models of salmon lice larval abundance and dispersal.

An alternative method that does not require plankton identification is the use of live fish held in the field in sentinel cages (Asplin et al. 2011, Bjørn et al. 2011). Previous applications of this experimental approach have involved the placing of a number of hatchery reared salmon smolts in a relatively small net cage at different locations within a fjord for a period of 1-3 weeks and subsequently counting the salmon lice on the fish. The method has been criticized because the interaction between salmon lice and fish is most likely strongly affected by the fine mesh net and the fact that fish will not swim naturally over an extended range and thereby encounter salmon lice copepodids in a manner that reflects their variation in the local habitat. Thus, the results cannot directly be translated to a concentration of free-living stages of lice or to the potential infestation pressure encountered by wild sea trout (Bjørn et al. 2011). However, it can be used to provide an index to assess the between- and within-season variation in localized infestation pressure, as well as that between a given area and among regions (Bjørn et al. 2011). Furthermore, it can be used to validate hydrographic models of pelagic salmon lice larval dispersal and their spread (Asplin et al. 2011, see also below).

A potentially promising indirect method to quantify the local salmon lice levels is so-called hydrodynamic lice dispersal modelling. Coupled biological−hydrodynamic lice dispersion models have become numerous over the last 10 years. The spread of larval salmon lice has been simulated in Norway and in many salmon-producing countries (Gillibrand & Willis 2007, Asplin et al. 2011, 2014, Adams et al. 2012, Johnsen et al. 2014), and international collaboration on dispersion modeling is currently ongoing.

Numerical modeling of currents and hydrography which are the basis for salmon lice dispersion modeling, are performed with the state-of-the-art hydrodynamic ocean model, ROMS (Haidvogel et al. 2008, Shchepetkin & McWilliams 2005). This usually is implemented for a region with a high resolution grid of 160 m horizontal cells and 35 layers vertically. The model is forced with lateral boundary conditions (hourly fields of currents, salinity and temperature) obtained from the coarser model, NorKyst800 (800m grid cells), covering the Norwegian coast (Albretsen et al. 2011, technical report) and including tides that are based on a global inverse barotropic model of ocean tides (TPXO7.2). Further, the model is forced by high resolution winds (3 km) obtained from the WRF-meso-scale-atmospheric model (www.wrf.model.org) providing wind fields representing the local winds within fjords (Myksvoll et al. 2012), in addition to river runoff data from the Norwegian Water Resources and Energy Directorate (NVE) (Beldring et al. 2003). The ocean model output is of instantaneous fields of currents, temperature and salinity saved every hour in every grid cell in all model layers. These fields are applied for modeling advection of salmon lice larvae with a modified version of the Lagrangian Advection and Diffusion Model (LADIM, Ådlandsvik & Sundby 1994, Asplin et al. 2011, 2014, Johnsen et al. 2014). LADIM computes the advection of the planktonic stages of the salmon lice, represented in the model as individual particles with ascribed behaviour, growth and mortality. The particles can be representative of “super-particles” representing cohorts of lice larvae and given a variable mortality. The model particles migrate vertically in response to light, temperature and salinity. For details about the parameterization, see Johnsen et al. (2014). The development of the particles is calculated as degree days, where the infectious copepodid stage is estimated to last from 50 to 150 degree days. Thus, for example, with water temperature constant at 10°C the copepodid stage will be reached at day 5 post-hatching and last until day 15 post-hatching. A constant mortality rate of 0.17 d^{-1} is applied, as estimated by Stien et al. (2005), and the particles are defined as “dead” after 150 degree days. Particles representing salmon lice are “released” in the model at the real positions of salmon aquaculture sites. The numbers of released lice nauplii at each site are computed according to Stien et al. (2005) and Jansen et al. (2012), from weekly reported salmon lice counts from Norwegian Food Safety Authority and biomass data from the Directorate of Fisheries (Jansen et al. 2012).

The modeled larval lice distribution and abundance in the fjord system depend on the currents advecting the lice (particles), the spreading of lice larvae (mixing, eddies, convergence/divergence zones etc.), the quantity of lice nauplii released from the fish farms, the position of the fish farms, the temperature (affecting growth and development), the salinity (vertical migration, avoiding brackish water), and the parameterizations of growth and mortality in the model. Future work will compare the modeled development of salmon lice at/near the standard sampling sites for wild salmonids, on hatchery-reared smolts in sentinel cages and from plankton samples, and prepare a statistical relationship between the datasets. In short, this can be achieved by counting the model-predicted number of infective copepodids from fish farms within one or more grid cells (160x160 m) at/near field sampling sites, and correlating the numbers with salmon lice observations on wild salmonids, from fish in sentinel cages and from plankton samples. In addition, the mapping of temperature and salinity (CTD measurements) in the fjord system, as well as current measurements, can be undertaken to validate the physical components of the model (Asplin et al. 2014, Taranger et al. 2014). If one could predict the abundance and distribution of salmon lice originating from farmed fish in space and time by the use of hydrodynamic models (Asplin et al. 2011), and also determine the critical abundance threshold for infestation effects on wild salmonids, this could provide the basis for an area management system founded on “maximum sustainable lice loads” or “lice quotas” (Serra-Llinnares et al. 2014). However, despite the potential of hydrodynamic models, there are pitfalls that need to be considered carefully, especially when calibrating and validating the models and extrapolating models into new areas.

5.4 Monitoring programmes on salmon lice levels in sea trout

The main objective of monitoring programmes of salmon lice levels on sea trout is to obtain comparable samples in space and time and to be able to draw inferences on the local infestation risk (for example, by comparing “farm exposed” and “non-exposed” areas, and among seasons and years), possible effects on wild salmonid populations, and possible consequences of the amelioration measures taken by management and the salmon farming industry (Serra-Llinnares et al. 2014). Because of the logistical difficulties of sampling in the field, and the aggregated or over-dispersed distribution of salmon lice on individual fish, monitoring programmes usually are based both on direct and indirect methods, the combinations of which vary between programmes. The combined analysis of data arising from the different methods will give the most robust picture of the salmon lice level in given region. The nature of the monitoring programmes (designed primarily to provide scientific advice for authorities or regulatory bodies – e.g. the National Food Safety Authority in Norway), is such that the results generally are reported in the grey literature rather than in peer-reviewed international publications. However, a small number of key peer-reviewed sea trout-salmon lice publications based on monitoring programmes or related activities exists both for Norway (Bjørn et al. 2001, 2007, 2011, Bjørn & Finstad, 2002, Finstad & Bjørn 2011, Serra-Llinnares et al. 2014), Ireland (Tully et al. 1993b, 1999, Gargan et al. 2003, see chapter 10 for details) and for Scotland (Butler & Watt 2002, Butler & Walker 2006, Hatton-Ellis et al. 2006, see chapter 10 for details).

Since the mid-1990s, Norway has enacted a National Salmon Lice Monitoring Programme as part of the National Strategy to protect important stocks of wild salmonids (Finstad & Bjørn 2011), and salmon lice levels on wild salmonids have been systematically monitored and reported to the Norwegian management authorities since 1992 (Finstad & Bjørn

2011). The programme has varied in intensity throughout the years, but has been comprehensive since 2010 and includes up to 41 sampling locations distributed in 15 different fjord systems covering the length of the Norwegian coastline (Serra-Llinares et al. 2014). The programme incorporates a combination of gill net monitoring (Bjørn et al. 2001, Serra-Llinnares et al. 2014), sea trout traps (Barlaup et al. 2013), sentinel cages (Bjørn et al. 2011, Asplin et al. 2011), trawling for post-smolts (Finstad et al. 2000), electrofishing and studies of premature migratory return (Birkeland 1996, Bjørn et al. 2001, Skaala et al. 2014). A central protocol in the programme has been to sample annually at the same localities both in intensively farmed and control areas. There has been an especial focus on Norwegian national salmon fjords, in order to address questions about the relationship between fish farming and salmon lice epizootics, to assess the consequences of salmon lice on wild salmonid populations and to measure the success of the measures taken by management and the fish farming industry.

Trawling to collect wild sea trout for monitoring of salmon lice in the Sognefjord in Western Norway. Photo: Steinar Kålås.

Since 1991 Ireland has conducted a long-term monitoring programme of sea trout in west coast catchments (see chapter 10). Monitoring of 10-12 west coast rivers for salmon lice-infested prematurely returning sea trout has been ongoing annually since 1991. A larger national monitoring programme involving 15-52 rivers close to, and distant from, salmon aquaculture facilities was conducted over the period 1992-2001 (Gargan et al. 2003), with sampling undertaken primarily using gill nets in inner estuaries and river mouths. Since 2002, sampling has concentrated on rivers entering aquaculture bays on the west coast (see chapter 10 for details).

Effective and large-scale monitoring programmes require considerable logistical effort and infrastructural investments to provide for the necessary data requirements, and are especially resource-intensive if they are continued over extended periods (e.g. Gargan et al.

2003, Serra Llinnares et al. 2014). Despite the obvious value of continuous high-quality monitoring data collated in a consistent manner over extended periods, there is pressure to revert to less demanding indirect methods to estimate the salmon lice levels on wild salmonids. One approach suggested by Serra-Llinnares et al. (2014) is to use the lice count data and biomass production values from aquaculture as a resource in estimating the regional and temporal infestation pressure, and to couple these with the hydrodynamic−biological lice dispersion and abundance models (see above) in predicting the infestation rate and risk and consequences for wild salmonid populations. In Norway, lice surveillance programmes are rapidly developing in that direction (Serra-Llinnares et al. 2014), and a preliminary version may be in operation throughout the Norwegian coastline by spring 2015 (Taranger et al. 2014).

5.5 Challenges in data analysis of salmon lice on sea trout

Notwithstanding the difficulties in obtaining representative samples both of fish and salmon lice, the analysis and interpretation of count data of salmon lice on sea trout remains challenging due to the nature of the data themselves. Several statistical approximations are possible, however none are ideal. There are three main statistical measures for occurrence of salmon lice that are used in parasitological analyses and statistical tests. These are: presence/absence of salmon lice (binary response variable), the percentage of fish with a certain level of salmon lice (proportional response variable) and the total number of lice on each fish (poisson or negative binomial which are usually zero-inflated). These three response variables vary in their data requirements and accuracy, and the choice of statistical measure therefore depends on the research question at hand. For example, if the question is to compare two regions it is perhaps sufficient to use presence/absence and a lower sample size; if, however, the goal is to estimate the number of salmon lice on fish in a given cohort for comparison with a given threshold level, a much higher accuracy is required.

Another central challenge in data analysis of salmon lice effects is that of autocorrelation; the individual fish is the analytical replicate and, for example, fish caught close to each other cannot necessarily be considered as independent observations. Salmon lice observations may be autocorrelated both in time and space, as the salmon lice level builds up and spreads geographically over time. This can in theory be corrected for in statistical models by introducing random variables. Such statistical challenges should be considered during planning of sampling programmes.

Helland et al. (2012, technical report), analyzed all available data from the Norwegian National salmon lice monitoring programme from 2004-2010 including 4890 fish (sea trout and char) from 41 stations and 15 fjord systems. They concluded that despite the large dataset at hand, it remained difficult to draw firm conclusions regarding the relationship between salmon lice levels and the environment due to the large variation in occurrence of salmon lice between individuals. They suggested that: (1) a larger sample of fish to be taken at each station, (2) there is a need to confirm threshold levels for salmon lice infestations, (3) sampling should be coupled to hydrodynamic modelling, and (4) there should be a coupling of such models to counts of salmon lice on farmed fish. In Norway, these recommendations have already been implemented (Serra-Llinnares et al. 2014), or are in progress (Taranger et al. 2014).

5.6 Concluding statements

- Unless deployed for short sampling periods, both gill nets, and trawl-caught fish are subject to physical removal of salmon lice during the capture process. Both methods might show a sampling bias towards certain size-classes of fish. The FISH-

LIFT trawl is an effective means of sampling fish with minimal effects of loss of parasites from the captured fish.

- Sea trout net traps provide representative samples of all the size classes of sea trout while retaining the salmon lice. Trapping also is a non-destructive method, which makes it usable also in areas with depleted stocks. However, live fish also present problems such as a vulnerability to predation within capture chambers, and salmon lice may move between the captured host fish and thereby affect prevalence and abundance estimates.
- A sampling and survey strategy over time and space and which incorporates a combination of different sampling methods should be used in order to more accurately and representatively sample the entire sea trout population of interest.
- Statistical pre-requisites and assumptions about the data should be considered during planning of sampling strategies and monitoring programmes.
- Hydrodynamic lice dispersal models using real fish farm positions, farm biomass and the associated salmon lice data are potentially powerful tools for inclusion in future monitoring and advisory programmes, provided that the models are appropriately calibrated and validated.

5.7 Knowledge gaps

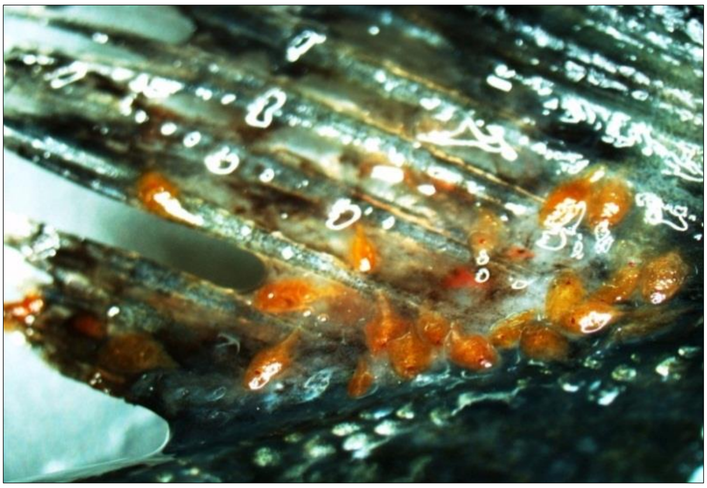
- Few of the capture methods used in monitoring programmes have been quality controlled. Therefore, there is a need for methodological and behavioural analyses comparing the sampling techniques, gear placement and sampling timing in order to obtain indicative and reliable sampling for entire sea trout populations.
- There is a general lack of standardized methods and enumeration protocols between studies.
- The sampling should include a larger number of fish than has been customary in order to be able to draw reliable and robust statistical inferences.
- Studies of sea trout migration routes and marine habitat use in relation to salmon aquaculture facilities and salmon lice levels are needed to determine the actual consequences of the infestation.
- Hydrodynamic lice dispersal models should be developed, validated and calibrated and used in risk analyses and assessments in coastal areas with intensive fish farming activity.

6 Effects of salmon lice on individual sea trout in laboratory studies

In this chapter, an overview is given of laboratory results relating to the physiological and pathological effects of salmon lice on individual sea trout. These studies include both hatchery-reared and wild post-smolts, and they were based on single-pulse exposures to copepodids being added to the tank water in the laboratory (hatchery-reared: Bjørn & Finstad 1997, 1998, Dawson 1998, Dawson et al. 1998, wild: Wells et al. 2006, 2007). The ontological development of salmon lice through the moult stages and host fish responses were monitored for 28-35 days in these particular studies. Such acute exposures of experimental fish to high concentrations of salmon lice larvae are necessary in order to ensure parasites developing on the fish are of similar age, but it has to be acknowledged that these do not necessarily mimic the chronic (lower) levels of natural exposure rates.

6.1 Mechanical damage of fish skin and tissue

Salmon lice feed on mucus, skin and the underlying tissue of host fish, including blood (Brandal et al. 1976, Costello 2006). Chalimus larvae may cause severe tissue erosion when occurring in large numbers (Bjørn & Finstad 1998), and especially of the fins, but it is generally the mobile preadult and adult stages that cause the most severe skin and tissue damage. In laboratory studies of artificially infested sea trout post-smolts, the copepodids tend to show an attachment preference for gills and fins, especially the dorsal fin. The consequential damage to host tissues caused by the attached chalimus remains typically rather minor except in dorsal fin areas where damage may be severe (Bjørn & Finstad 1998, Dawson 1998, Dawson et al. 1997, 1998, Wells et al. 2006, 2007). The mobile preadult and adult stages typically cause rather more severe general skin damage, especially on the preferred head and dorsal areas, but also in the anal region. Tissue damage by the mobile stages ultimately causes mortality of the most heavily infested fish (Bjørn & Finstad 1998, Dawson 1998, Dawson et al. 1998, Wells et al. 2006, 2007).



Dorsal fin of wild sea trout infested with chalimus stages of salmon lice. Photo: Patrick G. Gargan

6.2 Osmoregulatory problems and physiological stress responses

Salmon lice impacts have been shown to create an osmotic and ionic imbalance in sea trout, which is likely due to the mechanical damage of the skin and tissue *per se*, but also attributable to an additional and more general stress response (Bjørn & Finstad 1997, Wells et al. 2006). Stress responses may impact the fish negatively in various ways. The effects both of mechanical damage in itself, and the different stress responses, are elucidated below.

In freshwater fish, the body fluids have a higher salt concentration than the surrounding water. Water enters the fish body by osmosis, whereas salts tend to be lost. Fish would gradually become hydrated if they did not compensate by excretion of dilute urine and an active salt uptake (Na^+ and Cl^-) through the gills (Evans 1979, Marshall & Grosell 2006). Anadromous fishes such as sea trout experience a challenging environmental shift when they migrate from freshwater to saltwater and must adapt to the increased salinity. In seawater, where salmon lice occur, the fish body fluids are less concentrated than the surrounding water (fish 340 mOsm, seawater 1000 mOsm; i.e., fish are hypo-osmotic). Water is lost from the fish by osmosis, whereas salts tend to be gained. The fish would gradually become dehydrated if it did not compensate, which most fishes (including sea trout) achieve by drinking seawater and actively excreting the excess salts through the gills (Na^+ and Cl^-) and kidneys (Mg^{2+}, Ca^{2+} and SO_4^{2-}) (Evans 1979, Marshall & Grosell 2006). This process of drinking saltwater and actively excreting excess salts is the basis of osmoregulation.

The mechanical damage of the skin, mucus surfaces and dermal tissue caused by salmon lice impairs the barrier between the fish body and seawater, and results in increased leakage of water from the fish body and thereby an osmotic and ionic imbalance (Bjørn & Finstad 1997). Reduced haematocrit (volume percentage of red blood cells in blood) observed in infested and moribund fish (Bjørn & Finstad 1997, Wells et al. 2006) may be attributable to leakage of blood components (bleeding) due to mechanical damage of skin and tissue, possibly in combination with erythrocyte (red blood cell) shrinkage (dehydration) (Bjørn & Finstad 1997).

Salmon lice have been shown to elucidate chronic stress responses in fish (Bjørn & Finstad 1997, Dawson 1998, Wells et al. 2006, 2007). Physical, chemical and sensorally perceived stressors can evoke non-specific responses, which are considered compensatory and/or adaptive, to enable the fish to confront the disturbance and maintain its homeostatic state (Pickering 1981, Wendelaar Bonga 1997). However, if the stressor is severe or prolonged to the point that the fish is not capable of regaining homeostasis, then the responses themselves may become harmful and threaten fish health (Pickering 1981, Wendelaar Bonga 1997). Physiological responses to stress can be grouped into (1) primary responses, which involve the activation of brain centres and include endocrine changes such as measurable levels of circulating catecholamine and corticosteroid hormones; (2) secondary responses, which are the effects of these hormones at blood and tissue level, including changes in features related to metabolism, hydromineral balance, and cardiovascular, respiratory and immune functions; and (3) tertiary responses, which arise from primary and secondary responses and are whole-animal changes in performance, including growth, disease resistance, behaviour, capacity to tolerate subsequent or additional stressors and predation risk (Pickering 1981, Wendelaar Bonga 1997). Salmon lice can induce all three levels of stress responses in sea trout (Bjørn & Finstad 1998, Dawson 1998, wild: Wells et al. 2006, 2007).

An elevation in plasma cortisol is a primary stress response and is the most widely used stress indicator in fish (Wendelaar Bonga 1997). When a stressor is chronic, levels of this hormone may remain elevated (Wendelaar Bonga 1997). Measuring baseline cortisol is difficult because of the stress that is induced by the capture and handling of the fish (Poole et al. 2000), and minor increases in cortisol due to stress from salmon lice may be masked because the cortisol levels are compared with control groups that may also have elevated cortisol levels due to handling (Bjørn & Finstad 1997). Salmon lice-infested sea trout in the laboratory typically show higher levels of circulating cortisol compared to un-infested control fish in the early days post-exposure, and when the lice are at the attached chalimus developmental stages (Bjørn & Finstad 1997, Wells et al. 2007). Even from the earliest stages of initial copepodid attachment, an acute stress was indicated by elevated cortisol levels (Wells et al. 2006). Hence, both the attached chalimus stages, but particularly the mobile preadult and adult salmon lice, can cause a stress reaction in the fish as shown by increased cortisol levels.

Osmoregulatory disturbance as indicated by increased plasma chloride levels have been observed by the time that the second chalimus stage has developed, with a more severe effect emanating from increasing chalimus densities (Bjørn & Finstad 1997). Hence, late chalimus larvae can cause minor osmoregulatory disturbance in heavily infested sea trout. Serious osmoregulatory problems, as indicated by highly elevated plasma chloride levels and increased plasma osmolality, have been demonstrated when the preadult and adult stages of salmon lice develop and the lice become mobile (Bjørn & Finstad 1997, Dawson 1998, Wells et al. 2006, 2007). The plasma chloride levels increased with increasing densities of preadult and adult lice, confirming that heavily infested fish were most affected (Bjørn & Finstad 1997). Moribund fish suffered from a complete osmoregulatory breakdown (Bjørn & Finstad 1997).

The osmoregulatory disturbance indicated by increased plasma chloride levels may, as described above, be associated with the mechanical damage of fish skin and tissue caused by the grazing of the salmon lice, but also with secondary stress responses on osmoregulation. Disturbance of hydromineral balance is one of the most characteristic features of stress in fish (Wendelaar Bonga 1997). Osmoregulation in saltwater depends on active salt excretion through the chloride cells in the gills. Primary stress responses, such as release of catecholamines and cortisol, may cause structural changes in the gill tissues themselves, and osmoregulatory disturbance may therefore arise as a secondary response from such stress-mediated structural changes (Wendelaar Bonga 1997, Wells et al. 2007).

Acute and chronic stress also are typically associated with increased metabolic rate as a secondary stress response, because response to a stressor is energy demanding. Elevated plasma glucosis (hyperglycaemia), decrease in liver glycogen and elevated plasma lactate all have therefore been used as stress indicators in fish (see references in Wells et al. 2006, 2007). These measures can be further influenced by the metabolic status and feeding history of the host fish. Thus, when preadult and adult stages of salmon lice had developed on infested experimental fish, lice-induced elevation of plasma glucosis and plasma lactate (Wells et al. 2006, 2007), as well as depressed liver glycogen (Wells et al. 2007), all were recorded.

6.3 Growth, behaviour and disease resistance

Primary and secondary stress responses as described above may in the long term lead to tertiary stress responses, which include whole-animal changes in performance such as behaviour, decreased growth rate and increased susceptibility to disease (Pickering 1981, Wendelaar Bonga 1997). Salmon lice-infested sea trout have shown a reduced body mass and condition factor compared to control fish in laboratory studies (Bjørn & Finstad 1997, Dawson 1998). This may be due to harmful stress responses and dehydration of the fish (Bjørn & Finstad 1997). Reduced feeding activity in salmon lice-infested fish has also been recorded, typically once the salmon lice had moulted to the preadult and adult stages (Dawson 1998, Wells et al. 2006, 2007); but in one study (Wells et al. 2006) this was noted within only 10 days of initial exposure and prior to the development of mobile salmon lice.

Behavioural effects of salmon lice other than feeding behaviour of the host fish are not well studied in the laboratory. However, Wells et al. (2006, 2007) and Birkeland & Jakobsen (1997) noted that during the first 2-3 days of the infestation with copepodids, sea trout showed a distinct “flashing” behaviour (lateral turning) or increasing leaping activity in experimental tanks. Flashing behaviour is recognisable as the individual fish showing unusual burst swimming, leaping from the water, or rapidly flicking the body onto its side. This behaviour ceased after seven days, but subsequently was observed again when the salmon lice had reached the mobile stages. Such fish behaviour has also been described previously in response to sea lice (Wootten et al. 1982).

The fish mucus and skin are mechanical barriers that protect fishes from microbial infections, and the damage by feeding salmon lice can compromise this barrier. Bacterial or fungal infections of previously infested fish were recorded when fish were transferred from seawater to freshwater in the laboratory (Wells et al. 2007). Reduced disease resistance as a consequence of salmon lice infestations in sea trout has not been extensively studied. However, both the mechanical damage to the skin and the primary and secondary stress responses described above are indicative of a compromised immune system and thereby an increased risk of secondary infection. Primary and secondary stress responses may result in reduced disease resistance, as shown by a reduced lymphocyte-leukocyte ratio in sea trout infested with salmon lice that had developed only to the early chalimus stage. A reduced lymphocyte-leukocyte ratio is indicative of a reduced immune system, and this was likely induced by the increased cortisol levels (Bjørn & Finstad 1997).

6.4 Effects related to timing of seawater transfer and fish origin

The first laboratory studies on the effects of salmon lice on individual sea trout were undertaken on seawater-acclimated hatchery-reared post-smolts (Bjørn & Finstad et al. 1997, 1998). In addition, a comparison was made between hatchery-reared sea trout infested with salmon lice 2 and 6 weeks after transfer to seawater (Dawson et al. 1998). The physiological effects, reduced feeding and skin damage caused by salmon lice were more severe in fish infested 2 weeks after transfer to seawater than those infested 6 weeks after transfer to seawater, indicating that salmon lice may have a more detrimental impact on sea trout smolts shortly after transfer to seawater than when they have resided for several weeks in seawater.

Irrespective of the effects of salmon lice, physiological acclimation of the host fish to seawater is itself a stressful process, and a simultaneous challenge from salmon lice infestation during the early marine migration may constitute an important additional stressor. Wells et al. (2006, 2007) argued that it was a more realistic laboratory study to infest post-smolts immediately after transfer to seawater because salmon lice exposure in the natural environment can commence once the sea trout enters seawater. Furthermore, hatchery-reared smolts may differ from wild post-smolts in many traits and characteristics (Finstad & Jonsson 2001), and experimental results from salmon lice exposure of hatchery-reared smolts may therefore not be representative of wild smolts. Wells et al. (2006, 2007) therefore used wild post-smolts in their studies. In this context, therefore, it is important to note that the results from studies of salmon lice effects on wild and hatchery-reared smolts, and from those of seawater-adapted or newly transferred post-smolts, were both comparable and similar (Bjørn & Finstad 1997, 1998, Dawson et al. 1998, Wells et al. 2006, 2007).

6.5 Mortality

Salmon lice-induced mortalities both of hatchery-reared (Bjørn & Finstad 1997, 1998) and wild (Wells et al. 2006, 2007) sea trout post-smolts were observed to commence within 10-20 days of exposure, when the salmon lice had reached the mobile preadult and adult life stages. Salmon lice development rates are known to generally increase with increasing water temperatures (Wootten et al. 1982, Johnson & Albright 1991a, Stien et al. 2005). At water temperatures approximating 10°C, most (80%) of the salmon lice on hatchery-reared sea trout had attained the preadult stage after 19 days (Bjørn & Finstad 1998). Time from exposure to attain the adult stage was shorter for male lice (~29 days) than for female lice (~38 days) (Bjørn & Finstad 1998). The salmon lice developmental rate was similar, or slightly faster, on wild sea trout post-smolts at water temperatures of 14°C (Wells et al. 2006, 2007). Less than 40% of the salmon lice survived and developed to the adult stage, which may be due to active rejection of parasites by the sea trout, the sea trout physically removing the lice by rubbing their bodies against the tank and/or natural mortality of the lice (Bjørn & Finstad 1997, 1998).

6.6 Salmon lice threshold values

Bjørn & Finstad (1997) showed that for fish of average mass 91 g the most heavily infested sea trout died as a result of infestation. They concluded that the relative density of parasites found on moribund fish indicated that >1.0 lice g^{-1} fish body mass, or 50 preadult and adult lice $fish^{-1}$, may cause death of small (60 g) sea trout post-smolts. Given an average lice survival of 63%, a lethal relative density of approximately 1.6 chalimus larvae per gram fish mass, or >90 larvae for a small sea trout post-smolt (60 g) was suggested (Bjørn & Finstad 1997, Finstad & Bjørn 2011) as a critical level. Density dependent mortality of salmon lice on a fish may, however, have an effect on the estimates of such threshold values, and the assumption of a simple linear relationship between lice numbers and lice mortality may not be correct.

Wells et al. (2006) concluded that 12-13 preadult and adult (i.e. “mobile”) salmon lice per fish was the critical abundance which elicited sublethal stress responses in post-smolt sea trout (body mass range 19-70 g). Based on that study, and those referred to above, it has been suggested that a simple, conservative and precautionary approach to manage and protect wild sea trout populations would be to adopt a critical level of <10 mobile lice per fish for sea trout during their first year at sea (Finstad & Bjørn 2011, Finstad et al. 2011).

Scientists from the Institute of Marine Research in Norway, the Norwegian Veterinary Institute and Norwegian Institute for Nature Research have in a recent report suggested a classification system for the expected salmon lice-induced mortality of first-time migrant sea trout based on existing knowledge (technical report by Taranger et al. 2012, and also outlined in the scientific publications of Serra Llinares et al. 2014 and Taranger et al. 2014). They predict no extra mortality for sea trout with 0-0.1 lice per gram fish body mass, 20% extra mortality for sea trout carrying 0.1-0.2 lice per gram, 50% extra mortality for sea trout with 0.2-0.3 lice per gram and 100% extra mortality for sea trout with >0.3 lice per gram. Studies on the effects of salmon lice on veteran migrants and maturing sea trout are lacking, but a complementary study of Arctic char (Tveiten et al. 2010) suggested that the effects of salmon lice on maturing fish may be more severe than for first-time migrants. Based on this study, Taranger et al. (2012) assumed for veteran migrant and maturing sea trout no additional mortality risk for sea trout with <0.025 lice per gram body mass, 20% extra mortality for sea trout with 0.025-0.05 lice per gram, 50% extra mortality for sea trout with 0.05-0.10 lice per gram, 75% extra mortality for sea trout with 0.10-0.15 lice per gram and 100% extra mortality for sea trout with >0.15 lice per gram.

It is important to note that threshold levels referred to above (Taranger et al. 2012, 2014, Serra Llinares et al. 2014) are based on effects in relatively short-term laboratory experiments, and that values are indicative and not absolute. As emphasized by Taranger et al. (2012), these values need further verification and validation, especially if the objective is to determine critical parasite burdens to guide conservation and management criteria. Mortality in the natural environment may be higher than that seen in laboratory studies as a consequence 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). Furthermore, compromised fish in the natural environment may experience an elevated mortality risk from predators (Thorstad et al. 2012). A reduced or compromised immune system (Bjørn & Finstad 1997) may therefore incur additional mortality over a longer term, and yet other environmental effects may also exacerbate the effects of salmon lice and the aforementioned critical threshold levels.

Wild sea trout infested with chalimus stages of salmon lice. Photo: Steinar Kålås

6.7 Concluding statements

- Salmon lice feed on the mucus, skin and underlying tissue including blood, causing mechanical damage to the host sea trout. The mobile preadult and adult stages of salmon lice cause more severe tissue erosion than do the attached chalimus stages.
- Laboratory studies of sea trout post-smolts have shown that salmon lice may induce osmoregulatory dysfunction, physiological stress responses, anaemia, reduced feeding and growth, increased susceptibility to secondary microbial infections, reduced disease resistance and increased mortality in individual fish.
- Osmoregulatory dysfunction is likely caused both by the mechanical damage of the skin and tissue *per se* and to the overall physiological stress responses. The mechanical damage impairment of the physical barrier between the fish body and seawater results in increased leakage of water from the fish body, and thereby osmotic and ionic imbalance.
- Sub-lethal physiological stress responses may be triggered by salmon lice developmental stages as early as the chalimus stages, and perhaps especially so when occurring in large numbers. Physiological stress responses become more severe when the salmon lice develop into the mobile preadult and adult life stages.
- Salmon lice-induced fish mortality starts to occur within 10-20 days of exposure to copepodids in the laboratory, by which time the salmon lice have developed into preadult and adult stages.
- Preadult and adult salmon lice are, in general, more pathogenic to sea trout than the earlier (attached) chalimus stages.
- Effects of salmon lice in laboratory studies of sea trout reflect similar effects found in studies of Atlantic salmon post-smolts (as summarized by Finstad & Bjørn 2011, Finstad et al. 2011).

- Laboratory studies of sea trout indicated that >1.0 lice per gram fish body mass may cause death of small sea-trout post-smolts of average 90 g, or 50 preadult and adult lice per fish may cause death of small sea trout post-smolts of 60 g.
- The critical intensity that elicited a sublethal stress response in wild sea trout post-smolts was 12-13 mobile salmon lice per fish (fish body mass 19-70 g).
- Experimental results of lice impacts for fish held in captivity in laboratory studies may be influenced also by stress and tank effects. Conversely, estimates of threshold levels for mortality based on short term laboratory studies may be conservative. The minimum levels for salmon lice-induced mortality in the natural environment may be influenced by additive effects, elevated predation of compromised individuals, and longer-term effects attributable to a reduced immune system and elevated risk of secondary bacterial and fungal infections.

6.8 Knowledge gaps

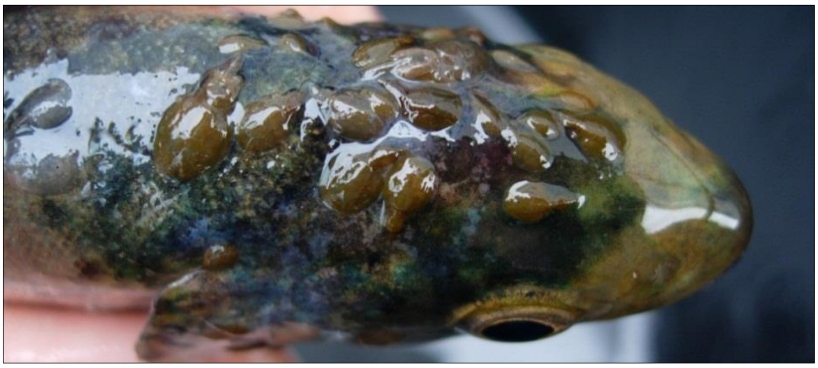
- The data basis for deriving and predicting threshold louse levels for mortality should be strengthened in order to adjust and fine-tune threshold classifications for different fish sizes and life history stages. Also, the effects of the variable salinity and water temperature regimes in the natural environment need to be incorporated. For example, experimental studies typically are undertaken at a salinity of 34 (representing full-strength seawater), whereas the typical habitat for sea trout may be at a markedly lower salinity. There also is a need for more information on salmon lice population dynamics and possible density dependent effects on host fish in order to translate quantifications of chalimus levels into host mortality threshold levels.
- Nearly all threshold studies have been undertaken with hatchery-reared sea trout smolts artificially infestated with a single pulse of salmon lice copepodids. There is a need for stress/mortality threshold studies on wild sea trout post-smolts and adults with natural levels of lice abundances and appropriately structured populations of the lice developmental stages.
- It is not known to what extent the mortality threshold levels derived from laboratory studies are applicable to field data. One way to strengthen the laboratory estimates could be to analyse frequencies of occurrence of preadult and adult salmon lice on wild sea trout captured through monitoring programmes in Ireland, Scotland and Ireland.
- Laboratory studies of effects of salmon lice on individual sea trout are based mainly on post-smolts that represent first-time migrants to the marine environment. There is a lack of knowledge on the effects of salmon lice on veteran (adult) migrants and maturing sea trout.

7 Effects of salmon lice on individual sea trout in field studies

In this chapter, an overview is provided of results from field studies on the effects of salmon lice on individual sea trout. Field studies are important to verify the extent to which laboratory studies are representative of wild fish in natural systems. Field studies also aid understanding of the effects of the parasite at the population level. There are several categories of field studies. Effects have been studied in relation to mechanical damage of fish skin and tissue, osmoregulatory disturbance and physiological stress responses (chapter 6), growth and survival. Premature migratory return of salmon lice-infested sea trout to freshwater also has been monitored and examined. Salmon lice levels of wild sea trout and population effects are considered in later chapters (chapter 8, 9 and 10).

7.1 Mechanical damage of fish skin and tissue

The attached chalimus larval stages may cause severe erosion when present in large numbers and, similar to results from laboratory studies (chapter 6), fin erosion and haemorrhage at the base of the dorsal fin have been frequently recorded in wild-captured sea trout with heavy burdens of chalimus larvae (McVicar et al. 1993, Dawson 1998, MacKenzie et al. 1998). For example, Skaala et al. (2014a) reported that between 80 and 90% of sea trout returning to a Norwegian river had dorsal fin damage attributable to salmon lice. The pattern reported from laboratory studies, with attachment of chalimus larvae to the dorsal fin and mobile stages present along the dorsal or more anterior body regions, are confirmed from numerous field studies in Scotland and Ireland (Tully et al. 1993a,b, Dawson 1998, MacKenzie et al. 1998, Marshall 2003, Urquhart et al. 2008). Cranial lesions and grazing marks on the gill opercula, and along the ventral body surfaces, also have been described (McVicar et al. 1993, Tully et al. 1993b). Tully et al. (1993b) observed blood seepage in body areas impacted by salmon lice when fish were removed from the water.



Wild sea trout with preadult and adult salmon lice collected in western Norway. Photo: Steinar Kålås

7.2 Osmoregulatory problems and physiological stress responses

Primary and secondary physiological stress responses have been documented in wild sea trout post-smolts captured in the marine environment, as exemplified by elevated plasma cortisol, plasma chloride and blood glucose levels (Poole et al. 2000, Bjørn et al. 2001). The elevated cortisol levels were similar to those found in laboratory studies (chapter 6), and stress responses have been noted as being more severe with increasing salmon lice levels (Bjørn et al. 2001, Poole et al. 2000). Because chalimus larvae were the dominating life stage, and only limited skin erosion was observed, Bjørn et al. (2001) concluded that the tendency for minor osmotic imbalance and a consequential need for mobilisation of energy stores may have been the result of the integrated stress response attributable to the infestation rather than a result of the mechanical damage caused by tissue grazing of the salmon lice. Fish body sizes in these studies were <150 g body mass (Bjørn et al. 2001), or an average body length of 18 cm (Poole et al. 2000).

Blood plasma of sea trout captured in the marine environment (mean fork length 23 cm, body mass 126 g), and carrying of mobile salmon lice, showed a reduction in total protein, serum albumin and cholesterol compared with sea trout lacking salmon lice or those with copepodids or chalimus stages only (Dawson 1998). Furthermore, plasma glucosis levels increased with lice numbers when all stages salmon lice were pooled (Dawson 1998). No other physiological effects by the salmon lice were detected (Dawson 1998).

In a controlled field experiment in Norway, downstream-migrating sea trout were captured in freshwater and held in tanks; one group of fish was exposed to seawater (and thereby the natural concentration of lice larvae), whereas an unexposed control group was held in filtered seawater from which salmon lice larvae had been removed (Birkeland & Jakobsen 1997). Salmon lice-induced mortality commenced 11 days after exposure to un-filtered seawater, by which time some lice had developed to the preadult stage (water temperature, 17-20°C; mean abundance and intensity of salmon lice per fish, 59). Fish in the exposed group showed severe osmotic problems by this stage, with elevated plasma chloride levels and lower plasma total protein and albumin levels.

The highest estimated cortisol levels in wild-captured sea trout occurred in the period when post-smolts had recently entered the sea, as recorded by Poole et al. (2000). They suggested that post-smolts may be more vulnerable to salmon lice during the early marine phase, when they are physiologically actively adapting to seawater, rather than later in the season.

7.3 Growth

Growth patterns of sea trout in freshwater and saltwater are generally complex, and selective salmon lice-induced mortality may mask other potential and observable effects on sea trout growth. Moreover, it is also especially difficult in field studies to isolate the effects of salmon lice from other possible anthropogenic effects in correlative time series studies because multiple factors may have changed either independently or in concert over the observational period.

Notwithstanding the above-mentioned caveat, Fjørtoft et al. (2014) undertook comparative scale analyses of growth of sea trout from a river in south-western Norway during 1976-82, in the absence of local salmon farming, and in 2000-2007 when farming was intensive in the area. They showed the fish to grow more slowly during both their first and second summers at sea over the latter observational period, but there was no difference in growth rate of the same individuals whilst resident in freshwater. The growth reduction after the first summer in the sea corresponded to a body mass reduction of 20-40%. These authors concluded that although changes in food availability may have played a part in the reduced growth during the marine feeding period, the negative growth trend for sea trout was most likely related to the high salmon lice levels observed in the fjord system.

A gradual decrease in marine growth rates was also detected from scale analyses of sea trout from a Scottish river adjacent to salmon farms (data from 1980 to 1989-1990, 1992-1993 and 1997-2001; Butler & Walker 2006). Thus, from 1980 to the period 1997-2001, maximum sea age was found to have been reduced from 11 to 5 years. When comparing scale samples from 1926 and 1980, the sea age and marine growth rates did not differ greatly. Butler & Walker (2006) concluded that the decline in growth after 1980 was at least partly caused by salmon lice epizootics emanating from the fish farms established 4 and 7 km from the river mouth in 1987.

7.4 Behaviour and migration patterns

There are few studies of the effects of salmon lice on sea trout behaviour and their migration patterns, although observations of premature freshwater return are an exception.

7.4.1 Premature migratory return to freshwater

Sea trout smolts and adults often migrate to sea in the spring or early summer and return to freshwater during the autumn in order to over-winter and/or undergo spawning. There may, however, be considerable variation in life history patterns and the timing of migrations both within and among populations (**box 2** and chapter 2). Premature migratory return to freshwater of sea trout carrying large numbers of salmon lice has repeatedly been recorded for sea trout that clearly had spent only a few days or weeks at sea. This has been consistently interpreted as an adaptive behavioural response of the fish to salmon lice-induced osmoregulatory dysfunction (Birkeland 1996, Birkeland & Jakobsen 1997, Bjørn et al. 2001, Wells et al. 2007). The migratory return to freshwater may enable the infested sea trout to regain its osmotic balance and survive. The return to brackish or freshwater may also allow “de-lousing” because salmon lice have a low tolerance to hyposaline or freshwater conditions (Birkeland 1996).

The first reports of post-smolt sea trout returning to freshwater prematurely in poor physical condition and with heavy salmon lice infestations, within only a few weeks of their seaward migration, date from the late 1980s and early 1990s in Ireland (Whelan 1991, Tully et al. 1993a,b, Tully & Whelan 1993). Subsequent studies from Ireland, Norway and Scotland have reported similar observations of this phenomenon (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). In terms of timing, it was apparent from relatively early studies of this phenomenon that premature migratory return to freshwater may occur as soon as within the first few days, or within the first 1-2 weeks, of freshwater emigration (Birkeland & Jakobsen 1997, Bjørn et al. 2001).

It is important to note that these behavioural and physiological impacts on the host fish extend beyond those induced by the chalimus and mobile stages of salmon lice: high levels of copepodids alone also can cause premature freshwater return of sea trout (Birkeland & Jakobsen 1997). Birkeland (1996) concluded that the high salmon lice levels recorded in her study indicated that the post-smolts that returned to freshwater would not have survived had they not returned to freshwater. But premature migratory return does carry a cost in reduced growth opportunities for the individual fish (Birkeland 1996), which can be manifest as reduced resources available for egg production, and thereby reducing fecundity and reproductive success of females.

The timing of freshwater return of sea trout was monitored by operating a fish trap in the lower part of a Norwegian river (Birkeland 1996, Birkeland & Jakobsen 1997). Nearly half (41%) of prematurely returning post-smolts migrated to sea again that same summer season, with a median freshwater residency of 38 days following river return (Birkeland 1996). Those subsequently returning to sea were among the smallest post-smolts recorded ascending the river. By the time of second descent, most fish had lost all their salmon lice, but they also had lost one quarter of their body mass during their brief freshwater residence. Birkeland (1996) estimated that those post-smolts returning to sea had lost 30% of their potential sea growth for that year, whilst post-smolts that remained in freshwater throughout that summer had inevitably lost the remainder of their sea growth potential for that season. A few individual post-smolts were found dead in the river. Older sea trout were noted to return to freshwater later in the season than did comparable post-smolts, and it is questionable whether this could be characterised as a true premature migratory return (Birkeland 1996). However, older sea trout suffered considerable mortality in freshwater. Thus, within one week following river ascent, 20% of the older migrants were found dead in the river, and they had considerable skin lesions from salmon lice infestations that had become secondarily infected by fungi or bacteria in the river. Whereas the post-smolts mainly carried copepodid and chalimus stages of salmon lice, the older migrant fish carried a larger proportion of preadult and adult louse stages.

The physiological consequences of premature freshwater return by sea trout were studied by Wells et al. (2007) in a laboratory study. Salmon lice intensity was reduced following transfer from seawater to freshwater 19 days after initial exposure, and a wide range of physiological measures returned to levels similar to the un-infested control group following transfer of infested fish to freshwater. Wells et al. (2007) concluded that premature migratory return of infested sea trout post-smolts to freshwater conferred significant short-term physiological benefits across a range of osmoregulatory, metabolic and stress markers. For infested fish subsequently transferred to freshwater – and thereby experimentally mimicking premature migratory return − mortality was reduced compared to fish maintained infested in seawater. However, secondary bacterial or fungal infection was recorded on a number of the infested fish following their transfer to freshwater.

Collection of sea trout by electrofishing for salmon lice monitoring in a river mouth in western Norway. Photo: Bernt Olav Økland

7.5 Mortality

The direct observation of mortality is difficult to achieve for free-ranging individual fish in marine waters. Thus, whilst Tully et al. (1993a,b), Tully & Whelan (1993) and Birkeland (1996) all have reported direct observations of dead and moribund sea trout in estuaries linked to salmon lice infestations, it has to be acknowledged that fish in the marine environment may die from multiple causes, such as predation, before they may be lost as a direct result of a pathological disease or parasite infestation (Thorstad et al. 2013).

Advances in fish telemetry methods have opened the possibility of comprehensively following the movements, behaviour and survival of individual fish tagged with acoustic transmitters and released to the natural environment. Initial studies have shown that sea louse-infested hatchery-reared sea trout and Atlantic salmon smolts did not show increased mortality during fjord migration compared with control (unifected) groups (Sivertsgård et al. 2007). However, that detailed study extended only over a short time period in the fjord, and during which the salmon lice could develop only to the chalimus stage of the life cycle. Temporally more extensive telemetry data are necessary to evaluate the effects of all life cycle stages of salmon lice on post-smolt and adult sea trout. Moreover, there are logistic and practical limitations in terms of equipment and manpower resources that would need to be deployed in seeking to increase the detail, frequency and geographic extent of telemetry detections of individual fish.

7.6 Salmon lice and the spread of disease agents

The relatively newly discovered microsporidian *Desmozoon lepeophtherii* (= *Paranucleospora theridion*, Freeman & Sommerville 2011) is a parasite that includes both Atlantic salmon and salmon lice as hosts during its life cycle. The first developmental cycle takes place in Atlantic salmon in endothelial cells of blood vessels and in leukocytes, and it is expected that the parasite can reduce the immune defence of the host, increasing its susceptibility or permitting the proliferation of pathogens already present in the fish (Nylund et al. 2011). *D. lepeophtherii* has been linked to gill disease causing mortality in farmed Atlantic salmon both in Norway and Scotland (proliferative gill inflammation, PGI; Matthews et al. 2011, Nylund et al. 2011). Atlantic salmon probably are infected by *D. lepeophtherii* through waterborne spores that initiate infections in the gills (Sveen et al. 2012). Salmon lice became infected during autumn, possibly when they fed on infected fish, and developed extensive infections during winter. Lice mortality in winter and spring is likely responsible for a reservoir of spores in the water (Sveen et al. 2012).

The parasite has also been shown to be present in brown trout (Nylund et al. 2011). It is not known to what extent *D. lepeophtherii* may affect survival and reproduction in wild Atlantic salmon and sea trout, but negative effects cannot be excluded.

7.7 Concluding statements

- There is agreement between laboratory and field studies regarding the patterns of mechanical damage induced by salmon lice, their physiological impacts, and the fact that salmon lice may cause mortality and reduced growth of individual fish.
- Field studies of sea trout post-smolts have shown that salmon lice may induce osmoregulatory dysfunction, physiological stress responses, anaemia, reduced growth, increased susceptibility to secondary microbial infections and increased mortality.
- Salmon lice may cause severe fin and skin/gill tissue erosion, especially of the dorsal fin by chalimus larvae, and across the more anterior body regions preferred by the mobile life cycle stages. Head erosions and grazing marks on the opercula and ventral body surfaces may also occur.
- Chalimus larval stages alone may cause severe erosion when present in large numbers.
- Primary and secondary physiological stress responses have been documented in wild sea trout post-smolts captured in the marine environment, and these data concur with those obtained from controlled and replicated laboratory studies.

- Field studies confirm that osmotic imbalance may be detectable at moderate levels of salmon lice, and certainly by the time lice have developed to the chalimus stages.
- Host fish stress responses increase with increasing salmon lice levels.
- Mobile preadult lice can cause severe osmotic problems for the host fish and mortality may commence within 11 days of exposure at water temperatures of 17-20°C.
- Premature migratory return of salmon lice-infested sea trout to freshwater has been documented in Ireland, Scotland and Norway. Premature return is interpreted as an adaptive response by the host to salmon lice-induced osmoregulatory dysfunction in seawater. 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 hyposaline conditions and survive only for short periods in freshwater. In the long term, however, growth opportunities and future fecundity of individuals may be greatly reduced by an abbreviated sea migration caused by salmon lice infestation.
- Secondary bacterial or fungus infections in wounds caused by salmon lice may occur and may themselves induce mortality of sea trout after their return to freshwater and consequential loss of their salmon lice.
- Mortality of individual fish is difficult to record and quantify in the marine environment, because dead fish are rarely found. Weakened fish in the marine environment also may die from predation before they die as a result of the direct physiological impacts of salmon lice.

Wild sea trout with dorsal fin damaged from salmon lice. Photo: Bengt Finstad

7.8 Knowledge gaps

- Field studies have been undertaken primarily for juvenile post-smolts, whereas there are few studies of the effects of salmon lice on veteran migrants and maturing adult sea trout.
- Telemetry methods have opened possibilities of studying individual behaviour and mortality of fish in near coastal areas. This enables studies of, for example, the effects of salmon lice on the behaviour, survivorship and predation risks of individual sea trout.
- The phenomenon of premature migratory return to freshwater is poorly studied, and information is needed on survival and growth of these fish, and whether there is geographic or among-population variation in the extent to which sea trout exhibit such behaviour.
- More comprehensive studies on growth effects of salmon lice for individual fish through measurement of otolith growth rings and scale reading and measurement of circulus spacings are warranted.
- The use of individual-based models, in conjunction with field data, can potentially be exploited to elucidate the complex non-linear relationships that are common occurrences in environmental research; for example, the relationships between direct-

ly attributable effects of salmon lice on host growth and selective mortality may exert complex, non-linear interactions with behaviour, maturation schedule, and ultimately fecundity.

Wild sea trout with damage from salmon lice on head and dorsal fin. Photos: Steinar Kålås

8 Salmon lice levels in samples of wild sea trout

In this chapter, we summarise salmon lice levels recorded for samples of wild sea trout, both in farm-free and intensively farmed areas. Published studies of salmon lice levels on wild sea trout in different areas, and over various time periods, are summarised in **Table 1**.

8.1 Salmon lice levels in areas before, or without, salmon farming

Ideally, in order to evaluate whether or not salmon lice levels have become elevated in wild populations, and their possible association with salmon farming, baseline information on lice levels and their year-round population dynamics would be required for time periods preceding the development of fish farming, or from areas lacking fish farming. Historical salmon lice levels on sea trout prior to the industry (Boxshall 1974), and data for areas lacking fish farming (Tingley et al. 1997, Schram et al. 1998, Heuch et al. 2002, Rikardsen 2004, Urquhart et al. 2010), generally show a relatively high prevalence, but low intensity of salmon lice. The “natural background” intensity of salmon lice on sea trout may be as low as 0-3 lice per fish, and with a prevalence of 0-20% during late winter and spring (Schram et al. 1998, Heuch et al. 2002, Rikardsen, 2004). Available data indicate intensities increasing to a peak of up to 4-8 lice per fish and higher prevalences in the late summer and autumn (Tingley et al. 1997, Schram et al. 1998, Rikardsen 2004, Urquhart et al. 2010). In areas lacking fish farms, prevalence may range up to 100%, but often is lower than 80% (**Table 1**). The peak in salmon lice levels on sea trout may occur 1-2 months later in the year at more northerly locations compared to more southern latitudes, perhaps reflecting seasonal contrasts in temperature and hence developmental rates for salmon lice. At more northern latitudes in Norway, the peak salmon lice level in sea trout often is noted during the period August-October (Bjørn & Finstad 2002, Rikardsen 2004), whereas at more southerly latitudes this may advance to June-August (Mo & Heuch 1998, Schram et al. 1998, Heuch et al. 2005).

Atlantic salmon, sea trout and Arctic char all are natural hosts of salmon lice, and due to the seasonality of their migration behaviour there are few of these wild hosts in coastal waters during the winter months. Atlantic salmon feed in offshore waters (e.g. Baltic Sea), or the open North Atlantic Ocean and typically traverse coastal areas relatively quickly during the outward migration of juvenile smolts in the spring or early summer (Thorstad et al. 2011). The rate of transit of returning adult salmon through coastal waters during the spawning migration also is typically relatively rapid. These return migrations usually occur during May-September in Norway, but with considerably more variation in timing in Scotland and other more southerly regions of salmon distribution (Thorstad et al. 2011). In contrast to Atlantic salmon, sea trout and Arctic char often spend weeks or months during the summer in coastal areas and the remainder of the year in freshwater, although a proportion of trout and char populations may stay at sea throughout the year (**box 2**, chapter 2). Because salmon lice cannot survive long in freshwater (McLean et al. 1990, Finstad et al. 1995), the persistence of the parasite population depends upon hosts at sea over the winter months. For wild host populations these winter components therefore include Atlantic salmon distant from near-shore waters and feeding in the open ocean, and on the small proportions of sea trout and Arctic char that remain in coastal areas. In areas lacking salmon farms, the salmon lice populations therefore have few available hosts and appear to encounter a host resource bottleneck in winter (Schram et al. 1998, Heuch et al. 2002, Rikardsen 2004). For example, prevalence of salmon lice was shown to decline between December and March-April on the Skagerrak coast in southern Norway (Schram et al. 1998, Heuch et al. 2002). In northern Norway also, prevalence and abundance of salmon lice have been shown to be low in winter (prevalence 13-20%, and abundance 0.1-0.4 in November-April), and adult life cycle stages dominated. Lice levels increased during the summer months from May to September to a peak prevalence of 80-81% and peak abundance of 3.6-6.8. These latter lice populations showed an increasing number of chalimus larvae, indicating recent exposure, which attained a maximum in September-October (Rikardsen 2004). Another example of the importance of seasonality for understanding salmon lice dynamics in areas lacking fish farming, derives from the English North Sea coasts of East Anglia and Yorkshire England and in the North Sea off the coast of. Salmon lice levels on sea trout were low and relatively stable over the years sampled (1972-1973 and 1992-1993, Tingley et al. 1997; data from 1972 also published by Boxshall 1974), but seasonality had a clear effect on salmon lice abundances, with differences in excess of an order of magnitude noted over the year. Prevalence was 67-81% in 1972-1973 and 81-89% in 1992-1993, and mean abundance was 1.17-3.19 in 1972-1973 and 4.42-4.66 in 1992-1993 (Tingley et al. 1997).

The highest level of salmon lice on sea trout reported for an area lacking fish farming was a mean abundance of 10.9 salmon lice per fish, and mean intensity of 11.6 salmon lice per fish (Oslofjord, southern Norway; Mo & Heuch 1998). However, most of the samples in that study showed abundances and intensities in the range of 0.5-8 salmon lice per fish. Overall prevalence was 51%. It is important to note, however, that four heavily-infested individuals (of a total sample of 102 fish) carried as many as 33-84 lice each (of which 43-72% of the lice were adults). This pattern of over-dispersion of occurrence of salmon lice shows that even in areas without fish farming a few individual sea trout may carry salmon lice levels that, according to laboratory studies (chapter 6), will induce stress on the host fish.

To the best of our knowledge there are no published records of outbreaks of salmon lice epizootics on sea trout populations that pre-date the commencement of sea pen salmon farming, or for areas that have lacked fish farms. Never the less, it is important to emphasize that salmon lice epizootics were reported in Atlantic salmon and brook trout (*Salvelinus fontinalis*) over the period 1939-1940 at Moser River in Nova Scotia on the Canadian east coast (White 1940, 1942). The infrequency of known and reported epizootics in areas without salmon farming may indicate that this is not a common phenomenon for salmon lice on wild sea trout and other salmonid populations (although there may be a publication bias).

__Table 1__. Overview of studies of salmon lice levels on wild sea trout published in peer reviewed international journals and book chapters. Abundance is the mean number of salmon lice per fish caught in a sample. Intensity is the mean or median number of salmon lice per infested fish in the sample. Prevalence is the percentage of salmon lice infested fish in the sample. In the abundance column, maximum number (max) of salmon lice on any individual sea trout is given if the information is available in the source. Information on salmon lice life cycle stage, time period when the study was undertaken, capture methods used to collect sea trout, fish size, study site and extent of fish farming in the area also is summarised.

Abundance (mean)	**Intensity**	**Prevalence**	**Lice life cycle stage**	**Study period**	**Capture method**	**Fish size**	**Study site**	**Extent of salmon farming in area**	**Reference**
3.2	Mean 4.0	81%	Not specified	1972-1973, month not specified	Research fishing vessels	Mean 520 mm.	North Sea off Yorkshire	No farms	Boxshall (1974)
1.0-77.5 (max 325)	Mean 7.0-104.8	14.3-100%	Dominated by chalimus stages	May 1992	Gill netting	Mean 164-273 mm	Rivers Clifden, Costello, Gowla, Owengarve, Burrishoole, Newport, Inny River, Owenduff, Ballynahinch, Killary, Currane, Dowras, Drumcliffe, Argideen on the west coast of Ireland	Fish farming area, but variation among embayments covered in the study	Tully et al. (1993a)
5.0-8.0 (max 46)	Mean 5.0-10.7	75-100%	20-26% chalimus	June-August 1991 and 1992	Rod and line	Not given	River Eachaig and Argyll rivers, west coast, Scotland	Information not given	Sharp et al. (1994)
7.0-63.9 (max 216)	Mean 7.0-63.9	75-100%	0-79% chalimus, increasing proportion chalimus with increasing lice abundance	June-August 1991 and 1992	Rod and line	Not given	Rivers Morar, Ewe and Burn, north west coast, Scotland	Information not given	Sharp et al. (1994)
1.4-5.0 (max 11)	Mean 1.4-5.0	25-100%	6-55% chalimus	June-August 1991 and 1992	Rod and line	Not given	Rivers Don, Ythan and Hope, north and north east coast, Scotland	Information not given	Sharp et al. (1994)
89.8-260.8 (max 1002)	103.0-272.4	87-96%	Mainly chalimus	June-July 1992	Fish trap in lower part of river capturing prematurely returned trout	Post-smolts mean total length 174 mm, mean mass 42.3 g, older migrants mean total length 374 mm, mean mass 581 g	Lønningdalselven, Hordaland, Norway	Intensive farming	Birkeland (1996)
53.5-623.0 (max 1179)	53.5-623.0	88-100%	Mainly copepodids and chalimus.	June 1992	Fish trap in lower part of river capturing prematurely returned trout	Mean total length 160 mm, mean mass 30 g	Lønningdalselven, Hordaland, Norway	Intensive farming	Birkeland & Jakobsen (1997)
4.66 and 4.42 (max 41 and 55)	Mean 5.26 (range 1-41) and 5.47 (range 1-55)	96% both years	Mainly preadults and adults	June-November 1992 and 1993	Gill net and market	Mean 29-32 cm fork (range 25-64)	East Anglia	No farms	Tingley et al. (1997)

Abundance (mean)	Intensity	Prevalence	Lice life cycle stage	Study period	Capture method	Fish size	Study site	Extent of salmon farming in area	Reference
3.19 and 1.17 (max 12 and 4)	Mean 3.96 (range 1-12) and 1.75 (range 1-4)	67 and-81%	Not specified	1972-1973, month not specified	Not given	Not given	North Sea off Yorkshire	No farms	Tingley et al. (1997). Data from 1972 were also published by Boxshall (1974)
42 (SE 35)	Not given in publication and not calculated here because prevalence is not given separately per district, but for Ballinakill and Connemara Districts combined.	82%	Mainly chalimus	May 1996	Gill netting	Mean fork length 228 mm, 126 g	Rivers Bunowen, Bundorragha, Erriff, Culfin, Dawros and Owenglin in Ballinakill District, Ireland.	Information not given	Dawson (1998)
71 (SE 45)	Not given in publication and not calculated here because prevalence is not given separately per district, but for Ballinakill and Connemara Districts combined.	82%	Mainly chalimus, but also preadults and adults	May 1996	Gill netting	Mean fork length 206 mm, 82 g	Rivers Gowla, Invermore, Furnace and Cashla in Connemara District, Ireland.	Information not given	Dawson (1998)
0.5-10.9 (max 84)	Mean 2.7-26.7	20-85%	Proportion between larvae and mobile stages varied among samples. Proportion of mobile stages always >30%	August-October 1992. May-September 1993.	Electrofishing in river mouth and gill nets	Mean length 245 mm in river and 426 mm in the fjord.	Akerselva and Oslofjord, southern Norway.	No farms	Mo & Heuch (1998)
0-72.7 (max 207)	Mean 0-46.4	0-100%	Mainly copepodids and chalimus, but increasing proportion of mobile stages from late May and onwards for many locations	April-September 1994	Seine netting, rod and line, gill netting	101-559 mm fork length	17 location on west coast, two on east coast and one on north coast of Scotland	Both from areas with and without intensive fish farming	MacKenzie et al. (1998)
Not given	Median <3-8	20-100%	March-April mainly preadults and adults. Dominated by adults also the rest of the summer, but with chalimus larvae appearing in April-October (never more than 15% chalimus)	March-December 1992-1995.	Beach seine	Mean 320 mm, 440 g.	Skagerrak coast, southern Norway	No farms	Schram et al. (1998)
20.1 (max 253)	Mean 27.9	72%	Information not given	May-June 1995	Gill nets, electrofishing and wolf trap	Not given	North Mayo, South Mayo, Galway and Kerry, all together ten locations, Ireland	Information not given	Byrne et al. (1999)
0-111	Mean 0-156	0-100%	Information not given.	May-June 1993-1997	Mainly gill nets. Some fish captured also by traps, draft nets and electrofishing.	Only fish <260 mm fork length were included in analysis	42 estuaries in Ireland	Both areas with and without intensive fish farming	Tully et al. (1999)
49.3-194.9 (max 471)	Mean 53-203	89-96%	Chalimus larvae dominated during the entire period	June-September 1997	Gill nets	Mean 119-209 g	Vesterålen, northern Norway	Intensive farming	Bjørn et al. (2001)*

Abundance (mean)	Intensity	Prevalence	Lice life cycle stage	Study period	Capture method	Fish size	Study site	Extent of salmon farming in area	Reference
0.6-8.9 (max 36)	Mean 1-13	55-89%	Chalimus larvae dominated in June, but up to 50% preadults and adults later in summer	June-September 1997	Gill nets	Mean 119-464 g	Ofoten, northern Norway	Low farming intensity	Bjørn et al. (2001)*
0.1-23.6 (max134)	Mean 0-29.5	0-95%	Mainly chalimus larvae	June-August 1992-1993	Gill nets	Not given (gill net mesh sizes 19-35 mm)	Altafjorden, northern Norway	Intensive farming	Bjørn & Finstad (2002)*
0.2-13.0 (max 84)	Mean 0-17.3	0-83%	Mainly chalimus larvae in July and increasing amount of preadults and adults in August	June-August 1992-1993	Gill nets	Not given (gill net mesh sizes 19-35 mm)	Lille Porsanger, northern Norway	Low farming intensity	Bjørn & Finstad (2002)*
0.75 and 0.33 (max 11)	Median 1-2	0-49%	Majority preadults and adults	October 1998-April 1999, October 1999-March 2000	Gill nets	Mean 328 g (SD 63)	Gill nets	No farms	Heuch et al. (2002)
0-68.4 (max 500)	0-46.4	0-100%	Mainly chalimus, but increased proportions of mobile stages in July-September	March-October 1998-2001	Sweepnet	Not given	Laxford Bay, Sutherland, Scotland	During fallow and production periods at nearby farm	Marshall (2003)
0-6.8 (max 33)	Mean 0-8.6	0-81%	Preadults and adults dominated in winter, chalimus in September-October	March-December 2001	Gill nets	Mean 668 g (SD 432)	Ranafjord, northern Norway	No farms	Rikardsen (2004)
0.1-3.6 (max 28)	Mean 1.0-4.7	6-80%	Preadults and adults dominated in winter, chalimus in September-October	March-December 2001	Gill nets	Mean 340 g (SD 314)	Balsfjord, northern Norway	No farms	Rikardsen (2004)
1.3 (June) - 21.2 (August) (max 59)	Mean 6.4 (June) - 26.5 (August)	21 (June) - 88% (August)	Chalimus dominated in June-July, and preadults and adults started to occur in August	June-August 2000	Gill nets	Mean 240 g	Løksefjord and Malangsbotn, northern Norway	Low farming intensity	Bjørn et al. (2007)*
0 (June) - 16.7 (August) (max 78)	Mean 0 (June) - 18.9 (August)	0 (June) - 80% August	Chalimus dominated in June - July, and preadults and adults started to occur in August	June-August 2000	Gill nets	Mean 170 g	Altafjord	Intensive farming	Bjørn et al. (2007)*
7.8 (95% CI 6.0-10.0)	Mean 7.8	100%	Preadults and adults	May and June 2005	Bag nets	Mean 1.16 kg (SD 0.32)	North Esk, east coast of Scotland	No farms?	Urquhart et al. (2008)
30 (max 69)	Mean 30	100%	Only copepodid and chalimus stage	May 2007	Electrofishing during return to freshwater	Mean 155 mm, 35 g	River Shieldaig, Scotland	Information not given	Pert et al. (2009)
0.82-7.87	Mean 0.24-7.87	29-100%	Information not given	July-December 2006-2007	Gill nets,	Mean 440-480 mm, 1.06-1.21 kg	Rivers Annan and Carron, west coast, Scotland	Close to salmon farms	Urquhart et al. (2010)
0.03-0.37	Mean 0.00-0.09	3-23%	Information not given	May-August 2005, 2006 and 2007	Bag nets, sweepnetting, gill nets	Mean 221-308 mm, 0.16-0.31 kg	Upper Forth Estuary, North Esk and Stonehaven Bay, east coast, Scotland	No farming	Urquhart et al. (2010)
0.2-20.5 (max 186)	Mean 3.5-30.2	4-77%	All stages in May, mainly chalimus in June, and increased proportion of adults again after that	May-August 2003-2004	Gill nets	Mean 97-383 g, 210-270 mm	Eresfjord in romsdalsfjord, Norway	Protection zone with low farm activity	Bjørn et al. (2011)

Abundance (mean)	Intensity	Prevalence	Lice life cycle stage	Study period	Capture method	Fish size	Study site	Extent of salmon farming in area	Reference
3.3-52.8 (max 130)	Mean 4.6-52.8	73-100%	All stages in May, mainly chalimus in June and July, and subsequently increased proportion of adults	May-August 2003-2004	Gill nets	Mean 364-490 g, 310-320 mm	Karlsøyfjord in Romsdalsfjord, Norway	Intensive farming	Bjørn et al. (2011)
0-8.1 (max 44)	Mean 0-12.0	0-83%	Information not given	May-August 2008-2012	Gill nets	Mean 131-457 g	Five large fjord areas in Norway with restrictions on fish farming (National Salmon Fjords)	>30 km to nearest farm	Serra Llinares et al. (2014)
0-106 (max 689)	Mean 1.8-114.8	0-100%	Information not given	May-August 2008-2012	Gill nets	Mean 85-823 g	Five smaller fjord areas in Norway with some restrictions on fish farming activity (National Salmon Fjords)	<30 km to nearest farm	Serra Llinares et al. (2014)
2-254 (max 759)	Mean 6-254	13-100%	All stages. Dominance of chalimus stages during epizootic outbreak in March 2014	March – June 2013-2014	Bag nets	Mean 31-35 cm, 263-405 g	Sognefjorden, Norway	Intensive farming	Vollset & Barlaup (2014)

*Lice levels are given for brown trout and Arctic char combined in this publication, because lice levels did not differ among the two species.

8.2 Salmon lice levels in areas with salmon farming

Salmon lice levels reported for sea trout vary considerably among studies in farm intensive areas (**Table 1**). This is to be expected because studies vary considerably in time of the year of the survey, fish sizes collected, sampling methods and sample sizes. There is a risk of skewness in such data, and the collected fish may not represent the salmon lice level in the entire local sea trout population. For example, only fish that survived infestation will be caught, whereas fish behaviour and catchability will to an extent depend upon infestation rate. Furthermore, fishing gear is size selective, may sample only a restricted habitat or depth, and also may affect the number of lice retained on the fish captured. Thus, fish captured in gill nets and seine nets may be subject to physical abrasion during capture and removal from the net, thereby resulting in the loss of some salmon lice, or, in the case of the retention of free-swimming fish in bag nets, lice may move between individual sea trout (chapter 5). Furthermore, the place and time of sampling may not be representative of the local sea trout population of the physical location. This latter problem is especially acute in relation to several studies based on sampling sea trout in river mouths and freshwater outfalls. For such specific and restricted locations the salmon lice level may be overestimated if only the most heavily infested trout that are actively returning prematurely to freshwater are caught. Conversely, salmon lice levels on fish captured in estuaries and river mouths may be underestimated because sampling might be biased towards fish that have only recently migrated down river and have not been at sea for sufficient time for salmon lice to attach. Underestimation of salmon lice intensities and abundances also is likely if sea trout have been resident in hyposaline waters at river estuaries for a sufficient period for the lice to become detached from the host fish. All of these caveats apply equally to samples from areas with or without fish farming. None the less, it is notable that salmon lice levels in areas lacking fish farming typically are considerably less variable than areas impacted by fish farming (**Table 1**). With specific reference to farm-impacted areas there also is likely to be considerable variation among studies with regard to fish number and biomass production in nearby farms, and the associated variation in salmon lice levels. Factors affecting salmon lice levels in sea trout are further discussed in chapter 9.

Many Irish, Scottish and Norwegian studies conducted in farming areas show that chalimus larvae dominate in early in summer and spring, and that the preadult and adult stages of salmon lice have been recorded on sea trout primarily in late summer and autumn (Tully et al. 1993a, MacKenzie et al. 1998, Bjørn et al. 2001, 2007, 2011, Bjørn & Finstad 2002). However, in areas with a locally high salmon lice level, chalimus stages dominate throughout, and sea trout rarely carry adult lice (Tully et al. 1993a, Sharp et al. 1994, Birkeland & Jakobsen 1997, Gargan 2000, Bjørn et al. 2001, Butler 2002, Gargan et al. 2003). The predominance of chalimus larvae in areas with high salmon lice levels may be explicable by heavily infested fish dying at sea or returning prematurely to freshwater (and not being sampled) before lice had attained the adult stage (Tully et al. 1993a, Birkeland & Jakobsen 1997, Bjørn et al. 2001).

If the proportion of fish carrying potentially lethal levels of a parasite is known, the consequences of the parasite for the host population may be estimated. Bjørn et al. (2001) found that 32% of the sea trout post-smolts captured at sea at their study site in northern Norway exhibited relative densities of salmon lice above the level that caused mortality in experimentally infested sea trout in the laboratory. The corresponding estimate from sea trout that returned prematurely to freshwater was 47% (Bjørn et al. 2001). Even though it is not known to what degree threshold levels based on laboratory results are directly applicable to field data, Bjørn et al. (2001) could conclude that excessive mortality of the most heavily-infested post-smolts most likely occurred in that study area. This conclusion was based on a substantial decrease in August of the infestation intensity to a level below that which is lethal level, a major concomitant reduction in the relative density and variance-to-mean ratio in August compared to July samples, and the absence of adult stages of salmon lice late in the season.

Several other studies report increased salmon lice levels in areas with salmon farming. In a large-scale Irish study, including 4600 sea trout sampled at 15-52 sites during 1992-2001, 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). The critical level applied in that study was ≥55 lice per fish and was based upon the level that was found to induce physiological dysfunction and osmoregulatory disturbances in the laboratory (Bjørn & Finstad 1997). In Norway, from a large-scale study in areas <30 km from the nearest farms (43 sites in five fjord areas in 2008-2012), salmon lice levels were found to vary among years. No increased mortality risk was recorded during at least one of the sampling occasions, but the maximum increase in mortality risk did affect between 12 and 90% of the sampled fish at one or more sampling occasion in all five fjord areas (Serra-Llinares et al. 2014). Those mortality risks were based on the threshold levels reported by Taranger et al. (2012), and which are outlined here in chapter 6 as well as by Serra-Llinares et al. (2014). Taranger et al. (2014) found that of 109 stations investigated along the Norwegian coast for salmon lice infection, 67 stations indicated moderate-to-high mortality of wild sea trout. Finally, 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 the threshold levels proposed by Wells et al. 2006).

In areas with fish farms, numbers of hosts can in theory curtail the natural bottleneck that salmon lice experience during winter months and create epizootics on wild fish even at lower temperatures. There are few studies of the salmon lice levels on sea trout during the winter in areas with fish farming. A recent study by Vollset & Barlaup (2014) demonstrated an epizootic outbreak of lice on sea trout in a fjord with intensive fish farming in March. They pointed out that there is little knowledge on how the component of the population that overwinters in the sea is affected by increased production of salmon lice from farms. These individuals may be important in maintaining population stability (chapter 2.3), especially in smaller watersheds that freeze or dry out during winter months.

8.3 Concluding statements

- Salmon lice levels on sea trout in areas without salmon farming, or in locations sampled prior to the commencement of farming, generally show relatively high prevalences but low intensities. The natural background salmon lice intensity on sea trout in farm-free areas may be as low as 0-3 lice per fish and with a prevalence of 0-20% in late winter and spring. This may increase to a peak of up to 4-8 lice per fish and higher prevalence in the late summer and autumn. In such farm-free areas, the salmon lice population appears to encounter a bottleneck in winter, whereas peak intensity often is noted in June-August at more southerly latitudes in Norway or August-October at more northern localities.
- The highest salmon lice levels reported for sea trout in a farm-free area in Norway showed a mean abundance of 10.9 lice per fish, and mean intensity of 11.6 lice per fish. However, even in areas lacking salmon farms, a few individual sea trout may carry salmon lice levels that laboratory studies have indicated to exert negative impacts on growth and survival of the host fish.
- There are no published records of salmon lice epizootics on wild sea trout in farm-free areas. There are historical reports of epizootics for other wild salmonid species in Canada in the early 20th century. This indicates that salmon lice epizootics are

not a common phenomenon for sea trout or other wild salmonids in farm-free areas.

- Salmon lice levels on populations of sea trout 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.
- In areas where sea trout are heavily infested, individual hosts rarely carry the adult lice stage and the chalimus larval stages predominate. This may be attributable to intense larval infestation pressure at that locality. Alternatively, it is possible that any heavily infested fish that carried preadult and adult lice stages had already died at sea, or returned prematurely to freshwater, before the lice could develop to the adult stage.
- Even though it is not known to what degree threshold levels based on laboratory results are directly applicable to field data, large-scale field studies from Ireland, Scotland and Norway indirectly indicate an elevated risk of salmon lice-induced mortality of sea trout in areas with high salmon lice levels. Due to uncertainties in how well the sampled fish actually represent the entire host population, it is difficult to extrapolate these data to a quantitative estimate of the population effects for sea trout in farm-intensive areas.

8.4 Knowledge gaps

- Monitoring of salmon lice levels on wild populations of sea trout needs to be strengthened in order to facilitate an inclusive analysis of the factors likely to influence the large variation in salmon lice levels noted for areas impacted by fish farms. Furthermore, additional studies are required to specify in detail the migration routes of sea trout in relation to salmon aquaculture installations and to determine the larval salmon lice levels to which local sea trout populations are exposed.
- Further, and more detailed, supportive information is needed on how, where and when to undertake sample monitoring of sea trout. This would enable improvements to the evaluation of how representative is the field sampling and thereby its extension to assessments of entire populations (see also chapter 5). More comprehensive information on the marine behaviour and movement of sea trout is also necessary to underpin assessments of potential impacts at the level of the entire host sea trout population.

Sea trout sampled in the Hardangerfjord, Norway.
Photo Bjørn T. Barlaup

9 Interactions between fish farming activity and salmon lice levels of sea trout in coastal areas

The increased host density associated with salmon 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 in a given locality 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). Hence, salmon lice originating from farmed salmon are more likely to infest wild salmonids than *vice versa*, although all salmon lice hosts potentially cross-infest one another (Todd et al. 2004), and wild sea trout, Arctic char and Atlantic salmon also act as vectors for salmon lice. Several studies have related salmon lice levels on sea trout to fish farming activity by correlating lice levels to distance from farms, or by comparing results from farming intensive and farm-free control areas. Results from these studies are reviewed in this chapter.

Several studies of wild sea trout in Ireland, Norway and Scotland have shown increased salmon lice levels with decreasing distance to salmon aquaculture sites (Tully et al. 1999, Gargan 2000, Bjørn et al. 2001, Bjørn & Finstad 2002, Gargan et al. 2003, Bjørn et al. 2011, Middlemas et al. 2013, Serra-Llinares et al. 2014). These studies support a link between salmon farms and salmon lice burdens in sea trout. The results from these studies correspond with others showing increased concentrations of salmon lice larvae in the water column with decreasing distance to salmon farms (Gillibrand et al. 2005, Penston et al. 2008a,b). Moreover, there is support for a correlation between salmon lice larvae in the water column and the number of gravid salmon lice larvae produced by adjacent farms (Penston & Davies 2009).

The correlation between salmon farming and lice production is even more apparent in farmed areas employing synchronized production cycles. Salmon farms in Scotland and some other areas typically operate a synchronised 2-year production cycle, over which the mean total biomass of fish, and thereby the potential for salmon lice larval production, increases with time (Butler 2002, Revie et al. 2002b, Gillibrand et al. 2005). Several studies have shown a relationship between the production cycle in salmon farms and salmon lice levels on sympatric 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), and thereby support a link between aquaculture farms and salmon lice burdens in wild sea trout. Biannual cycles of salmon lice epizootics have been observed only in areas with synchronised-year class production, whereas epizootics were observed every spring in areas with a mixed-year class production (Butler 2002).

Middlemas et al. (2013), Gargan et al. (2003) and Serra-Llinares et al. (2014) all included a large number of sampling sites during monitoring of salmon lice levels on wild sea trout over several years. In all three studies (respectively from Scotland, Ireland and Norway), the highest levels of salmon lice were found on sea trout sampled in coastal areas within 20-30 km of the farms. On the west coast of Scotland, the distance to the nearest farm did not influence the probability of infestations above the critical level for physiological impact by salmon lice (based on Wells et al. 2006, Bjørn & Finstad 1997) beyond 31 km, although there was considerable uncertainty around this cut-off distance (95% confidence limits: 13-149 km, Middlemas et al. 2013). In the Irish study (Gargan et al. 2003), reduced lice levels on wild sea trout were recorded at distances >30 km from farms. Chalimus larval lice stages dominated at a distance to farms of <30 km, and preadult and adult lice stages dominated at distances >100 km. In the Norwegian study (Serra-Llinares et al. 2014), in areas where active fish farms existed within a distance of <30 km, 41% of the variance of the mean lice abundance on wild sea trout could be explained by the lice production in those farms.

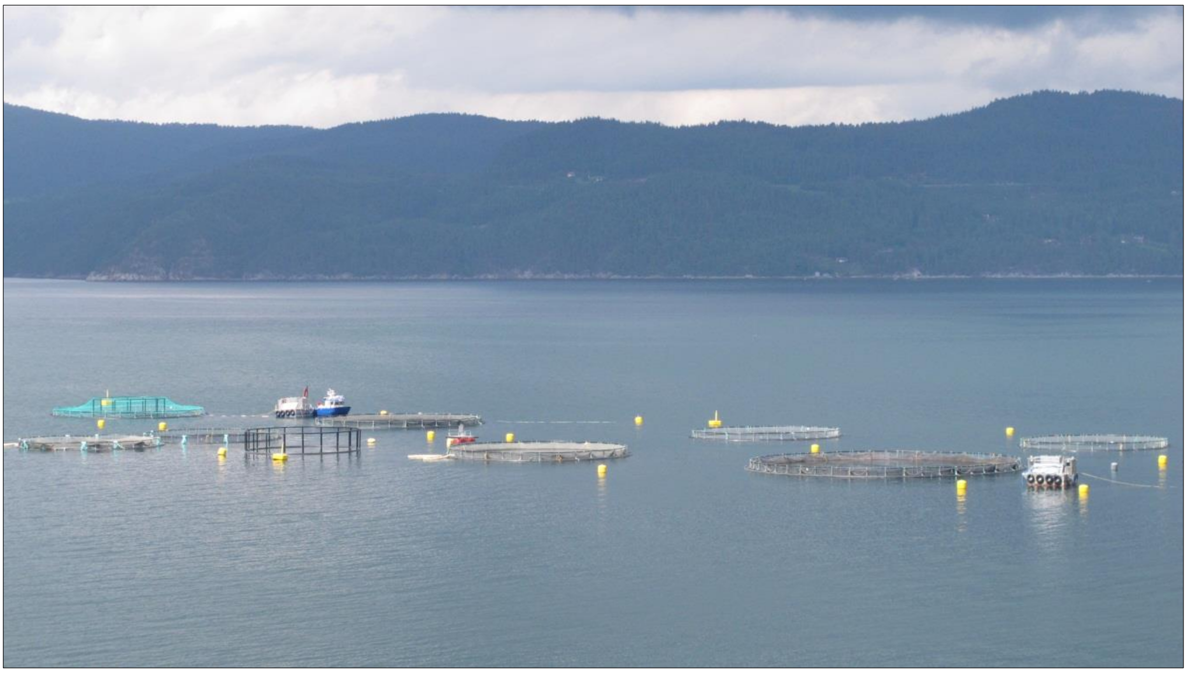
Elevated salmon lice levels on wild sea trout also have been recorded at greater distances from farms (>25-30 km, Bjørn & Finstad 2002, Bjørn et al. 2011). How far, and in which direction, salmon lice larvae are transported from their release source depends upon multiple variables, including salmon lice development rates, water temperature, currents and wind-driven circulation (Gillibrand et al. 2005, Asplin et al. 2011, 2014). Development rates of salmon lice larvae increase with water temperature (Wootten et al. 1982, Johnson & Albright 1991a, Stien et al. 2005). At lower temperatures, salmon lice larvae may therefore have the potential to spread further than during otherwise similar conditions at higher temperatures. Salmon lice larvae have a pelagic phase of up to one month from hatching, dependent on water temperature, by which time they must locate and attach to the host fish (Heuch et al. 2005). Larval nauplii and copepodids may be transported up to 100 km from their source, although numerical models indicate typical dispersal distances of perhaps only up to 25 km (Asplin et al. 2011, 2014). Salinity influences salmon lice survival and behaviour (Heuch 1995), which also affects the density of salmon lice in a given area. Hence, the variability of effective dispersal of salmon lice is potentially considerable, although it is likely that the majority of lice remain relatively close to their source. None the less, under certain circumstances the highest abundance of infective larvae is not necessarily restricted to the source area (Asplin et al. 2011, 2014). For example, aggregation of larvae may occur in certain areas, typically close to land and in embayments (Asplin et al. 2014), and larval distribution commonly is spatially and temporally patchy within a given area (Murray 2002). The movements of wild sea trout themselves in coastal areas (chapter 2) also will contribute to variation in their risk of exposure to salmon lice and they may move between sites of high and low risk, and not necessarily be captured close to the site where they may have been actually infested. This can be manifest as heavily infested fish moving towards low-risk estuarine or fresh waters in response to osmoregulatory stress (Birkeland 1996, Birkeland & Jakobsen 1997). Hence, considerable variation in salmon lice levels on wild sea trout, as has been observed in rivers close to farms in Ireland (Gargan et al. 2003), is to be expected. Such complexities may underlie the occasional reports of the lack of a relationship between salmon lice levels and distance to nearby farms, or between lice levels in wild sea trout and those on a nearby fish farm (e.g. MacKenzie et al. 1998, Marshall 2003).

9.1 Concluding statements

- A number of comparative field studies in several countries have demonstrated a link between Atlantic salmon farms and salmon lice levels in wild sea trout, with increased salmon lice levels on wild sea trout closer to salmon farms.
- Several studies have shown elevated salmon lice levels on wild sea trout, and particularly within 30 km of the nearest farms.
- Several studies have shown temporal correlations between salmon lice levels on wild sea trout and biomass of salmon in adjacent farms, with increased salmon lice levels on sea trout correlating with increased total fish biomass in those farms.
- Elevated salmon lice levels on wild sea trout also may be recorded at distances exceeding 25-30 km, and numerical models have shown that salmon lice larvae can be passively dispersed on currents to distances >100 km. How far, and in which direction, salmon lice larvae are transported depends upon numerous variables, including salmon lice development rate, water temperature, currents, wind-driven circulation and salinity. Movements of the host sea trout in coastal areas also will contribute to variation in their risk of salmon lice encounters because sea trout may move between sites with high and low risk, and not necessarily be captured close to the site where they may have been initially infested.

9.2 Knowledge gaps

- Numerical models and their data basis relating to the production, release and distribution of infective salmon lice larvae from farms need to be improved. More quantitative information is needed on how salmon lice larvae may spread and be dispersed in coastal areas, and which environmental factors determine the resulting salmon lice level on wild sea trout in a given area. Such information is necessary to optimise and evaluate mitigation measures, such as designating protective areas without salmon farming, and to evaluate potential or existing farm sites in order to predict their likely impact on wild sea trout populations.



Salmon farm in Central Norway. Photo: Eva B. Thorstad

10 Population effects of salmon lice

10.1 Effects of salmon lice on fish stocks

Salmon lice epizootics have been recorded for populations of wild sea trout following the establishment of salmon farms in Ireland, Scotland and Norway (Revie et al. 2009 technical report, Finstad et al. 2011), and often have been attributed to proliferation of salmon lice larval production from captive stocks of farmed Atlantic salmon (Tully & Whelan 1993, Heuch & Mo 2001, Butler 2002). These parasite epizootics can impact both individual fish (e.g. tissue damage, physiological stress, and reduced marine growth and somatic condition factor (see chapters 6 and 7)), and cohorts or entire populations (e.g. premature migratory return to freshwater, and changes in population structure arising from mortality).

To obtain even simple quantitative data − such as measures of overall abundance and population age-class structure – for stocks of anadromous salmonids within even small river catchments is a very complex undertaking. Monitoring methods applied in Europe to assess salmon and sea trout populations in rivers range from the deployment of automated counters, video recording, snorkel surveys, capture-mark-release-recapture and interceptory trapping or netting. In addition, visual surveys of spawning and redd counts may be supplemented by electrofishing surveys aimed at enumerating the embryonic and juvenile components of the population in freshwater. Tagging studies require a reliable means of initially sampling, and subsequently recapturing, large numbers of individuals within the population and either partial (e.g. fyke net or screw net) or total barrier traps provide the best means of monitoring a population as the juveniles migrate downriver or adult fish return from the sea. Whilst full trapping facilities which intercept the entire stock could be argued to be the ideal, these facilities are capital-intensive and may require year-round maintenance and operation. Such research facilities are few in number in Europe and, as a consequence, for many Atlantic salmon and sea trout sport fisheries the rod catch is commonly used as an index of overall stock size and health.

Estimates of stock size from rod catch data before/after the onset of marine salmon farming in estuaries or areas close to those rivers allow assessment of the effect of salmon lice on sea trout populations. Such a comparison does, however, require that the introduction of salmon farming is the only major change for the region in question although it may be possible in modeling the population data to statistically isolate confounding factors. Since 1974 in Ireland, the sea trout rod catch has been monitored consistently for 18 west coast fisheries in the Connemara district. The data show annual sea trout rod catches of ~10,000 fish during the period 1974-86, a decline during 1987-88, and a collapse to 240 fish caught in 1990 (Whelan & Poole 1996, Gargan et al. 2006a). Sampling of sea trout in estuaries was initiated in the Irish mid-west in 1990, and sea trout post-smolts were recorded in all rivers with high salmon lice levels of predominantly juvenile salmon lice life-cycle stages (Tully et al. 1993b). This documented collapse in sea trout rod catch coincided with the development of salmon aquaculture in inshore bays and estuaries in western Ireland during the mid-1980’s, and was latterly linked to salmon lice infestation on sea trout in aquaculture bays (Tully & Whelan 1993, Tully et al. 1999, Gargan et al. 2003).

In determining whether any reduction in rod catch is reflective of an overall reduction in sea trout stock size, it is important to consider catch per unit effort (CPUE) for the fishery. In this context, the “catch and release” byelaw introduced in western Ireland in 1990 may have affected angling effort for some fisheries. Gargan et al. (2006b) examined sea trout CPUE for three Connemara sea trout fisheries over more than five decades and found that that the sea trout catch collapse recorded between 1988 and 1990 was not related to reduced angling effort, although a marked reduction in CPUE had indeed occurred.

In Scotland, during the late 1980's, unprecedented declines in sea trout rod fisheries were recorded throughout the west coast region (Walker 1994, Northcott & Walker 1996). Loch Maree is a large freshwater lake in Wester Ross which discharges to coastal waters through the River Ewe. Traditionally, Loch Maree has featured as the foremost wild sea trout fishery in western Scotland and was famous for both the abundance and large maximum size and age of its sea trout population. A collapse of the River Ewe sea trout rod catch, beginning in 1988 and linked to salmon lice epizootics following the establishment of marine salmon farms near the river mouth, was reported by Butler & Walker (2006). Butler (2002) further estimated that farm salmon probably were the primary source of salmon lice (78-97% of parasites) on salmon and sea trout populations, and that aquaculture facilities comprised the major risk of louse transmission to emigrating wild salmon and sea trout smolts in springtime on the west coast of Scotland. As an indication of the potential mortality impact of salmon lice on individual wild salmonids in western Scotland, Gargan et al. (2003) estimated that 31% of sea trout sampled in aquaculture bays in western Ireland over the period 1992–2001 carried potentially lethal louse burdens.

10.2 Population-reducing effects on sea trout

Ford & Myers (2008) examined temporal trends in the abundance and survival of wild salmonids in an inclusive analytical effort to determine global population level impacts of salmon farming on wild salmonids. They contrasted trends in abundance of wild salmonid populations "exposed" to potential aquaculture impacts, with those of "unexposed" populations. Their analysis indicated a significant differential decline in survival of populations exposed to salmon farms, and correlated this effect with the increase in farmed salmon production in five regions. Combining the regional estimates statistically, they found an average reduction in survival or abundance of wild populations associated with salmon farming of >50% per generation. However, one notable complication in their analysis was the use of nominal reported catch data as a proxy for population abundances. As noted in chapter 10.1, strictly one should assess catch data in relation to fishing effort. Certainly for the Scottish data analyzed by Ford & Myers (2008), commercial fishing effort had declined markedly over the time period they analyzed, due to the closure of many net fisheries, and this will have implications for any estimate of population abundances derived for both salmon and sea trout. Ford & Myers (2008) did not include Norway in their analyses because they found that Atlantic salmon farming was so widespread that it was difficult to establish control areas, many adult populations of Atlantic salmon contained large proportions of escapees from fish farms, and there were confounding effects from acidification and disease. It is evident also that the geographical areas which lend themselves to the establishment of salmon farms are restricted by environmental parameters. Thus, whilst many Norwegian fjords might present suitably sheltered farm locations, in the British Isles only on the west coasts of Scotland and Ireland are the coastlines physically sheltered. The possibility of geographical autocorrelation between the presence of salmon farming and responses of adjacent populations of salmonids to more pervasive environmental change or perturbation should, therefore, be considered in broad-scale analyses of the impacts of salmon aquaculture on wild populations.

Bjørn et al. (2001) quantified salmon lice levels on two Norwegian sea trout stocks; one ("exposed") stock was located in an area subject to extensive salmon farming and was compared with an "unexposed" stock in an area with little farming activity. At the exposed location, 47% of the fish caught in freshwater and 32% of those captured at sea carried salmon lice at intensities above the level that has been shown to induce mortality in laboratory experiments (Bjørn & Finstad 1997). Furthermore, almost half of all fish from the exposed locality had salmon lice intensities that probably would cause osmoregulatory imbalance. Bjørn et al. (2001) concluded that high salmon lice levels may therefore have profound negative effects upon wild populations of sea trout as a result of (i) reduced fish growth arising from post-smolts returning prematurely to freshwater, (ii) stress effects and homeostatic perturbations, and (iii) exposure of the most heavily-infested fish to an increased risk of mortality due to behavioral changes.

Also in Norway, Serra-Llinares et al. (2014) evaluated the efficacy of fjords being designated for protection in order to prevent infestation by farm-derived salmon lice of specific populations of wild salmonids that might be considered to be of special conservation importance. Their evaluation focused on quantifying the lice levels for wild salmonids, derived from salmon lice counts on wild-caught sea trout within one third of these protected fjords. The effects of small protected fjords were strongly dependent on the production pattern of the aquaculture industry in the surrounding area, and they found a clear correlation between salmon lice levels on wild salmonids and lice production in nearby salmon farms. Serra-Llinares et al. (2014) applied the index proposed by Taranger et al. (2012) to predict the increase in mortality risk due to salmon lice for sea trout carrying varying levels of parasite burdens. Salmon lice levels on wild sea trout caught in small protected areas were found to be very high during most of the period investigated, and ‘medium’ to ‘high’ risk indices for population-reducing effects often were recorded for wild sea trout sampled in these fjords. But risk levels are likely to vary among years, according to changes in the biomass and year class structure of cultured fish held in farm facilities. For example, Atlantic salmon typically are cultured on a two-year production cycle in many areas (Revie et al. 2002b). In a western Scotland sea loch, Middlemas et al. (2010) reported a significant and fluctuating relationship between production cycle year and the incidence of sea trout with parasite burdens exceeding a threshold level considered by Wells et al. (2006) to provide “a clear indication of the proportion of sea trout within a population that are subject to physiological stress and potential death from sea lice infestation”.

Contemporaneous data on salmon lice intensities on marine salmon farms, and on wild sea trout populations, in addition to observations of the incidence of premature migratory return by sea trout within a population, all have proven to be strongly indicative that salmon lice from marine salmon farms were a significant contributory factor in observed stock collapses in western Ireland (Tully & Whelan 1993, Tully et al. 1999, Gargan et al. 2003). The overall conclusion of these authors was that salmon lice had a negative effect on stock and population abundances. Undoubtedly, the population-reducing effects of caligid parasites on sea trout can best be assessed where trapping facilities have been in place prior to, and following, the establishment of marine salmon farming in the adjacent area. For example, Irish data on upstream migrant sea trout are available since 1970 from the Burrishoole upstream trap and 1985 for the Tawnyard (Erriff) sea trout kelt trap; both time series predate the onset of marine salmon farming in the estuaries of both rivers. Rod catch data and trap records from both fisheries indicate a stable sea trout population structure typical of the west of Ireland prior to 1989, dominated by a peak of finnock (0+ sea age trout of length ~32 cm), a second peak of 1 sea-winter maidens (length up to ~40 cm) and some older and larger sea-age classes and previous return spawners of >40 cm (Poole et al. 1996, Gargan 2000). Subsequent to the 1989 sea trout stock collapse in western Ireland, this typical population structure changed markedly; there was a reduction in the number and proportions of sea age classes and stocks were characterised by low returns of finnock and fewer veteran sea trout in the older age classes (Whelan 1993, Poole et al. 1996, Poole et al. 2006, Gargan 2000). Long-term monitoring of sea trout population structure for these two west of Ireland catchments was the first to document comprehensively a complete stock collapse and a significant change in population structure which could be linked to premature migratory return and to salmon lice infestation.

A number of studies focusing on sea trout population declines in rivers, freshwaters lochs and sea lochs of the west coast of Scotland have been undertaken, and from an early juncture Butler (2002) highlighted the possibility of salmon lice epizootics on wild salmonids originating from adjacent farmed salmon stocks. Butler & Walker (2006) recorded a collapse in sea trout rod catch in the river Ewe/Loch Maree system in Wester Ross, Scotland in 1988 with an apparently unprecedented reduction in marine growth and survival reflected in marked shifts in the population structure before and after the collapse. Between 1980 and 1997-2001, maximum sea age fell from 11 to 5 years and marine growth rates declined. This was reflected in the River Ewe rod catch with significant changes in the body mass distribution of fish between 1971-1980 and 1992-2001, with the mean falling from 0.54 kg to 0.34 kg over the time period. Taken together, the changes in the River Ewe stock structure could be related to declines in marine growth and survival which were deduced to have been at least partly attributable to salmon lice epizootics emanating from salmon farms in the adjacent coastal waters of the marine embayment of Loch Ewe (Butler & Walker 2006). This contention was supported in a further publication (Walker et al. 2006) by comparisons with contemporaneous catch data for east coast Scotland sea trout stocks. The east coast of Scotland has essentially remained non-impacted by commercial salmon farming throughout the history of the industry, and sea trout stock structure remained stable over the same period that the west coast collapses were reported. Further corroborative reports of contemporaneous collapses in other, smaller, sea trout fisheries in the west of Scotland include those for rivers draining into Loch Torridon (McKibben & Hay 2004). Notwithstanding the clear contrasts in these sea trout stock assessments for east (non-farmed) *versus* west (farmed) coasts regions, it has to be acknowledged also that the presence/absence of salmon farming is not the only difference between the two Scottish coastlines. Ideally, comparisons would be drawn between areas or rivers in farmed and non-farmed regions within the Scottish west coast itself; but the development history and extent of the industry is such that suitably large non-farmed, or “non-impacted” areas are not present. Furthermore, even drawing comparisons among specific sea lochs within western Scotland is fraught with difficulty because of the problem of pseudoreplication – no two sea lochs are identical in terms of their size, depth or hydrography. The absence of extensive areas of western Scotland which lack salmon farming, and which might be designated as “controls” for experimental comparison with salmon farm “impacted” areas, has proven to be a major obstacle to scientists investigating the likely impacts of salmon farming on adjacent wild stocks of sea trout and salmon. Lack of access for scientists to detailed data on lice levels and number and size of fish held in fish farms also hampers analyses of the likely impacts of salmon farming on wild sea trout and Atlantic salmon stocks.

10.3 Population-reducing effects on Atlantic salmon

In recent years, there have been numerous experimental studies on the mortality impact of salmon lice on out-migrating populations of Atlantic salmon smolts, using chemically treated and control groups of untreated fish in both Norway and Ireland. These studies have been conducted largely in rivers discharging into salmon aquaculture bays, although not exclusively so, with the presumption being that salmon lice originating from local farm sources might confer increased mortality risk to the untreated control smolts, and that this effect will extend to the wild Atlantic salmon smolt population. These studies are reviewed in this chapter because of their relevance for drawing interferences relating to population effects for sea trout.

Two experimental approaches have been adopted in manipulating hatchery-reared Atlantic salmon smolts in a controlled manner and then releasing these fish to undergo the natural emigration from the river. In all experiments, one group of smolts was chemically treated to provide short-term protection from salmon lice whilst a separate, un-treated, group provided the experimental control. Two active chemical agents have been deployed. Substance EX (Alpharma) is applied topically to smolts in a bath treatment, whereas emamectin benzoate (Slice™, Schering-Plough) is provided as an in-feed additive over a period of days or weeks prior to the release of the smolts into the river. Emamectin also can be administered by interperitoneal injection (Skilbrei et al. 2013). Both emamectin and Substance EX provide short-term protection of smolts from salmon lice, and are shown to be effective for the first 1-2 months after release (Stone et al. 2002). Releases of Atlantic salmon (Substance EX) in areas of Norway with heavy fish farming activity have resulted in higher recaptures (0.90%) compared to unprotected control fish (0.03%) (Finstad & Jonsson 2001). Similarly, Skilbrei & Wennevik (2006) compared the returns of emamectin-treated and control (untreated) juvenile salmon smolts released on three occasions in springtime of the one year in large Norwegian fjords and found protected fish in their third experimental release to show significantly higher return rates as maiden mature adults. Other studies of Atlantic salmon in rivers in central Norway (Hvidsten et al. 2007) and southwest Norway (Finstad & Jonsson 2001) have demonstrated that in years of high salmon lice levels, the returns of chemically-protected fish tended to be higher than unprotected control groups.

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

Jackson et al. (2011a) tagged and released emamectin-treated and control groups of ranched salmon in 10 experimental releases over 9 years in one location with salmon aquaculture in western Ireland. Whilst the return rate of treated fish was higher in nine of their ten releases, they concluded that salmon lice infestation was only a minor component of overall marine mortality for the particular stock studied. In a further report, which included additional release locations, Jackson et al. (2011b) reiterated their previous general conclusion; but that conclusion was subsequently challenged by Krkošek et al. (2013, 2014) and is discussed further below. Independent results of returns of emamectin-treated and control salmon smolts from three other locations in western Ireland (Gargan et al. 2012) show that salmon lice-induced mortality on adult salmon returns can be significant: Gargan et al. (2012) concluded that salmon lice outbreaks have the potential to be an important factor reducing wild Atlantic salmon stock sizes. In a complementary and corroborative analysis, Krkošek et al. (2013) conducted an extensive meta-analysis of all the foregoing Irish and Norwegian field experiments in order to quantify the potential influence of salmon lice on the marine survival of Atlantic salmon. The compiled data included 24 trials in which tagged smolts (totaling 283,347 fish; 1996–2008) were released as paired control and parasiticide-treated groups into 10 areas of western Ireland and Norway. Treatment against salmon lice had a significant positive effect on survival to adult recruitment leading to an estimated risk ratio between treated and untreated groups of 1.29:1, which corresponded to a loss of 39% of adult Atlantic salmon recruitment (Krkošek et al. 2013). Because the chemical protection is known to apply only to the first few weeks of the marine migration of the post-smolt (Stone et al. 2002), it was concluded that the result for treated *versus* control groups was attributable to salmon lice infestations acquired early during the marine migration. Although their meta-analysis was not explicitly structured to assess the impact of farm-derived salmon lice on free-ranging Atlantic salmon post-smolts, these results do provide unequivocal experimental evidence from the natural environment that parasites can have large impacts on marine survival of salmonids, and thereby have implications for fisheries management and conservation.

In assessing the potential for salmon lice to impact survival of Atlantic salmon post-smolts, it is important to emphasize that all the aforementioned experimental release trials have involved the use of hatchery-reared Atlantic salmon smolts. Hatchery smolts typically are larger than wild smolts and the former generally show lower marine survivorship, perhaps attributable to hatchery smolts showing poorer "quality" compared to wild counterparts (Jonsson et al. 2003); the larger size of hatchery smolts may, however, at least partially offset their lower survivorship arising from any reduced overall "quality". One consequence of such differences in overall survivorship of (small) wild and (larger) hatchery smolts is that the estimates of salmon lice-induced reduction in adult recruitment attributable in the experimental releases analyzed by Krkošek et al. (2013) might well, in fact, be even greater than reported when applied to (smaller) wild Atlantic salmon smolts. Conversely, because sea trout smolts typically are larger than Atlantic salmon smolts (chapter 2.2.2), salmon lice at a given intensity might exert a lesser percentage impact on early survival of sea trout post-smolts when they first migrate to sea.

More recently, Jackson et al. (2013) have reported on a further re-analysis and extension of their data arising from releases of emamectin-treated and control salmon smolts in western Ireland. Jackson et al. (2013) found a significant treatment effect but they contend that the level of salmon lice-induced mortality was only approximately 1% of the overall marine mortality, and that salmon lice present only a minor and irregular component to marine mortality of salmon. 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, technical report from the International Council for the Exploration of the Sea, ICES), when the majority of the experimental releases in their study were undertaken. 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. To put this average 1% reduction in return rates, as reported by the Jackson et al. (2013), into context: if a return of 3,000 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 510 fewer fish returning. This level of additional mortality 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. The validity both of the analyses and the interpretations reported by Jackson et al. (2011a,b, 2013) have been questioned by Krkošek et al. (2014), who showed at least three fundamental errors in the two original papers and reaffirmed that meta-analysis of these same data showed that salmon louse-induced mortality of post-smolts ultimately can result in a 34% reduction in adult salmon returning to coastal waters. In their reply, Jackson et al. (2014) raised several statistical issues but did not explicitly address or answer the fundamental errors identified by Krkošek et al. (2014). Their greatest concern was that Krkošek et al. (2014) ignored the heterogeneity (variation in estimated effect size) in the meta-analysis and argued that the presentation of a single value estimate of the effect of treating salmon smolts is invalid. Put in simpler terms, treating fish will lead to significantly higher returns of adult salmon. However, in some release groups the effect is small, while in other release groups the effect is very large.

Following on from these initial experimental reports, Skilbrei et al. (2013) further examined the survival of outward-migrating Atlantic salmon smolts by comparing the adult returns of sea-ranched smolts treated against salmon lice using emamectin benzoate or Substance EX with untreated control groups in the River Dale in western Norway. The effect of treatment was significant and showed a higher probability of treated fish being recaptured (risk ratio 1.17:1). Torrissen et al. (2013) also cite closely similar estimates from Ireland and Norway of survivorship of salmon lice-protected Atlantic salmon smolts to survive marine migration compared to untreated smolts. The most recent study on releases of hatchery reared salmon treated or not treated against salmon lice (Vollset et al. 2014) concluded that salmon lice effects may increase the mean age of returning salmon, either by influencing their age at maturity or by disproportionately increasing mortality in those fish that mature early.

The experimental protection of salmon and sea trout − by the application either of Substance EX or emamectin benzoate, to the juvenile fish in freshwater and prior to their release − is confined to only the first few weeks at sea. Sea trout post-smolts in coastal waters will remain exposed to the local inshore salmon lice level throughout their time at sea. In the case of Atlantic salmon, which emigrate rapidly from coastal waters, the experimental fish that survive those first few weeks at sea will be exposed latterly only to ongoing natural levels and infestation rates throughout the remainder of their migration in the open North Atlantic. That a significant difference in return rates of “treated” and “control” Atlantic salmon smolts can be detected amongst the adults returning to freshwater some 12+ months following their release is indicative that mortality attributable to salmon lice in the early weeks of the marine migration is markedly elevated above background and can exert considerable impacts at the population level (Krkošek et al. 2013, 2014). Furthermore, it is important to note that an elevated rate of early post-smolt mortality during the marine migration both of Atlantic salmon and sea trout will compromise the ability of an impacted population to respond positively to possible improvements in the feeding and predation regimes encountered later in the marine migration. The converse argument is that post-smolt populations that are heavily impacted by salmon lice mortality will respond even more negatively to declines in later feeding opportunities, or increases in other mortality risks, in the latter phases of the marine migration.

It is clear that all of the studies conducted to examine the potential impact of salmon lice as a mortality factor in out-migrating Atlantic salmon smolts in aquaculture bays have found greater return rates of treated fish, but not in every location each year. The estimated average risk ratio of protected fish returning to their natal rivers to spawn compared to unprotected fish range from 1.14-1.41:1 (Jackson et al. 2013, Gargan et al. 2012, Krkošek et al. 2013, 2014, Skilbrei et al. 2013). In any given release group a risk ratio of 1.14-1.41:1 reflects that 14-41% fewer unprotected than protected fish ultimately are recaptured as adults. However, within these studies the estimates vary and this likely reflects both the variation in treatment effect and the variation in exposure of the fish to salmon lice. For example, Skilbrei & Wennevik (2006) showed that the oral administration of emamectin as an in-feed additive can result in considerable variation in uptake by individual fish, perhaps to the extent of leading to a suboptimal protection of some fish in the treated group. For their experiments involving the emamectin treatment and release of salmon smolts in western Ireland, Gargan et al. (2012) chemically assayed subsamples of all treated fish and they also found that some individuals in the treated group probably did not acquire emamectin to a concentration likely to provide protection from salmon lice. Accordingly, it is apparent that the true level of salmon-lice induced mortality derived from survivorship estimates in these experimental releases will be even higher than is indicated by the comparisons between the numbers of adults returning from the treated and control groups of smolts because not all the treated smolts will have been adequately protected.

Each of the foregoing studies compared large groups of protected and un-protected Atlantic salmon that were released, and each experiment represents a snapshot in time and space. Despite the large numbers of smolts released, the numbers recaptured in such experiments typically are rather low and one should, therefore, be cautious in extrapolating data from single studies to a population level. None the less, clear differences between the groups recaptured within experiments have consistently been shown to be statistically significant. Meta-analyses and long-term studies, and similar results from an increasing number of experimental studies, support that these are levels of extra mortality (i.e., 14-41% fewer spawners) that can be expected for Atlantic salmon populations in farm-intensive areas. The overall pattern, therefore, is one of a significant treatment effect; and the scale of effect will depend on a range of factors including differences among rivers, the location and size of farms, levels of larval salmon lice during the smolt migration, wind-driven lice dispersal, and freshwater influences. Sea trout are known to spend the majority of their marine feeding phase in near coastal or inshore areas (Klemetsen et al. 2003), as opposed to Atlantic salmon which migrate to offshore feeding grounds and may undertake extensive ocean migration. Monitoring of salmon lice of return adult wild Atlantic salmon has shown that infestation continues throughout the marine residence of the host fish – even for sub-adult fish in the open North Atlantic (Jacobsen & Gaard 1997, Todd et al. 2000). The near-shore distribution of sea trout results in their exposure to infective larval salmon lice over a prolonged time period and therefore to potentially greater lice levels than Atlantic salmon. It could be argued that if population-reducing effects of lice can be demonstrated for out-migrating salmon smolts, then the greater overall salmon lice infestation pressure experienced by sea trout in near-shore waters is likely to have an even greater population reducing effect. Nevertheless, estuarine areas and freshwater outfalls in coastal areas do potentially provide a refuge from salmon lice for sea trout.

Deploying an ocean trawl net for Atlantic salmon post-smolts off the Irish coast.
Photo: Patrick G. Gargan

In reviewing salmon lice-host interactions between farmed and wild Atlantic salmon and sea trout, Todd (2007) emphasized that the early evidence of farm-wild parasite interactions was primarily circumstantial or correlative. None the less, and prior to the recent publications of the numerous large-scale experimental releases of “treated” and “control” Atlantic salmon and sea trout smolts cited above, Revie et al. (2009, technical report) latterly reviewed the available literature to date and concluded that “the weight of evidence is that salmon lice of farm origin can present, in some locations, and for some host species populations, a significant threat. Hence, a concerted precautionary approach both to sea lice control throughout the aquaculture industry and to the management of farm interactions with wild salmonids is expedient.” That conclusion would therefore appear substantially reinforced by the aforementioned recent experimental results arising from the various large-scale trials with Substance EX and emamectin benzoate.

10.4 Effects on stages of sea trout life history

The effect of parasites on sea trout populations can be assessed at various life stages of the host fish. Two west of Ireland sea trout fisheries (Burrishoole and Tawnyard) have shown an increase the proportion of finnock (0+ sea age sea trout) returning, with fewer older fish in the stock after the observed sea trout stock collapses that had been associated with salmon lice infestation (Poole et al. 2006, Gargan 2000). The 1989 spawning stock collapse in western Ireland significantly reduced both the total number of ova deposited and subsequent levels of recruitment (Poole et al. 2006). The number of ova deposited by sea trout in the Burrishoole system, estimated to range between 0.49 and 1.61 million before 1987, decreased to <60,000 by 2000 and showed a low of 27,500 in 2003 (Poole et al. 2006). O’Farrell et al. (1989) considered sex ratio, percentage maturation, fecundity and relative abundance of each sea age group with regard to egg deposition in the Tawnyard catchment. They calculated that the percentage contribution to ova deposition of 0+ sea age fish was 5.6%, whereas that of 1+ sea age fish was 40.6% and 2-sea age fish and older contributed 53.7% to ova deposition. Hence, reduced marine survivorship of larger, older spawners which perhaps contribute disproportionately to overall egg deposition can exert considerable and rapid impacts at the population level. These large, veteran migrants should, therefore, perhaps remain a focus for especial protection in developing sea trout conservation strategies.

In Norway, Birkeland (1996) examined the consequences of premature migratory return of sea trout to freshwater, and concluded that unless fish experience compensatory growth when they return to sea their growth must be reduced compared to fish spending the full growth season in the sea. Therefore, loss of body mass and reduced growth as a result of sea louse infestation may reduce resources available for egg production, thereby reducing individual fecundity and population reproductive success. In Scotland, Butler & Walker (2006) recorded a marked reduction between the late 1980s and early 1990s in the proportion of older and larger sea trout in the catch data for the river Ewe/Loch Maree system in Wester Ross. They showed a reduced longevity of sea trout from a maximum of 11 to 5 sea years and concluded that the combination of reduced abundance, size, longevity and hence frequency of spawning adults probably had a major influence on total sea trout egg deposition. Given that the abundance, maximum sea age and mean spawning frequency of this sea trout stock decreased further between 1993-93 and 1997-2001, total egg deposition probably was yet further compromised (Butler & Walker 2006). From comprehensive empirical data such as these, it is evident that the collapses in sea trout stocks – and especially the loss of older age classes observed both in the west of Ireland and the west coast Scottish fisheries – have had significant impacts of sea trout ova deposition and population structure.

The impact of salmon lice on sea trout has been shown to affect subsequent smolt output. In spite of wide annual variation, there was no significant change in smolt output from the Burrishoole river in western Ireland between 1970 and 1989. However, following the collapse in sea trout spawning stock, smolt output decreased significantly to below the previous recorded minimum (Poole et al. 1996). A steady decline in sea trout smolt output also was observed for the nearby Owengowla fishery following a collapse in marine survival (Gargan et al. 2006b).

10.5 Effect on sea trout marine survival

Long-term monitoring data for sea trout from Ireland, and which precede the development of intensive salmon aquaculture, may permit BACI (before-after control-impact; Smith et al. 1993) assessment. In the Burrishoole system in western Ireland, prior to the onset of marine salmon aquaculture, the percentage of smolts that survived to return as 0+ sea age finnock in the same calendar year ranged from 11.4 to 32.4% with a historical mean of 21%. In 1988, marine survival (as measured from upstream trap interceptions) fell below the previous recorded minimum to 8.5%, and in 1989 to an all-time low of 1.5%. Throughout the 1990's there was a saw-tooth pattern of finnock return rates, rising in 1999 to 16.7% and which was the highest return rate since 1986. The mean for the 1990s – excluding 1999 – was 6.8%, which was three times lower than the historical average (Poole et al. 2006). Sea lice emanating from sea farms were implicated in this additional mortality (Tully & Whelan 1993, Gargan et al. 2003, Poole et al. 2006). Data from two other upstream trap facilities in western Ireland provide an insight into sea trout marine survival following the observed stock collapse. Marine survival was <1% for seven out of ten years on the Owengowla, and <2% for seven of eight years on the Invermore (Gargan et al. 2006b). The highest marine survival (19%) over the period was observed on the Owengowla in 1994, coinciding with whole-bay spring fallowing of salmon aquaculture. Although survival estimates under circumstances of local farm fallowing would require replication in multiple years and locations, these data indicate that infestations by salmon lice from marine Atlantic salmon farms made an important contribution to the sea trout stock collapse on Ireland's west coast (Gargan et al. 2006b). Whilst no marine survival data exist for Scottish west coast rivers prior to the sea trout collapse in the late 1980's, low smolt-to-finnock marine survival rates of 0.8-8.1% and 1.0-4.6% respectively over the 1999-2001 period were also recorded for the rivers Tournaig and Shieldaig (Butler & Walker 2006) and have been related to salmon lice infestation.

Skaala et al. (2014a) assessed the marine survival rate of sea trout from the River Guddalselva, in the central part of the Hardangerfjord in Norway, and tested the hypothesis that populations in this area are depressed by salmon lice infestation. From 2001 to 2011, all descending smolts and sea trout returning from the fjord were captured in traps. Samples of the smolt cohorts were treated with Substance EX to prevent early salmon lice infestation and smolts also were marked with individual tags. The results show a very low marine survival rate of only 0.6-3.4% for tagged smolts, with the highest survival rates in years with the lowest registrations of farm salmon lice in springtime. The survival rate of Substance EX-treated smolts and controls was 3.41% and 1.76%, respectively, with a significantly higher recapture rate for treated smolts. These findings suggest that salmon lice infestation in local fjordic waters is an important contributor to the high mortality of anadromous trout populations in the Hardangerfjord, and is one of the first studies to present quantitative empirical evidence of induced mortality due to salmon lice infestation at the population level for sea trout.

10.6 Effects on residency time at sea and premature migratory return

Sea trout were observed in the lower pools of the Delphi fishery in Connemara, western Ireland in late May 1989 with large numbers of juvenile salmon lice. These sea trout were post-smolts, which had returned prematurely from the sea after only two or three weeks, and showed little or no marine growth. This was the first documented evidence of premature migratory return of lice-infested sea trout (Tully et al. 1993a). Sampling of other rivers in western Ireland commenced in 1990 with the objective of determining whether or not this phenomenon was widespread. Sea trout post-smolts and some sea trout kelts with salmon lice were recorded in all rivers; the juvenile stages of salmon lice were predominant and this indicated recent transmission. Dead and dying fish were observed in the estuaries where salmon lice levels were highest (Tully et al. 1993a). The latter authors suggested that premature return might be adaptive in evolutionary terms and could be positively selected for because it removes the fish from the infective parasite population and increases their chances of survival, albeit at a probable cost of reduced growth and reproductive output in the short-term. Tully et al. (1993) did, however, further comment that for a proportion of prematurely returned sea trout the physiological impact of salmon lice infestation probably was severe and the fish may have reversed their migration in response to osmotic stress.

Birkeland (1996) and Bjørn et al. (2001) reported the premature migratory return of salmon lice-infested sea trout in Norway, and Butler & Watt (2003) and Hatton-Ellis et al. (2006) have done so similarly for Scotland (see also chapter 7.4.1). Butler & Walker (2006) noted that timing of primary sea trout return to freshwater advanced by one month, from July to June, and that finnock returned earlier in May and June in the River Ewe system in western Scotland. These authors note that the presence of salmon lice epizootics in the marine embayment of Loch Ewe related to farm production cycles and the resulting premature return of post-smolts, finnock and older sea trout suggest that this is the primary anthropogenic factor concerned. A field experiment conducted in the River Lønningdalselven (Norway) in spring 1992 (Birkeland & Jakobsen, 1997) supports the hypothesis that salmon lice infestations may cause premature migratory return of sea trout juveniles, either to the reduced salinity estuary or to the river itself. In all of these instances, even if infested fish survived their initial return to freshwater, it is clear that their marine growth (and hence future fecundity) will have been compromised by their abbreviated marine migration and its associated benefits of greater feeding and growth opportunities compared to freshwater residence.

Wild sea trout with salmon lice. Photo: Rune Nilsen

10.7 Effect on reduced marine growth

For the Burrishoole sea trout stock in Ireland, ratios of sea growth to freshwater growth showed no discernible trend until 1990, after which this ratio showed a marked decrease over the period 1990-1992, and a significant reduction in marine growth most likely linked to premature migratory return of salmon lice-infested fish (Poole et al. 1996). Fjørtoft et al. (2014) examined freshwater and marine growth both of sea trout and Atlantic salmon from the River Etneelva in relation to river, fjord and ocean temperatures during the periods 1976-1982 and 2000-2007. Unlike salmon, sea trout grew more slowly through their first and second summers in the sea during the latter observation period compared to the initial period, and there were more growth 'checks' (or hiatuses) in the spacing of the circuli on the scales sampled from the last period. The reduced growth in length corresponds to a weight reduction of approximately 20-40%. They concluded that the negative trend observed in marine growth for sea trout was most likely related to the high salmon lice levels observed in the central and outer parts of the Hardangerfjord. In a similar manner, higher marine mortality of predominantly post-smolt and 1+ sea age sea trout from 1990-1992 in Ireland was paralleled by poor growth of the surviving fish (Poole et al. 1996). Furthermore, Butler & Walker (2006) recorded significant declines in marine growth of sea trout and a collapse in sea trout rod catch in the River Ewe system in western Scotland following the establishment of marine salmon farms. All of these results therefore converge on salmon lice infestations of post-smolt and adult sea trout having the potential to exert clearly definable impacts on sea trout populations, manifest as changes in individual marine migration timing and behaviour, growth and survivorship. However, it should be emphasised that there often is a correlation between growth and recruitment in marine fish stocks that is most likely independent of parasites, and that effects of salmon lice on marine growth may be difficult to isolate from other impacts.

Collection of sea trout by electrofishing in a river mouth in western Norway.
Photo: Bjart Are Hellen

10.8 Predominance of freshwater resident brown trout

Sea trout progeny may adopt variable life history and migratory tactics depending on environmental conditions (Walker 1994, Klemetsen et al. 2003), and increased freshwater growth rates reduce the tendency for juvenile sea trout to undergo smoltification and migration to sea (Morgan & Paveley 1993). Butler & Walker (2006) noted an increase in the abundance of resident (non-anadromous) trout following the sea trout stock collapse in the River Ewe/Loch Maree system in western Scotland. Given the reductions in egg deposition resulting from the collapse in adult sea trout abundances, it is possible that lack of competition – and related improvements in freshwater growth rates – might lead to a greater prevalence of freshwater-resident trout in some impacted populations (Butler & Walker 2006). Poole et al. (2006) similarly speculated that the reduction of sea trout smolt numbers could be a response of the Burrishoole population to changed environmental conditions whereby freshwater competition had been substantially decreased, thus reducing the benefit of a marine phase to the life cycle.

In a study of sea trout smolt output and marine survival following a collapse in sea trout stocks in two west of Ireland fisheries, Gargan et al. (2006b) recorded that substantial sea trout smolt runs continued to be recorded for a number of years despite the very small numbers of adult trout returning from the sea. Trend analysis indicated a reduction in sea trout smolt output from both fisheries over the study period, which suggested that although freshwater resident trout contribute significantly to sea trout smolt runs, a reduction in smolt output can be expected after a relatively short period of very poor marine survival. If the individuals which adopted the anadromous strategy have very low marine survival, there would be selection in favour of those with higher genetic propensity for freshwater residence. The declining numbers of smolts produced by the freshwater stock therefore could be explained by such selection against the anadromous life history strategy within a population, perhaps to the extent of its eventual loss for a given stock (Gargan et al. 2006b).

10.9 Effect on increased predation

For pelagic fish in the marine environment the risk of mortality from predation may vary according to the depth occupied in the water column, and swimming and diurnal migratory behaviour (and hence vulnerability to predators) may be altered by parasitic load. For example, Gjelland et al. (2014) found a more surface-oriented behaviour in highly-infested sea trout in the Etnefjord in Norway. For sea trout, swimming closer to the surface may represent a trade-off between reduced exposure to parasites and elevated predation risk due to increased exposure to predatory birds (Ward & Hvidsten 2011). Salmon lice infestation may also increase predation mortality in infested individuals as a consequence of their reduced predator vigilance and reduced burst swimming performance (e.g. Wagner et al. 2008, Krkošek et al. 2011).

10.10 Effect on different genetic sea trout populations

The effects of salmon lice on sea trout populations may vary according to the genetic structure of a target population. In this regard, Glover et al. (2001) recorded a clear difference in susceptibility to salmon lice between a freshwater resident brown trout population and an anadromous population, as measured by their respective salmon lice abundances, and postulated that this host difference may be genetic in origin. Subsequently, Glover et al. (2003) found significant differences in abundance, density, and development rate of salmon lice among three sea trout populations in south west Norway. Their results suggest that the observed differences in salmon lice level among the three sea trout populations reflect host genetic differences, and may also be linked with host adaptation. Coughlan et al. (2006) sampled DNA from scales of sea trout in the Burrishoole River, in the west of Ireland, before and at intervals during aquaculture activities. Amongst these samples, allelic variation at a microsatellite marker, tightly linked to a locus critical to immune response (Satr-UBA), was compared with variation at six neutral microsatellite loci. No substantial evidence of the variability of a genetic signal for the immune response genes was observed at neutral microsatellite loci. A significant decline in allelic richness and gene diversity at the Satr-UBA marker locus, which preceded a severe sea trout stock collapse, appears to be associated with aquaculture activities. These data therefore suggest that salmon farming-mediated disease can indirectly affect the genetic structure of sympatric sea trout populations by reducing variability at major histocompatibility genes.

10.11 What is a sea trout population – and how can sea trout populations be affected by reduced marine survival and growth as induced by salmon lice?

Salmon lice may reduce marine survival and growth of individual sea trout, as outlined in the previous chapters. To discuss the outcome of reduced survival and growth in individuals for brown trout as a species and for sea trout populations in particular, it is necessary to outline what is a sea trout population. Much of the following outline derives from thorough reviews by Ferguson (2006), Jonsson & Jonsson (2006b, 2011) and Solomon (2006). From this outline, we discuss the possible outcomes of salmon lice-induced reduced marine survival and growth in terms of effects of brown trout in general, and sea trout populations in particular, in the latter paragraphs of this chapter.

Brown trout populations did not survive the glaciations of the last Ice Age throughout most of north-western Europe (Ferguson 2006). Colonisation by brown trout of these areas following the Ice Age was by sea trout straying from ice-free refuge areas, and non-glaciated regions further south, where populations had survived. In respect of recent evolutionary history, anadromy is therefore the ancestral state of brown trout over much of north-western Europe. For this reason, evolution from sea trout to freshwater brown trout has occurred independently in each watershed within the past 10 000 to 14 000 years. As pointed out by Ferguson (2006), this means that it is difficult to generalise on the relationship among freshwater resident and sea migratory types because freshwater trout have evolved independently in each catchment, and what may apply in one catchment may not be the case in others.

Brown trout populations in river stretches accessible from the sea differ genetically among catchments (Hansen et al. 2002, Hovgaard et al. 2006), which indicates that straying and gene flow among watersheds is limited. Even tributaries within a river system can have genetically different brown trout populations (Hindar et al. 1991). Some of this variability is likely the result of local adaptation to the conditions in specific rivers and tributaries (Hansen et al. 2002, Ferguson 2006, Jonsson & Jonsson 2006b), as has been shown for other salmonids including Atlantic salmon (Garcia de Leaniz et al. 2007). Known straying rates (i.e. the proportion of individuals in a river that originate from other rivers and which successfully breed and contribute to succeeding generations in the new river; Ferguson 2006, Jonsson & Jonsson 2006b) for sea trout approximate to 1-3%. If effective straying rates were higher than a few individuals per generation, the genetic differences that are documented among populations would not exist (Ferguson 2006). It should be noted that a larger number of individuals may stray between rivers, but that all straying does not necessarily result in successful spawning and genetic introgression.

Within populations and rivers, there is little genetic differentiation between sea-migrating and resident individuals (reviewed by Ferguson 2006, Jonsson & Jonsson 2006b, 2011, see also Hindar et al. 1991, Charles et al. 2005, 2006). This reflects that there is significant interbreeding between the two types, and that they usually do not comprise reproductively isolated populations (Ferguson 2006). However, migrant and resident brown trout within rivers can spawn separately, or they may spawn together successfully, and constitute freely interbreeding fractions of a single spawning stock (Jonsson & Jonsson 2006b). The proportion of females undertaking marine migration often is greater than that of males, probably because of the greater advantage to females of a sea migration and a consequential larger body size and fecundity (see Chapter 2). Extensive interbreeding is implicated in rivers where the freshwater trout are almost exclusively males.

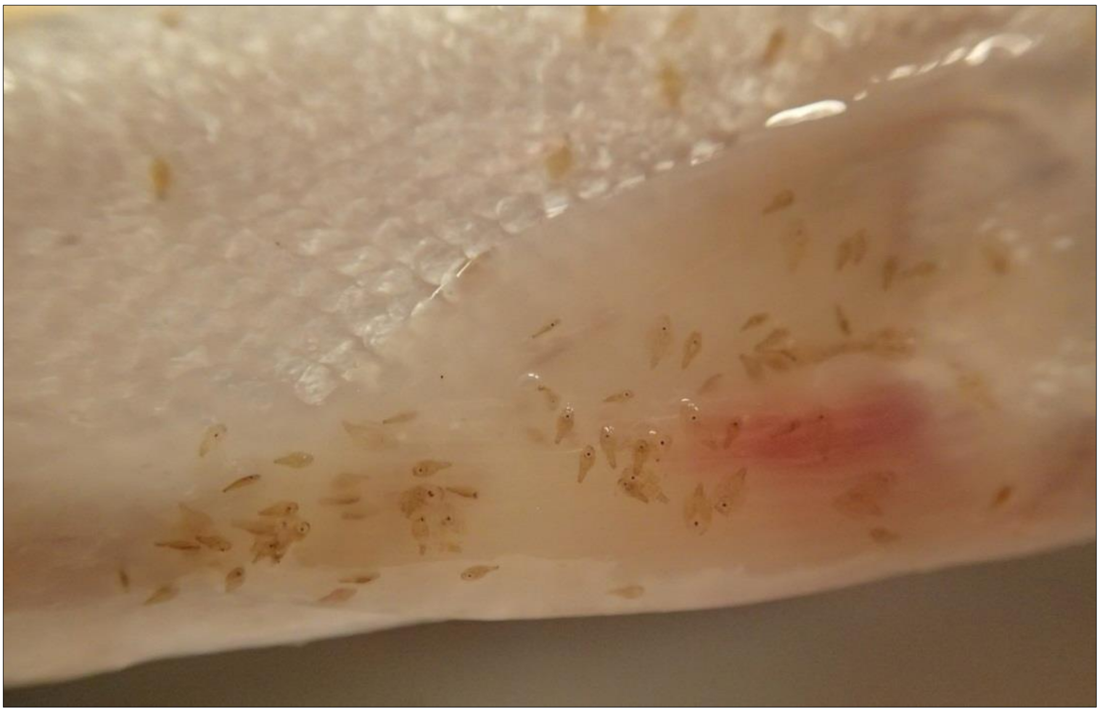
A lack of genetic differentiation between anadromous and resident individuals does not mean that there is no genetic basis for the marine migratory strategy. There is, for example, a genetic basis to the physiological adjustments necessary to allow anadromy and to the behavioural process of migration, and genetic effects also can indirectly influence anadromy (or freshwater residency) manifest as the maturation schedule, energy efficiency and other proximate traits (summarised by Ferguson 2006). Further evidence for a genetic control of migratory behaviour in brown trout includes observations of the loss of anadromy in brown trout populations above impassable waterfalls, distinct sea trout populations showing different migration patterns at sea, and more anadromous offspring being produced from anadromous parents than from freshwater resident adults (summarised by Ferguson 2006). However, there are no estimates of the relative contributions of genetic and environmental influences to the occurrence of anadromy for brown trout (Ferguson 2006).

Ferguson (2006) explained anadromy in brown trout as representing a threshold quantitative trait that is controlled both by multiple genes and by environmental influences, and is expressed such that anadromy occurs when this combination of factors exceeds a threshold level. Anadromy evolves in response to trade-offs between costs and benefits of migration compared with residency, and the costs and benefits are balanced through their effect on fitness (Bohlin et al. 2001, Ferguson 2006, Jonsson & Jonsson 2006b, Solomon 2006). Various combinations of genetic and environmental influences can result in the threshold being exceeded with a low genetic propensity being offset by a high environmental influence and *vice versa* (Ferguson 2006). Hence, the energetic threshold level coding for migration probably differs among populations, and an energetic state triggering migration in one population may result in residency in others (Jonsson & Jonsson 2006b).

In given catchments, the balance of costs and benefits may result in evolution of different life-history strategies (including freshwater residency *versus* anadromy) coexisting within the one system and arising from frequency-dependent selection (Ferguson 2006, Solomon 2006). Frequency-dependent selection refers to a particular strategy that is advantageous only when a proportion of the population participates and the advantage decreases as the frequency of the trait increases. Anadromy also can be inversely density-dependent, but this may be purely environmentally induced, although potentially there could be a genetic component to density where, for example, higher survival is genetically based (Ferguson 2006).

The differential occurrence of freshwater and anadromous forms within and among large catchments, and the stability of related environmental factors over time, suggests that the costs and benefits are in fine balance (Ferguson 2006, Solomon 2006). That sea trout can be present in one river and rare or absent in another, together with the co-occurrence of anadromous and freshwater resident trout in many systems, suggest that the fitness advantage of the two life history strategies is similar, and that there is a knife-edge balance (Ferguson 2006, Solomon 2006). Only relatively minor changes in environmental conditions and/or genes can, therefore, result in a shift in life-history strategy. The likelihood of moderate heritability of anadromy as a trait, together with the higher fecundity of larger sea trout, can result in substantial population changes occurring within perhaps only a few generations. Thus, increases in marine mortality and reduced growth of sea trout induced by salmon lice both can shift the selective balance in favour of the freshwater resident life history.

The widespread occurrence of freshwater resident brown trout populations (Klemetsen et al. 2003) ensures that an impact factor such as salmon lice cannot increase the extinction risk of the brown trout as a species. Anadromy as a trait can remain dormant in a population and only be expressed when environmental conditions change (Ferguson 2006). If so, the phenomenon of sea-migrating trout may not readily be lost even though existing sea trout populations disappear (Gargan et al. 2006b, Kallio-Nyberg et al. 2010). However, reduced sea survival and growth as a result of increased salmon lice infestations in farm intensive areas will likely lead to a decreased frequency of sea run brown trout and a corresponding increase in the frequency of freshwater resident brown trout (as indicated by Gargan et al. 2006b), and can perhaps even result in the loss of sea trout from some watersheds if there is a chronic and appreciable increase in marine mortality. Catchments offering poor environmental conditions for brown trout during some periods of the year (for instance due to drought and/or freezing) will face the greatest risk of losing their brown trout populations. Larger catchments with more suitable year-round conditions for brown trout may not face such a risk, but severe reduction or loss of the sea-run migratory form will result in altered genetic composition of populations (which may be regarded as the effective loss of a sea trout population and its replacement by a freshwater resident population with differing population genetic characteristics), reduced genetic diversity and a greater uniformity in life history characteristics. The loss of the improved growth opportunities offered by the marine environment compared with the freshwater environment will also lead to lower abundance of brown trout, lowered recruitment and loss of the large migratory individuals popular among fishers.



Wild sea trout with chalimus stage salmon lice collected in western Norway.
Photo: Bjørnar Skår

10.12 Concluding statements

- Salmon lice epizootics have been recorded for populations of wild sea trout following the establishment of salmon farms in Ireland, Scotland and Norway and often have been attributed to the proliferation of salmon lice larval production from captive stocks of farmed Atlantic salmon.
- In Ireland there was a marked collapse of several west coast sea trout populations during the late 1980s. Contemporaneous data on salmon lice intensities on marine salmon farms, and on wild sea trout − in addition to observations of the incidence of premature migratory return by sea trout within a population − all have proven to be strongly indicative that salmon lice from marine salmon farms were a significant contributory factor in the observed stock collapses.
- In Scotland, during the late 1980's, unprecedented declines in sea trout rod fisheries were recorded throughout the west coast region. It has been estimated that farm salmon probably were the primary source of salmon lice on salmon and sea trout populations, and that aquaculture facilities comprised the major risk of louse transmission to emigrating wild salmon and sea trout smolts in springtime on the west coast of Scotland.
- Long-term monitoring of sea trout population structure for two west of Ireland catchments documented comprehensively the late 1980s stock collapse and the significant change in sea trout population structure which could be linked to salmon lice infestation.
- The 1989 spawning stock collapse of sea trout in western Ireland significantly reduced both the total number of ova deposited and subsequent levels of recruitment to the populations.
- In the Irish Burrishoole system, prior to the onset of marine salmon aquaculture, the percentage of smolts that survived to return as 0+ sea age finnock in the same calendar year ranged from 11.4 to 32.4% with a historical mean of 21%. In 1988, marine survival fell to 8.5%, and in 1989 to an all-time low of 1.5%. The mean for the 1990s, excluding 1999, was 6.8%, which was three times lower than the historical average. Salmon lice emanating from sea farms were implicated in this additional mortality.
- In Scotland, during the late 1980's, unprecedented declines in sea trout rod fisheries were recorded throughout the west coast region. It is along the western coasts of mainland Scotland that the salmon aquaculture industry is concentrated.
- For a western Scotland sea loch, a recent study showed there was a significant and fluctuating relationship between salmon farm production cycle year (i.e. the likely salmon lice infestation pressure) and the incidence of sea trout with parasite burdens exceeding the stress threshold level.
- For the river Ewe/Loch Maree system in Wester Ross, Scotland there was an apparently unprecedented reduction in sea trout marine growth and survival during the late 1980s, which was reflected in marked shifts in the population structure before and after the collapse. Between 1980 and 1997-2001, maximum sea age of mature sea trout fell from 11 to 5 years.
- The effects of the west Scotland collapse of sea trout stocks and reduced longevity/maximum size of fish were manifest in a published estimate which showed that the potential lifetime egg deposition of a typical female sea trout decreased from 30,000 in 1980 to 6,000 in 1993.
- The east coast of Scotland has essentially remained non-impacted by commercial salmon farming throughout the history of the industry, and sea trout stock structure remained stable over the same period that the west coast collapses were reported.
- In Norway, high proportions (up to 47%) of sea trout within populations of sea trout exploiting marine waters subject to salmon farming have been recorded as bearing salmon lice at intensities above the level that has been shown to induce mortality in

laboratory experiments. Similarly in western Ireland, an estimated 31% of sea trout sampled in aquaculture bays carried potentially lethal louse burdens.

- In recent years, there have been numerous large-scale, experimental studies to assess the mortality impact of salmon lice on out-migrating Atlantic salmon smolts. These experiments, both in Norway and Ireland, have concerned the tagging and release of large groups of chemically treated and control groups of untreated fish. Recapture of tagged fish following their completion of marine migration and return to freshwater to spawn has permitted the statistical analysis of the effects of salmon louse infestation on salmon return.
- The overall pattern is one of a significant treatment effect with greater survival of treated fish. The scale of effect will depend on a range of factors including the location and size of farms, levels of larval salmon lice production during the salmonid smolt migration, wind-driven lice dispersal, and freshwater influences.
- It is important to note that all experimental releases of salmon smolts in assessing salmon louse impacts involve the use of hatchery-reared smolts. These typically are larger than wild smolts and hatchery-reared smolts generally have lower overall marine survivorship. Nevertheless, the estimated average risk ratio of protected fish returning to their natal rivers to spawn compared to unprotected fish range from 1.14-1.41:1. Meta-analyses and long-term studies, and similar results from an increasing number of experimental studies, support that these are levels of extra mortality (i.e., 12-44% fewer adult spawners) that can be expected for Atlantic salmon populations in farm-intensive areas.
- Atlantic salmon smolts typically migrate quickly away from inshore waters to the outer coast and open ocean. Sea trout typically spend their entire marine residence in near-shore waters and therefore are likely to be exposed to higher levels of infective larval salmon lice over a prolonged time period than are Atlantic salmon.
- Chemical treatment and release studies to investigate the effects of salmon lice on survival and return of sea trout are few in number compared to those undertaken with Atlantic salmon smolts. One such study assessed the survival rate of chemically protected smolts and un-treated controls and the results showed respectively 3.41% and 1.76% returns, with a significantly higher recapture rate for treated smolts. These findings suggest that salmon lice infestation in local fjordic waters can be an important contributor to the high mortality of anadromous trout. That study was the first to present quantitative empirical evidence of impacts attributable to salmon lice infestation at the population level for sea trout.
- Premature migratory return may be an adaptive strategy adopted by the fish in response to heavy infestations of salmon lice, which may induce stress and osmoregulatory dysfunction, or even death of the fish. Return to freshwater is viewed as being potentially adaptive because the parasite cannot survive hyposaline conditions. None the less, premature migratory return does comprise an energetic cost to the host fish, as a result of the reduced feeding and growth opportunities at sea. This cost also may be manifest in reduced future fecundity and spawning success.
- Studies in Ireland, Scotland and Norway have recorded premature migratory return and reductions in marine growth of sea trout related to high salmon lice levels. These results converge on salmon lice infestations of post-smolt and adult sea trout having the potential to exert clearly definable impacts on sea trout populations, manifest as changes in individual marine migration timing and behaviour, growth and survivorship. The overall effects are measurable as declines in sea trout abundance, changes in size and age distributions, and in total egg deposition.
- In western Scotland, following the late 1980s stock collapses, several studies affirmed an increase in the proportion of trout residing permanently in freshwater following the collapse. Such a shift in demography and migratory behaviour may be explicable by an overall reduction of trout abundance (and thereby competition) in

freshwater, perhaps mediating against the growth advantage of temporary migration to sea.
- Genetic data suggest that salmon farming-mediated disease can indirectly affect the genetic structure of sympatric sea trout populations by reducing their variability at major histocompatibility genes.
- The evolution and maintenance of anadromy *versus* freshwater residency within populations of trout is complex and likely influenced by the interaction of genetic and environmental factors.
- If individual trout of the anadromous strategy have very low marine survival, there may be selection in favour of those individuals with a higher genetic propensity for freshwater residence.
- Within populations and rivers, there is little genetic differentiation between sea-migrating and resident individuals. This reflects that there is significant interbreeding between the two types, and that they usually do not comprise reproductively isolated populations. However, migrant and resident brown trout within rivers can spawn separately, or they may spawn together successfully, and constitute freely interbreeding fractions of a single spawning stock.
- In given catchments, the balance of costs and benefits may result in evolution of different life-history strategies (including freshwater residency *versus* anadromy) coexisting within the one system and arising from frequency-dependent selection.
- The widespread occurrence of freshwater resident brown trout populations ensures that an impact factor such as salmon lice cannot increase the extinction risk of the brown trout as a species. However, reduced sea survival and growth as a result of increased salmon lice levels in farm intensive areas will likely lead to a decreased frequency of sea run brown trout and a corresponding increase in the frequency of freshwater resident brown trout, and can perhaps even result in the loss of sea trout from some watersheds if there is a chronic and appreciable increase in marine mortality.

10.13 Knowledge gaps

- More detailed, comprehensive and consistently acquired monitoring data of salmon lice levels on wild sea trout populations is required. Such data would facilitate more inclusive analyses of the various factors likely to contribute to the variation in salmon lice levels noted for areas impacted by fish farms.
- The most important knowledge gaps are related to effects at the population level and in quantifying the reduction in wild sea trout populations as a result of increased mortality and reduced growth of individual fish caused by salmon lice in fish farming areas.
- The effects of salmon lice on life history traits – especially trout age and size at maturation – and selection against anadromous behaviour in favour of permanent freshwater residence also are not well understood.
- For robust and informed evaluation of the effects of salmon lice on sea trout populations, more field experiments comparing recapture rates and growth of fish released to the environment following prophylactic treatment against salmon lice should be undertaken. These experimental releases need to be of large numbers of fish, with suitable control (un-treated) groups released in parallel, and experiments should be repeated across multiple rivers and years in order to account for temporal and spatial environmental variation. Ideally, these release experiments would include quality-control checks of uptake of the prophylactic chemical treatment by the experimental fish, and of the osmoregulatory status of fish at release. The latter data are of especial importance in instances where percent survivorship at the cohort or population level is a specific research objective.

- Individual-based, and dynamic state-variable, models offer powerful and informative means of obtaining clear insights relating to the effects of salmon lice on sea trout populations and the expression of variation in life history traits. In order to effectively pursue that modeling strategy, there is a need for concerted efforts to parameterize these models with suitably comprehensive empirical data, both from field and laboratory studies.
- In contrast to Atlantic salmon, wild sea trout populations generally have been rather poorly studied, monitored and mapped, although there is variation in this respect among watersheds, regions and countries. Even the status of sea trout populations and a basic understanding of putative anthropogenic factors potentially impacting them are not well known for many watersheds.
- With specific regard to the marine environment, the behaviour and survival of sea trout is less well understood than for many other salmonid species. More information is required on sea trout marine migration and foraging areas, relative to marine salmon aquaculture. The migration distance of sea trout at sea from home rivers is poorly understood and more information is required to be able to assess the potential impact of salmon lice from marine salmon aquaculture on sea trout stocks from rivers close to any more distant from such installations. This information is critical in assessing whether sea trout from rivers remote from salmon farms undertake migrations which may bring them under the influence of salmon lice produced by farms. Such information is essential when interpreting salmon lice monitoring data on farmed and wild fish, in evaluating the likely efficacy of any adopted mitigation measures and permitting the formulation of appropriate and relevant scientific advice on possible mitigation measures.

11 Sea trout as proxy indicator of salmon lice levels in Atlantic salmon

In order to monitor salmon lice levels of outward-migrating Atlantic salmon, the post-smolts ideally need to be captured in outer coastal areas for registration of salmon lice levels attained during their migration through any farm-intensive areas. Trawls have been used to sample Atlantic salmon post-smolts, but catches have been low (e.g. Bjørn et al. 2007, Serra-Llinares et al. 2014), which may be expected when considering the large areas and water volumes in which a relatively low number of post-smolts can spread. The capture of wild sea trout often is less labour-intensive than is the case for Atlantic salmon post-smolts, and capturing sea trout often can be achieved by using smaller boats. Hence, capturing sea trout is less expensive than capturing Atlantic salmon. Salmon lice levels on sea trout can potentially therefore be used as a proxy indicator of salmon lice levels in Atlantic salmon. Such is the case with the scientific advice given to management authorities in Norway (Taranger et al. 2012, Serra-Llinares et al. 2014) although this approach has not been extended to Scotland. The annual monitoring of lice levels on prematurely returned sea trout in rivers entering salmon farming bays in western Ireland informs management regarding the potential impact of salmon lice from farm sources on out-migrating wild salmon smolts.

In this chapter, we outline and discuss how effectively the recorded salmon lice levels on sea trout captured along the coast may reflect the salmon lice levels and pressures for Atlantic salmon post-smolts during their initial outward ocean migration. To use sea trout as a proxy for salmon lice in Atlantic salmon, it is important to consider whether the two species have the same affinity for salmon lice, with regard to possible host species differences in vulnerability to salmon lice, the size of the monitored fish, their timing of migration, duration of exposure to salmon lice, and host behaviour and habitat use in the sea prior to capture. The following questions are therefore considered in this chapter:

1. Are immune responses against salmon lice similar in Atlantic salmon and sea trout?
2. Does the difference in body size of Atlantic salmon (smaller) and sea trout (larger) post-smolts affect their salmon lice levels?
3. Do Atlantic salmon and sea trout emigrate from rivers and enter the sea at the same time?
4. Do Atlantic salmon and sea trout differ in swim speeds through coastal waters?
5. Might differences in horizontal habitat use (e.g. open waters *versus* littoral shorelines) between Atlantic salmon and sea trout post-smolts affect their salmon lice levels?
6. Might differences in vertical habitat use (influenced by depth and salinity) between Atlantic salmon and sea trout affect their salmon lice levels?
7. Do salmon lice levels on sea trout at monitoring sites reflect the lice levels on Atlantic salmon in terms of migratory progression rates from the river mouth and the duration of exposure time?

11.1 Are immune responses against salmon lice similar in Atlantic salmon and sea trout?

The susceptibility of a fish to salmon lice determines the relative numbers of parasites successfully establishing on the fish (MacKinnon 1998). Host susceptibility is determined by numerous interactive factors, including host stress level, nutritional status and immune responses, all of which have a genetically determined component (MacKinnon 1998). Different salmonid species vary in their susceptibility to salmon lice (Johnson & Albright 1992, MacKinnon 1998). Immune responses to salmon lice occur in some salmonid species, and the fish may therefore reject the majority of salmon lice before the parasites develop to the mobile preadult stages (Wagner et al. 2008). Atlantic salmon apparently are more susceptible to salmon lice than are Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) (Johnson & Albright 1992). Coho salmon were initially infested at similar salmon lice densities as Atlantic salmon (Fast et al. 2002), but salmon lice rapidly reduced in numbers within 10-14 days (Johnson & Albright 1992). Coho salmon produced a cell-based immune reaction, which killed many attached chalimus larvae, rendering these fish relatively more resistant to salmon lice than the two other tested host species (Johnson & Albright 1992). It also has been shown that salmon lice themselves may react differently towards mucus from the different salmonid species, and it was suggested that the resistance of coho salmon to salmon lice may be attributable to agents in their mucus (Fast et al. 2003). Wagner et al. (2008) concluded in a review that there is little evidence of a host tissue response in Atlantic salmon at the body surface sites where salmon lice attach and feed, regardless of developmental stage, and the inflammatory response seen in coho salmon appears to be the primary mechanism by which most salmon lice are rejected by that species within the first week of exposure.

Atlantic salmon and sea trout belong to the same genus (*Salmo*), and are more closely related than Atlantic salmon are to the Pacific salmonids (genus *Oncorhynchus*) referred to above. Based on a study of the development of salmon lice on sea trout post-smolts, Bjørn & Finstad (1997) concluded that salmon lice seem to have developmental rates, host distribution, and pathogenicity on sea trout post-smolts similar to those recorded for Atlantic salmon. Sea trout did not appear any more or less susceptible to salmon lice, and the results indicated no major differences in louse-rejection mechanisms. However, they undertook no experiments comparing the two species directly and based their conclusion on a comparison of their independent results for sea trout with previously published studies on Atlantic salmon.

Few studies have directly compared the resistance to salmon lice of Atlantic salmon and sea trout. However, Dawson et al. (1997) investigated the relative susceptibility of Atlantic salmon and sea trout to salmon lice in the laboratory using hatchery-reared fish. For the first two weeks post--exposure, the mean number of chalimus was significantly higher on sea trout than Atlantic salmon, which suggested that there was a reduced settlement or survival of copepodids and chalimus on Atlantic salmon. When the experiments ended, significantly more salmon lice were found on sea trout than on Atlantic salmon. There was no difference in the developmental stages of the salmon lice and no difference in morphological damage from the lice between the two species during the experiment. Dawson et al. (1997) discussed whether salmon lice reared on one species might prefer to settle on that same species after the free-living stages. They dismissed this as an explanation for the higher lice settlement on sea trout than Atlantic salmon in their study, because copepodids reared for the experiment were hatched from eggs of salmon lice taken from farmed Atlantic salmon. Dawson et al. (1997) therefore concluded that either there may be a differential host specificity of *L. salmonis* for sea trout rather than Atlantic salmon, or that Atlantic salmon may have evolved a more effective immunological strategy in response to salmon lice.

Glover et al. (2003) found that farmed Atlantic salmon displayed a higher abundance and density of salmon lice than did sea trout, which contrasted the results of Dawson et al. (1997) referred to above. However, salmon lice levels − and also the development rate of salmon lice on the host fish − may differ among sea trout populations (Glover et al. 2003), and this alone may explain the contrasting results among studies. Glover et al. (2003) suggested that differences in salmon lice level among sea trout stocks may reflect genetic differences, and that the stock with the lowest levels and slowest developmental rate was that which may have been exposed to more frequent and more intensive salmon lice levels than the other stocks included in their experiment. They could not determine whether differences among stocks were due to differences in settlement of lice, differences in lice mortality after settlement, or both. Within stocks, there were no differences in salmon lice levels between mature and immature fish, or between genders. For the Atlantic salmon included in the experiment, there was no difference in salmon lice level between anal fin-clipped and non-clipped individuals. In an earlier study, fish from a land-locked brown trout stock that had not been exposed to salmon lice in its natural habitat, displayed a higher salmon lice level than did trout from an anadromous stock with a history of salmon lice infestation (Glover et al. 2001). With regard to wild Atlantic salmon populations, these also may differ (genetically) in their susceptibility to salmon lice (Glover et al. 2004).

Whether or not resistance to salmon lice can develop in veteran migrant sea trout (that had been infested by salmon lice in previous years), or in sea trout that had been de-loused by premature migratory return to freshwater, has yet to be studied. If previously-infested fish can develop an immune response to new exposures, sampling of veteran migrants or prematurely returned fish may influence the results of a monitoring programme regarding local infestation levels.

Salmon lice display no significant differences, or only weak population genetic variation throughout the North Atlantic Ocean; there is no evidence of isolation of genetically different populations on farmed hosts and different wild host species (Todd et al. 2004, Todd 2007, Glover et al. 2011). Hence, differences in salmon lice levels between Atlantic salmon and sea trout due to genetic differentiation among salmon lice themselves are not expected.

In summary, studies of immune responses in sea trout, and studies comparing immune response differences between Atlantic salmon and sea trout, are few. The existing studies have provided contrasting results regarding the affinity of salmon lice to Atlantic salmon and sea trout. One reason for this may be that sea trout differ between populations in their immune responses. The physiological and pathological responses to salmon lice, as outlined in chapter 6 and 7, seem generally very comparable for the two species.

Wild sea trout (upper) and Atlantic salmon (lower) smolt captured in trap during downstream migration in the River Eira in Middle Norway.
Photo: Eva B. Thorstad

11.2 Does the difference in body size of Atlantic salmon and sea trout post-smolts affect salmon lice levels?

Fish body size has been shown to influence salmon lice levels in salmonids, with the number of lice on a fish tending to increase with fish size (Jaworski & Holm 1992, Tucker et al. 2002, Genna et al. 2005, Todd et al. 2006). Bigger fish have a larger body surface area potentially available to salmon lice. Because surface area increases approximately as the square of fish length, the number of lice should increase at a higher rate than as a proportion of fish length (Jaworski & Holm 1992). Jaworski & Holm (1992) therefore suggested expressing salmon lice intensity as number of lice per unit total body surface, but comparative studies may be complicated by measurable differences in length/weight allometry of fish from differing populations.

Body size and shape (= length/weight relationship) of both sea trout and Atlantic salmon smolts may vary considerably within and among watersheds. Sea trout smolts have been reported to range in mean body length between 10.7 cm and 25.2 cm among 102 European populations (Jonsson & L'Abée-Lund 1993). The mean size of Atlantic salmon smolts may vary between 10 and 20 cm, with individual minimum and maximum values ranging between 7 and 30 cm (Thorstad et al. 2011). Went (1962) suggested that it is common for British and Irish sea trout smolts to be consistently larger than Atlantic salmon smolts. British sea trout display smolt sizes commonly ranging between 15 and 23 cm (Fahy 1978). In Irish rivers, smolt size was similarly reported as averaging 17-25 cm (Went 1962).

In two north Norwegian rivers, sea trout smolts also were larger than sympatric Atlantic salmon smolts (Berg & Jonsson 1989, Jensen et al. 2012a). In the Vardenes River, mean size of sea trout smolts was 18.7 cm, with Atlantic salmon smolts averaging 13.7 cm. In the River Halselva, the mean size of sea trout smolts was 19.5 cm, whereas Atlantic salmon smolts averaged 14.3 cm (Jensen et al. 2012a). Within Norway, population means for sea trout have been shown to vary between 10.7 and 22.6 cm (individuals from 6 to 32 cm), and mean smolt size increased with latitude but decreased with increasing adjacent sea temperature (L'Abée-Lund et al. 1989). Population means for Atlantic salmon within Norway varied between 11.5 and 16.2 cm (summarized in a technical report by Ugedal et al. 2014): mean smolt size generally was largest in the southern and northern regions of the country, with the smallest being recorded along the west coast and in central Norway (Ugedal et al. 2014). Atlantic salmon juveniles rearing in lakes may undergo smoltification at a larger size than those rearing in rivers (Klemetsen et al. 2003).

Tucker et al. (2002) compared groups of Atlantic salmon of average body masses of 43, 173 and 644 g under similar salmon lice exposure. They found that the largest fish were infested with the highest absolute number of salmon lice, likely due to their larger surface area, but that the smallest fish had the highest density of salmon lice in terms of surface area. Surface area correlated well with body length ($r^2 = 0.93$, linear analysis), but even better with body mass ($r^2 = 0.99$). Tucker et al. (2002) explained the higher density in the smaller fish as a consequence of the greater surface area of the fins relative to the total body surface area in the small fish. The fin area comprised 33% of the total area for the small group, 26% for the intermediate group and 23% for the large group. More than 65% of the lice settlement occurred on the fins in all size groups.

In summary, sea trout smolts typically are larger than Atlantic salmon smolts, but this may vary within and among catchments and geographic regions. Sea trout and Atlantic salmon also have different body shapes. It is likely that when comparing sea trout and Atlantic salmon post-smolts of similar body length, the body surface area of sea trout is the greater. However, the fin area of Atlantic salmon may be larger and this might influence settlement of salmon lice. If sea trout post-smolts captured for monitoring salmon lice are larger than the outward-migrating Atlantic salmon that they are intended to represent, they may have higher absolute numbers of salmon lice and lower densities per unit surface area. This also is the case when older and larger sea trout are sampled for monitoring purposes.

11.3 Do Atlantic salmon and sea trout emigrate from rivers and enter the sea at the same time?

The salmon lice levels in coastal waters often is lowest during the winter months, and increases during spring and summer (Bjørn & Finstad 2002, Bjørn et al. 2007, 2011). Chalimus larvae dominate on host fish sampled in early in summer and spring, and preadult and adult stages of salmon lice develop in late summer and autumn (MacKenzie et al. 1998, Bjørn et al. 2001, 2007, 2011), unless the salmon lice levels are very high in which case chalimus stages can dominate throughout the entire season (Sharp et al. 1994, Bjørn et al. 2001, Butler 2002, Gargan et al. 2003). Hence, the salmon lice levels on wild Atlantic salmon post-smolts and sea trout depend on the timing of sea entry.

With few exceptions, smolt migration of Atlantic salmon takes place during the spring and early summer (Thorstad et al. 2012). In general, the smolt migration in Norway extends over a three to seven-week period during April to July, with the earliest timing in southern populations. However, the majority of individuals in an annual cohort may migrate within a relatively short time period (1-2 weeks). It is believed that Atlantic salmon smolts use environmental cues in the rivers that may predict favourable ocean conditions to initiate downstream migration (Hvidsten et al. 1998, 2009). For example, smolts from Norwegian rivers enter the sea at different times of the season, but even though downriver migration is triggered by different environmental factors, the different populations appear to be adapted to enter the sea when a certain sea temperature is reached (Hvidsten et al. 1998, 2009). This implies that smolts from southern populations migrate earlier than smolts from northern populations, where the sea temperature reaches the preferable levels later in the season. Preference for specific ocean temperatures could be explained by increased smolt mortality due to low salinity tolerance at low sea temperatures (Sigholt & Finstad 1990). Increased survival at higher temperatures may also be linked to match–mismatch scenarios concerning increased prey availability and differential growth-mediated survival (Rikardsen & Dempson 2011), perhaps in combination with increased swimming performance that enhances predator avoidance at higher temperatures (Hvidsten et al. 2009). Hence, the timing of the Atlantic salmon smolt run may be adapted through natural selection to meet the most optimal environmental conditions in the sea.

Sea trout smolts typically migrate downriver to the sea in spring or early summer, and generally from February to June (see chapter 2.2.3). The timing of the smolt run may also be adapted through natural selection, similar to Atlantic salmon, to meet the most optimal environmental conditions at sea. However, there are few appropriate studies of sea trout at this particular life stage (chapter 2.2.3). Similar to Atlantic salmon, sea trout smolts from southern populations tend to migrate earlier than smolts from more northern populations (chapter 2.2.3).

In a river with sympatric populations both of Atlantic salmon and sea trout, considerable overlap in the smolt migration timing between Atlantic salmon and sea trout has been shown, although the Atlantic salmon smolts tended to migrate earlier than did sea trout smolts (median migration date 22 June vs. 4 July, Jensen et al. 2012a). The main migration period − expressed as the number of days between the 25% and 75% quartiles of smolts leaving the river − lasted on average 25 days for Atlantic salmon and 28 days for brown trout (Jensen et al. 2012a). There was substantial annual variation in median migration date among years, but the interannual variation in median migration time was significantly positively correlated between the species: in years with early descent of Atlantic salmon, the sea trout also migrated early. Water flow was included in the model to explain day-to-day variations in smolt runs for both species; water flow was the more important for Atlantic salmon whereas changes in water flow were more important for sea trout (Jensen et al. 2012a). For trout, water temperature also was included in the model. This, in combination with a more dispersed and longer migration period for trout, provided evidence that the parr-smolt transformation in sea trout occurred in a less punctual manner than in Atlantic salmon (Jensen et al. 2012a).

There are only few comparative studies of the smolt migration timing in Atlantic salmon and sea trout. In a technical report, Ugedal et al. (2014) summarized data on smolt migration dates from a number of other technical reports and concluded that the timing of smolt migration of Atlantic salmon and sea trout was similar in the studied catchments. However, in some cases there was a difference in timing between the species, with both earlier and later migration timing for sea trout, although in most cases trout migrated later.

For some catchments, a more dispersed and protracted migration period has been recorded for sea trout (Jensen et al. 2012a, Byrne et al. 2004, Jonsson & Jonsson 2009b). However, whether the migration is dispersed over a longer time period, or more concentrated during a 1-2 week period (Hembre et al. 2001) as for Atlantic salmon, may also differ among catchments. Larger sea trout smolts have been shown to tend to migrate earlier in the season than do smaller smolts (Bohlin et al. 1993, Gargan et al. 2006a, Jensen et al. 2012a).

In summary, the timing of Atlantic salmon and sea trout smolt migration appears similar within catchments, but might also differ in some locations. There is little information on timing of smolt migration in many catchments, and in variation of that timing among years. For monitoring of salmon lice infestation risk, and for using salmon lice levels of sea trout as a proxy for levels in Atlantic salmon, information on how long the post-smolts have been at sea and potentially exposed to salmon lice is important.

Older and larger sea trout show greater variation in marine habitat use, and in some locations they may reside in the marine environment throughout the winter or perhaps have only recently entered the sea (see chapter 2). It should therefore be acknowledged when using these individuals in salmon lice monitoring that they may reflect the integration of salmon lice levels over very different time-periods. The young stages of salmon lice on older and larger individual hosts will likely reflect the recent salmon lice levels in areas where these fish have resided.

11.4 Do Atlantic salmon and sea trout differ in swim speeds through coastal waters?

Bron et al. (1991) suggested that copepodid attraction to a fish is stimulated by rheotaxis, and therefore that swimming speed of the fish may play an important part in host infection. The ability of salmon lice to attach to a fish may be affected by local current speed around the fish (Bron et al. 1991). Hence, fish swimming speed *per se* may influence the salmon lice level on a given individual host.

Heuch & Karlsen (1997) showed that salmon lice copepodids responded to uniform linear accelerations, similar to those found in front of a swimming fish, and suggested that copepodids react to near-field accelerations produced within centimetres of a swimming fish by high-speed burst swimming and subsequent encounter and attachment to the host. Genna et al. (2005) suggested that the burst swimming response is likely to aid host attachment by increasing the chance of a copepodid physically encountering a host, or entering and remaining in the fish boundary layer, which is the region of reduced current flow and negligible current shear that exists around the host body. Copepodids may utilise the host boundary layer to facilitate presettlement behaviour on the host surface, and therefore boundary layer dynamics will influence the distribution of presettled copepodids. The boundary is thicker at lower swimming speeds, and low swimming speeds may therefore facilitate copepodid presettlement. In accordance with this, Genna et al. (2005) found the greatest salmon lice presettlement at slow host swimming speed (0.2 cm s^{-1}), and some presettlement at intermediate swimming speed (7.0 cm s^{-1}), but very little at a relatively high swimming speed (15.0 cm s^{-1}).

Atlantic salmon post-smolts appear to have a more deterministic and directed outward migration and faster progression rate through near-shore waters than do sea trout post-smolts (Thorstad et al. 2004, Sivertsgård et al. 2007, Aarestrup et al. 2014). However, a difference in the progression of outward movement from the river mouth may not necessarily imply differences in the swim speeds through the water column. Sea trout were, for example, shown to display movements in more random directions than did Atlantic salmon after entering the sea, and this will contribute to a slower linear progression rate (Thorstad et al. 2007).

When recording swim speeds relative to the ground, swim speeds are not corrected for the speed and direction of the water current; without so doing, the true swim speed through the water column is not known. Thorstad et al. (2004) therefore simultaneously recorded swim speeds of wild sea trout post-smolts (18-25 cm total length) and water currents. Mean swim speed through the water column was 0.68 body lengths s^{-1} (individual means from 0.48-1.11 body lengths s^{-1}). Similar recordings for hatchery-reared Atlantic salmon (23-30 cm total body length) showed mean swim speeds through the water column of 1.32 body lengths s^{-1} (individual means from 1.10-1.79 body lengths s^{-1}) (Thorstad et al. 2004). Recordings for wild Atlantic salmon (13-20 cm total body length) showed mean swim speeds of 1.17 body lengths s^{-1} (individual means from 0.33-1.89 body lengths s^{-1}, Økland et al. 2006).

The studies referred to above indicate that Atlantic salmon post-smolts may have faster swim speeds through the water column than do sea trout post-smolts, and this may affect the encounter probabilities for individual parasites and the ability of salmon lice to attach to the fish. However, these telemetry studies necessarily have included only few individual fish at only one study site. Larger sea trout can be expected to have higher maximum speeds than Atlantic salmon post-smolts due to their larger body size. Little is known of the swim speeds actually displayed by large sea trout in the marine environment and, although they may be able to obtain higher maximum speeds than Atlantic salmon post-smolts, the swim speeds most frequently observed may be the more important regarding salmon lice levels and estimates of exposure risk.

11.5 Might differences in horizontal habitat use between Atlantic salmon and sea trout post-smolts affect their salmon lice levels?

According to model predictions, the majority of salmon lice originating from a fish farm will remain relatively close to that source, but not necessarily with the highest abundance in the source area (Amundrud & Murray 2009, Asplin et al. 2014). How salmon lice larvae are dispersed from their source depends on multiple variables (see chapter 9). Aggregation of larvae may occur in certain areas, typically close to land and in embayments, according both to model predictions and field sampling of salmon lice larvae (Penston et al. 2004, Amundrud & Murray 2009, Asplin et al. 2014). If this is indeed the case, salmon lice levels on individual fish may depend on the horizontal area over which those fish actually ranged. Furthermore, if fish farms are located close to the littoral zone, this also may cause a generally higher concentration of salmon lice larvae in these habitats.

Sea trout in coastal areas exploit a range of habitats, and may reside in estuaries, at sea in full-salinity seawater, or may move repeatedly between estuaries and adjacent marine areas (e.g. Finstad et al. 2005, Pemberton 1976b, Middlemas et al. 2009, Jensen & Rikardsen 2012, Davidsen et al. 2014). Within fjords, sea trout post-smolts appear to exert a preference to remain close to shore rather than exploiting more open pelagic waters within the mid-fjord areas (Thorstad et al. 2004, 2007, Jensen et al. 2014). Mean distance to shore for post-smolts in a fjord and immediately following their entry to the marine environment was 125 m (Thorstad et al. 2004). Similarly, sea trout in Scottish sea lochs were captured largely within 200 m of the shore (Pemberton 1976b). In a study in northern Norway, results indicated that sea trout resided primarily within the inner and warmer parts of the fjord during the summer months, in contrast to Arctic char that moved to the colder outer areas (Rikardsen et al. 2007, Jensen et al. 2014).

A tendency for Atlantic salmon post-smolts to migrate along the shoreline has been reported in some studies (Lacroix et al. 2004). In other studies, post-smolts were found in the middle of embayments as well as closer to the shore (Thorstad et al. 2007, Davidsen et al. 2009, Kocik et al. 2009). Thorstad et al. (2007) concluded that Atlantic salmon post-smolts migrated in the middle of the fjord as well as closer to the shore, albeit with large individual variation. However, the results indicated that there were some patterns or consistencies in fjord migration routes, with more fish being recorded to one side of the fjord than the other. It is not known whether this reflected environmental patterns (such as currents) in the fjord system. For returning adult Atlantic salmon it has been shown that their horizontal distribution in fjord habitats can be affected by wind-induced spreading of river water across the fjord (Davidsen et al. 2013). There are few comparative studies of migration patterns of sea trout and Atlantic salmon in the same areas at the same time. None the less, from the comparative study by Thorstad et al. (2007), it was shown that Atlantic salmon post-smolts were distributed both along shores and in the middle of the fjord, whilst simultaneously recorded sea trout post-smolts were primarily recorded closer to the shore.

Bjørn et al. (2011) indicated that the infective salmon louse stages were distributed both in the pelagic and littoral areas of a Norwegian fjord, and that both Atlantic salmon and sea trout post-smolts were at risk of exposure to copepodids. However, at some localities, they did find differences in salmon lice levels for fish held in sentinel cages located in near-shore and pelagic areas.

If salmon lice larvae are unevenly aggregated horizontally in coastal areas − perhaps in response to current patterns, freshwater outfalls and other environmental parameters − a difference in horizontal habitat use between Atlantic salmon and sea trout may lead to different salmon lice levels between the two species. A higher salmon lice larval level in littoral areas may lead to higher burdens on sea trout than for Atlantic salmon, if sea trout use these areas more frequently. However, both salmon lice distribution patterns and fish migration routes can be complex, variable in time and vary among different coastal areas. It is therefore not obvious to what extent the differences in horizontal movement patterns may affect salmon lice levels on post-smolt Atlantic salmon and sea trout.

11.6 Might differences in vertical habitat use between Atlantic salmon and sea trout affect their salmon lice levels?

The copepodid is the infective stage of salmon lice, and these larvae appear to concentrate near the water surface, within the top 3 m of the water column during daytime, and to spread slightly deeper during the night (Heuch 1995, Heuch et al. 1995, Hevrøy et al. 2003, **box 4**). Hence, a fish swimming near the surface will be more vulnerable to being infested with salmon lice than those staying in deeper water. However, in near coastal areas with a surface freshwater layer due to snow melt and/or high river discharges in the spring, copepodids may be found deeper in the water column where the water is more saline, and therefore provide them with more suitable conditions (**box 4**). In such a case, a fish swimming near the surface will be less vulnerable to salmon lice than one residing on deeper water. Irrespective of these differences, the salmon lice exposure will be influenced by depth use of the host fish.

Atlantic salmon post-smolts usually swim close to the surface (1-3 m depth) during the early phase of the marine migration, but may make dives down to at least 6.5 m depth (LaBar et al. 1978, Davidsen et al. 2008, Plantalech Manel-la et al. 2009). They have been shown to swim closer to the surface (0–0.5 m) at night than during the day (McCleave 1978, Reddin et al. 2006, Davidsen et al. 2008). Various factors such as predation risk (avian predators from above and fish predators from below), orientation mechanisms and feeding may alone − or in combination − affect depth choice in marine environments (Thorstad et al. 2012). Atlantic salmon smolts may also prefer to swim at depths providing the most efficient energy use, either for locomotion or fundamental metabolic and physiological processes. For example, in a cold Norwegian fjord (7-12°C), the migrating smolts appeared to choose the warmest water layer available (Plantalech Manel-la et al. 2009). In that fjord, with a thin freshwater layer near the surface, the smolts did not show a preference for specific salinity and were frequently recorded to alternate between layers of different salinities, with a mean salinity of 19 at the migration depth (Plantalech Manel-la et al. 2009). In sum, the vertical distribution of Atlantic salmon post-smolts may be a trade-off between the combined benefits and disadvantages of the different depth layers and their characteristics (Thorstad et al. 2012).

Sea trout post-smolts have, like Atlantic salmon, been recorded in the upper 1-3 m of the water column, with a few individuals showing daily mean depths down to 4-5 m (Gjelland et al. 2014). Similar results have been recorded for large sea trout (body lengths 37-65 cm), which were shown to remain primarily in the upper 1-3 m (Rikardsen et al. 2007) or upper 5 m (Sturlaugsson & Johannsson 1996, technical report) of the water column, but with short dives down to depths of 26-28 m. Sea trout carrying salmon lice seemed to stay slightly closer to the surface (Gjelland et al. 2014). Rikardsen et al. (2007) compared depth use between day and night, and found some variation with a tendency for fish to stay deeper during the day; but this study was performed under Arctic conditions in summer, with little difference in light between day and night. There are very few studies of the depth use of sea trout in the marine environment.

In summary, both Atlantic salmon and sea trout generally swim in the upper part of the water column, where salmon lice copepodids also are gathered. The vertical movement between day and night seems to be in opposite directions for Atlantic salmon and salmon lice copepodids, with copepodids being closer to the surface during day, and Atlantic salmon being closer to the surface during night. This may mean that twice a day, Atlantic salmon smolts are swimming through the water layer with the highest density of salmon lice copepodids. Diel vertical migration in the marine environment has not been well studied in sea trout.

In coastal areas with a surface freshwater layer and salinity increasing with depth, salmon lice levels on Atlantic salmon and sea trout may be greatly affected by variation in fine-scale depth use by the fish and salmon lice copepodids. In a water column with stepped increases in salinity with depth, the copepodids were noted to aggregate in or just beneath the depths with salinity gradient steps, irrespective of light conditions (Heuch 1995). There is need for more information on depth use of both host species, but especially for sea trout, in order to permit detailed assessment of how their differential depth use might affect their relative salmon lice exposure risk.

Wild Atlantic salmon post-smolts captured by trawling at sea in Ireland.
Photo: Patrick G. Gargan

11.7 Do salmon lice levels on sea trout at monitoring sites reflect the lice levels on Atlantic salmon, in terms of migratory progression rates from the river mouth and exposure time?

When drawing conclusions on salmon lice levels based on wild fish captured during field monitoring, information on how long the fish has been at sea (and therefore vulnerable to salmon lice) clearly is needed. Fast migrating Atlantic salmon may, for example, already have migrated into the open ocean before salmon lice acquired in near coastal areas have developed into the more pathogenic preadult and adult stages (Sivertsgård et al. 2007). It is important to know also for how long fish captured for monitoring purposes in coastal areas have remained close to river outlets, where they possibly have been more protected against salmon lice due to their residing in brackish water, and how long they have stayed in more saline waters. Furthermore, salmon lice levels also may be influenced if the fish has returned prematurely to fresh water and thereby lost its burden before re-entering the marine environment (see chapter 7.4.1). Differences in progression rates between Atlantic salmon and sea trout in the marine environment may therefore affect their salmon lice levels when they are captured at a particular time and place in coastal areas for monitoring purposes.

Sea trout smolts in a Danish fjord showed slower horizontal progression rates after entry to the marine environment than was recorded in the river during the seaward migration (Aarestrup et al. 2014). Progression rate in the marine environment shortly after leaving the river was an average 3.2 km day^{-1}, or 0.02 body lengths s^{-1} (Aarestrup et al. 2014). In a Norwegian fjord, wild sea trout post-smolts tagged with acoustic transmitters were recorded 9 km from the release site in the river mouth within an average 18 days after release (corresponding to a progression rate of 0.07 km h^{-1}, or 0.11 body lengths s^{-1}, Finstad et al. 2005). Hatchery-reared Atlantic salmon in the same study showed a much faster progression, and spent only 28 hours before reaching the same site 9 km from the river mouth (corresponding to a progression rate of 0.54 km h^{-1}, or 0.41 body lengths s^{-1}, Finstad et al. 2005).

In a subsequent study in the same area, wild sea trout post-smolts required an average 15 days to reach the same receiver site 9 km from the river mouth (corresponding to 0.03 km h^{-1}, or 0.06 body lengths s^{-1}, Thorstad et al. 2007). Wild Atlantic salmon showed a faster progression rate, and spent an average 6 days to reach the 9 km receiver site (corresponding to a progression rate of 0.07 km h^{-1}, or 0.53 body lengths s^{-1}). In both studies, a smaller proportion of the sea trout than Atlantic salmon post-smolts were recorded at receiver sites located at 37 km and further away from the release site (Finstad et al. 2005, Thorstad et al. 2007).

Due to inter-specific differences in progression rates, a sea trout post-smolt may have had a longer exposure period to salmon lice when captured at a particular coastal monitoring site than an Atlantic salmon post-smolt captured at the same site. Conversely, the sea trout post-smolt may have spent more time, since leaving the river, in brackish water than in offshore and more saline areas.

Because sea trout post-smolts appear to typically remain in near coastal areas and close to their river of origin, this species may not reflect the total exposure risk for a comparable Atlantic salmon post-smolt migrating through the entire coastal areas and fjord. Hence, monitoring in inner and middle part of fjords may not reflect the salmon lice levels in the outer areas, which may or may not be different. In the case of farm-free areas in inner coastal areas, the salmon lice levels may be greater at the outer coastal areas, and monitoring of sea trout in near coastal areas may therefore underestimate the total exposure risk for Atlantic salmon. Given that sea trout post-smolts in many cases do not migrate long distances from the river mouth during the early weeks of the marine migration, a monitoring programme capturing sea trout in outer fjords may capture sea trout primarily from nearby rivers, and therefore not reflect the exposure risk for fish migrating from rivers discharging to the innermost fjord areas. During sampling in the Atlantic salmon post-smolt migration period, larger and older sea trout may to a larger extent than sea trout post-smolts have moved into more saline waters, and will have the newly attached stages of salmon lice that reflect the salmon lice level during this period. However, these patterns will depend on local conditions. In some areas, there are no brackish water areas outside the rivers, but the fish immediately enter full strength sea water when leaving the river.

In summary, neither sea trout post-smolts nor older sea trout alone will necessarily reflect the migration behaviour and resulting salmon lice levels of Atlantic salmon posts-smolts. Consequently, it is important to sample both sea trout post-smolts and older sea trout to obtain as complete a set of information as possible for that location of the salmon lice levels experienced by outward-migrating Atlantic salmon post-smolts.

11.8 Discussion

Sampling wild sea trout will provide valuable data on salmon lice levels over time, and between different areas that is also relevant to assessments of the risks encountered by Atlantic salmon post-smolts. However, the foregoing discussion does highlight characteristics of sea trout and Atlantic salmon that may affect salmon lice levels differently for the two host species.

In order to use sea trout as a proxy and to draw quantitative conclusions on salmon lice levels in Atlantic salmon, knowledge of local conditions should be used in each case to ascertain (1) how the body size of the sea trout captured may affect salmon lice levels compared to the Atlantic salmon post-smolts, (2) whether migration of the two species occurs at the same time, (3) which areas may have been transitted by trout in the period prior to sampling, (4) how freshwater layers and brackish water in the area (and vertical habitat use of the fish) may have influenced the results, and (5) the possibility that sea trout have remained for a longer time in inner, nearshore or freshwater-influenced areas. There is a need also to use local knowledge to ascertain whether the sea trout captured at a particular site in the coastal area reflect salmon lice levels over the entire early migration route of Atlantic salmon post-smolts from inshore to offshore waters.

For sea trout larger and older than smolts in the same springtime period, it is unpredictable how long they may have stayed in the sea prior to being captured; some may have resided at sea throughout the entire winter and spring (see chapter 2). However, larger sea trout may have transitted a greater coastal area (and wider range of habitat types) during the time period before capture compared to post-smolt fish. Older sea trout may therefore provide data reflecting salmon lice levels in broader regions in a more effective manner than is possible from monitoring captured sea trout post-smolts. Older sea trout may therefore also be more appropriate indicators of the local salmon lice levels than are sea trout post-smolts captured in some of the areas through which Atlantic salmon post-smolts also migrate. By separating the salmon lice on the sampled older sea trout into the different developmental stages, it is possible to use models to predict during the period over which the sea trout has been infested, and this will provide valuable information on the overall salmon lice level in the area.

To improve precision in the use of sea trout as a proxy indicator for quantitative salmon lice levels in Atlantic salmon, there is need to analyse separately the data on salmon lice levels from post-smolts and larger sea trout, and also to separate between the salmon lice developmental stages. Sea trout as proxies cannot be used alone to evaluate salmon lice levels in Atlantic salmon post-smolts, but sea trout data could be used in conjunction with other methods to analyze the overall local infestation pressure. Because sea trout populations are in decline, or at low levels, in many areas affected by salmon lice, there is a need to use and develop methods of capturing and monitoring fish alive such that they can be released unharmed.

Improved knowledge on the behaviour and habitat use of the two species will enhance precision in the use of sea trout as a proxy indicator for quantitative salmon lice levels in Atlantic salmon. Hence, there is need for further comparative studies of migration speeds, progression rates and horizontal and vertical habitat use of the two species. In addition, there is a need for increased knowledge on depth use especially for sea trout. There also is a need for studies examining possible differences in resistance against salmon lice between the two species and among populations.

11.9 Concluding statements

- In order to use sea trout as a proxy for estimating local salmon lice levels in Atlantic salmon, it is important to consider whether the two species have the same affinity for salmon lice.
- Studies comparing immune responses in sea trout and Atlantic salmon have provided contrasting results regarding their affinity for salmon lice. One factor might be population differences in immune responses. The physiological and pathological responses to salmon lice (outlined in chapter 6 and 7) appear to be comparable for the two species.
- Fish body size influences salmon lice levels. The number of lice on a fish tends to increase with increasing fish size because of the larger available body surface area. Surface area increases approximately as the square fish length, and the number of lice should increase at a higher rate than as a proportion of the fish length. If sea trout captured for monitoring are larger than the Atlantic salmon they are representing, they may have larger absolute numbers of salmon lice.

Modified bag net used to collect wild sea trout for salmon lice monitoring in Hardanger, western Norway. Photo: Bjørn T. Barlaup

- Salmon lice levels depend on the timing of sea entry. Whether smolt migration timing differs between Atlantic salmon and sea trout varies among catchments. For some river systems sea trout may have a more protracted migration period. Older sea trout may have resided in the marine environment throughout the entire winter, or perhaps have only recently entered the sea. When considering the use of salmon lice data from sea trout as a proxy for levels in Atlantic salmon, information on how long the fish have been at sea and potentially exposed to salmon lice is critically important.
- The ability of salmon lice to attach to a fish may be affected by local current speed around the fish. Atlantic salmon post-smolts may generally have faster swim speeds through the water column than do sea trout post-smolts, and this may reduce the ability of copepodids to encounter and attach to the host fish. Larger sea trout may be capable of higher maximum speeds than post-smolts. Studies of actual swim speeds, and how they may affect lice levels, are few.
- If salmon lice larvae are unevenly aggregated horizontally in coastal areas − in response to current patterns, freshwater outfalls and other environmental parameters − differences in horizontal habitat use between Atlantic salmon and sea trout may lead to contrasting salmon lice levels on the two species. A higher larval salmon lice level in littoral areas may lead to higher salmon lice intensities on sea trout than on Atlantic salmon, if sea trout use these areas more frequently. However, salmon lice distribution patterns and fish migration routes can be complex, variable in time and vary among areas.

- Atlantic salmon and sea trout generally swim in the upper part of the water column, where salmon lice copepodids also are gathered. In areas with a surface freshwater layer, copepodids may gather deeper in the water column where the water is more saline. In areas with a surface freshwater layer and salinity increasing with depth, salmon lice levels in Atlantic salmon and sea trout may be markedly affected by fine-scale variation in depth use by both the fish and the copepodids.
- Because of their slower horizontal progression rates, sea trout post-smolts may have had a longer exposure period to salmon lice than would comparable Atlantic salmon captured at the same monitoring site. Conversely, the sea trout post-smolts may have spent more of the time, since leaving the river, in brackish water than in more saline areas. Because sea trout post-smolts appear to typically remain close to their home river, they may not reflect the total salmon lice levels for Atlantic salmon post-smolts migrating through the entire coastal area and fjord. During sampling in the Atlantic salmon post-smolt migration period, older sea trout may to a larger extent have moved into more saline waters, and will have the newly attached stages of salmon lice that reflect the salmon lice levels during this period. However, these patterns will depend on local conditions. In some areas, there are no brackish water areas outside the rivers, but the fish immediately enter full salinity seawater when leaving the river.
- Neither sea trout post-smolts nor older sea trout alone will necessarily reflect the behaviour and resulting salmon lice levels of Atlantic salmon posts-smolts. Consequently, it is important to sample both post-smolts and older sea trout to obtain as complete a set of information as possible for that location of the salmon lice levels experienced by outward-migrating Atlantic salmon.
- Sampling wild sea trout will provide valuable data on salmon lice levels over time and between different areas that is also relevant to assessments of the risks encountered by Atlantic salmon post-smolts. However, this review does highlight characteristics of sea trout and Atlantic salmon that may affect salmon lice levels differently in Atlantic salmon post-smolts and sea trout.
- In order to use sea trout as a proxy and to draw quantitative conclusions on salmon lice levels in Atlantic salmon, knowledge of local conditions should be used to ascertain (1) how the body size of the sea trout captured may affect salmon lice levels compared to the Atlantic salmon post-smolts, (2) whether migration in the two species occurs at the same time, (3) exposure time to salmon lice, (4) which areas may have been transitted by sea trout in the period prior to sampling, (5) how freshwater layers and brackish water in the area may have influenced the results regarding vertical habitat use of the fish, and (6) the possibility that sea trout have remained for a longer time in inner freshwater-impacted areas.
- To improve precision in the use of sea trout as a proxy indicator, there is need to analyse separately the data on salmon lice levels from post-smolts and larger sea trout, and also to separate between salmon lice developmental stages.
- Sea trout as a proxy cannot be used alone to evaluate salmon lice levels in Atlantic salmon post-smolts, but sea trout data could be used in conjunction with other methods to analyze the overall local salmon lice level.

11.10 Knowledge gaps

- To improve precision in the use of sea trout as a proxy indicator for quantitatively estimating salmon lice levels in Atlantic salmon, there is need for further comparative studies of migration speeds and routes, progression rates and horizontal and vertical habitat use of the two species (and in sea trout for both post-smolt and older fish). In addition, there is a need for increased knowledge on depth use especially in sea trout. There is also need for studies examining possible differences in resistance against salmon lice between the two species and among populations.

Box 4 Behaviour and salinity tolerance of salmon lice

The copepodid, which is the infective stage of salmon lice, shows a diel vertical migration pattern in the water column and has been shown to gather near the surface during the day (top 0-3 m) and to spread to deeper layers at night (down to 3-7 m). This seems to be controlled by light intensity (Heuch et al. 1995). When experimentally held in homogeneous high salinity, copepodids were observed to gather in the upper section in the water column in response to 1 h of light from above, and to spread downwards in response to 4 h of darkness (Heuch 1995). This surface orientation of salmon lice was confirmed by observations of greater salmon lice intensities on farmed Atlantic salmon held in cages at 0-4 m depth compared to those held at greater depths (4-8 m and 8-12 m, Hevrøy et al. 2003).

In the field sampling reported by Heuch et al. (1995), nauplius larvae were found deeper than copepodids (8-9 m depth), and they showed smaller differences in depth between day and night. In a water column with step increases in salinity with depth, the copepodids aggregated at or just below those depths characterised by step salinity gradients, irrespective of light conditions (Heuch 1995).

Both nauplius larvae and copepodids have been observed to swim actively upwards followed by a passive sinking phase (Wootten et al. 1982). In salinity gradients, copepodids demonstrated avoidance of salinities <27, both by altering their swimming behaviour and changing the orientation of passive sinking (Bricknell et al. 2006).

Salmon lice are marine parasites, and cannot complete the life cycle at low salinities or in fresh water. In laboratory experiments, no egg development occurred at salinity 10 at water temperatures of 12°C and 10°C (Wootten et al. 1982, Johnson & Albright 1991a). At salinity 15, eggs developed, but failed to produce active nauplius larvae (Johnson & Albright 1991a). At higher salinities (20-30), active nauplius larvae were produced, but at salinities 20 and 25 most of the nauplius larvae died at the copepodid moult. Copepodids were obtained only at salinity 30 (Johnson & Albright 1991a).

Copepodids survived for less than one day in waters with salinity 10 or less. At higher salinities (15-30) and temperatures of 5, 10 and 15°C, average survival times ranged between 2 and 8 days (Johnson & Albright 1991a). Similarly, Bricknell et al. (2006) found that survival of free swimming copepodids was severely compromised at salinity levels <29. Attachment to a host did not aid copepodid survival during exposure to a low salinity environment, and a reduction in salinity appeared to reduce the ability of copepodids to remain attached to the host (Bricknell et al. 2006). Pre-exposure of copepodids to reduced salinity levels reduced their subsequent attachment rates to the hosts, and it was suggested that low salinity compromised the ability of the copepodid to detect and respond to the presence of a host (Bricknell et al. 2006). Sinking rates in the water column were also faster at reduced salinity (Bricknell et al. 2006). Adult salmon lice survived on average 9.5 days after removal from their host at salinity 10 and water temperature 10°C (Johnson & Albright 1991a).

Salmon lice attached to adult Atlantic salmon remained viable for up to 6 days when the returning Atlantic salmon were transferred from seawater to freshwater, but most lice were lost within the first 48 hours (McLean et al. 1990). In contrast, Finstad et al. (1995) found that salmon lice remained and survived on wild returning Arctic char for up to three weeks in fresh water.

12 Conclusions

In this report the knowledge of effects of salmon lice on sea trout has been reviewed, with the primary objective of assessing the effects of salmon lice on sea trout. 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 populations in the wild.

The scientific studies reviewed indicate that salmon farming increases the abundance of lice in the marine habitat and that salmon lice in the most intensively farmed areas have negatively impacted wild sea trout populations. The effects of salmon lice on sea trout ultimately are manifest as an increase in marine mortality, changes in migratory behaviour and reduction of marine growth. These conclusions are based on comprehensive studies of the effects by salmon lice which include:

1) Studies of individual sea trout in laboratory and field studies documenting (i) tissue damage, (ii) osmoregulatory dysfunction and other physiological stress responses, (iii) reduced growth, and (iv) increased susceptibility to secondary microbial infections and reduced disease resistance. One or more of these effects have frequently been reported as being incurred by 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 does compromise growth potential (and thereby future fecundity) by reducing the time spent feeding at sea. Sea trout with excessive skin lesions also might be more vulnerable to fungal and bacterial infection in freshwater than would undamaged fish.
3) Studies based on catch statistics and routine population monitoring utilizing in-river traps that have indicated salmon louse-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 arising from 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.

In sum, the combined knowledge from the reviewed studies provides evidence of a general and pervasive negative effect of salmon lice on sea trout 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 sea trout returning to freshwater for spawning, and in the surplus that can be harvested by recreational and commercial fisheries.

- **Quantification of salmon lice-induced mortality**

Salmon lice levels vary in time and space in fish farming areas. The reviewed studies have shown that sea trout using areas up to 30 km from fish farms can be negatively affected by salmon lice, but that sea trout using more distant areas also can be impacted because salmon lice larvae can be passively dispersed on currents >100 km from their origin. The effective dispersal distance achieved by salmon lice larvae in the plankton is locally very variable and dependent on local environmental conditions and fluctuations both in tidal currents and wind-driven circulation. The reduction of wild sea trout populations arising from increased mortality and reduced growth that may be caused by salmon lice in farm-intensive areas cannot, in most cases, be quantified because of a lack of field data in combination with associated studies of the population-level effects of salmon lice. In concluding a generally negative effect of salmon lice on wild sea trout populations, it has also to be acknowledged that there may be considerable variation of sea trout spawning populations among years that is attributable to factors other than salmon lice from farms. At present, the effects of salmon lice infestations on sea trout populations are demonstrably potentially significant, but are difficult to isolate from other potentially confounding influences.

Extensive and large-scale field studies of growth and marine survival of groups of tagged salmonids with prophylactic chemical treatment against salmon lice have permitted quantification of the host mortality effects of salmon lice by comparing these experimentally manipulated fish with un-protected control groups released in parallel. Such studies are expensive, labour-intensive and protracted in time, and they may also underestimate the effect of salmon lice for two reasons. First, in-feed chemical treatments, such as emamectin benzoate (that require the fish to consume an appropriate quantity of pellets), do not necessarily result in complete protection of all individual treated fish against salmon lice. Second, in order to ensure comparability of the experimental fish and to be able to release the required high numbers of fish at the same time, experiments on Atlantic salmon have invariably utilised hatchery-reared fish. Given the typical difference in size, and perhaps "quality", of hatchery-reared and wild smolts any extrapolation of experimental results to wild populations requires consideration of qualifying caveats. Pragmatically and logistically, the success of any tagging experiments requires an efficient means of re-capturing the fish – either from commercial fisheries, rod catches or experimental trapping facilities. Although scientifically and logistically challenging to achieve, such direct experimental data have been obtained in the past and clearly are essential to the objective quantification of the potential impacts of salmon lice on wild salmonid populations. There are few such studies on sea trout, but there are several relevant studies on Atlantic salmon, undertaken in multiple rivers and over several years in Ireland and Norway (Jackson et al. 2011a,b, 2013, 2014, Gargan et al. 2012, Krkošek et al. 2013, 2014, Skilbrei et al. 2013). All these studies have found greater return rates of Atlantic salmon treated against salmon lice, but not in every location each year. The estimated average risk ratio of protected fish returning to their natal rivers to spawn compared to unprotected fish has ranged from 1.14-1.41:1. Meta-analyses and long-term studies, and similar results from an increasing number of experimental studies, support that these are levels of additional mortality (i.e., 12-44% fewer adult spawners returning) that can be expected for Atlantic salmon populations in farm-intensive areas. The outcome of meta-analyses applied to all the available published data showed that treatment against salmon lice had a significant positive effect on survival to adult recruitment, leading to an estimated risk ratio between treated and untreated groups of 1.29:1 or 1.41:1 (Krkošek et al. 2013, 2014). This corresponds to a potential extra mortality loss of 34-39% of adult Atlantic salmon spawners, or a reduction in adult recruitment to spawning by approximately one third.

Atlantic salmon post-smolts migrate through farm-intensive areas in near-coastal areas only in the spring, and perhaps are present there for only a few days or weeks en route to ocean feeding grounds (Thorstad et al. 2011, 2012). Open-ocean studies of wild Atlantic salmon – including information on the incidence of chalimus and preadult stages of salmon lice – indicate persistent, but low levels or rates, of re-infestation of fish in offshore or oceanic waters by salmon lice (Jacobsen & Gaard 1997, Todd et al. 2000). The salmon louse-induced mortality impacts from Atlantic salmon studies cited above should therefore likely best be regarded as minimum estimates for sea trout mortality at the same sites, if protected and un-protected groups of sea trout were to be compared. Sea trout would normally remain for weeks, months or sometimes even a year or more in near coastal areas, and in association with high larval lice levels, and are therefore likely to be more affected by salmon lice than are Atlantic salmon. Sea trout also remain in coastal areas later in the spring and summer months than do post-smolt Atlantic salmon, and are therefore exposed to seasonally higher risks of salmon lice infestation. Finally, sea trout can remain at sea for longer periods than the short-term protection provided by the chemical treatment (e.g. emamectin benzoate, which is effective for perhaps 1-2 months, Stone et al. 2002, see chapter 10). Accordingly, results from studies applying these kinds of experimental methods to sea trout are most likely to be underestimates of the potential for salmon lice-induced mortality. There is only the one published study in which marine survival of sea trout prophylactically protected against salmon lice has been assessed (Skaala et al. 2014a). Skaala et al. (2014a) showed very low percentages of survival to return, with 3.41% of treated fish and 1.76% of un-treated controls returning. Although these levels of survival are low, they are significantly different and indicate the extent to which spawning abundances of adult sea trout may be reduced in local populations (i.e., in this case by almost one half).

In general, effects of salmon lice on sea trout summarised in this review resemble those shown in studies of Atlantic salmon, especially at the level of the individual fish (Finstad & Bjørn 2011, Finstad et al. 2011). Due to their contrasting life history strategies and habitat use in the marine environment, sea trout are expected to be more vulnerable to reduced marine survival and compromised growth due to salmon lice than are Atlantic salmon. Sea trout can, to some extent, counteract these effects by returning to brackish water and/or freshwater and to use these habitats as a refuge from salmon lice in order to survive. But inevitably there is a cost to the individual attributable to the reduced growth opportunities from loss of feeding at sea and, for survivors, ultimately this will be manifest as reduced reproductive potential.

- **Possible effects by reduced marine growth and increased mortality on population and species level**

In contrast to the density-dependent freshwater mortality of sea trout that occurs especially during the earliest embryonic and post-emergence life stages, marine mortality of sea trout seems not to be density-dependent, as is the case for Atlantic salmon. Mortality in the freshwater phase therefore can have a population *regulating* effect, whereas mortality in the marine phase (including that attributable to salmon lice) is not regulatory, but has a population *reducing* effect (see for example Milner et al. 2003, Einum & Nislow 2011). Elevated mortality during the freshwater phase can, to a varying extent, be compensated by increased growth and survival of the remaining juveniles, whereas there are no compensatory mechanisms for additional mortality in the marine phase. Hence, elevated rates of marine mortality, such as that induced by salmon lice, can result in a proportional reduction in the number of spawning adults. Because sea-run brown trout typically are female, any additional marine mortality has the potential to affect recruitment even more negatively than would be the case with an equal sex ratio.

The widespread and world-wide occurrence of freshwater resident brown trout populations (Klemetsen et al. 2003) implies that a marine impact factor such as salmon lice in the North Atlantic region does not increase extinction risk of the brown trout as a species. However, because the brown trout is a partially migrating species, reduced marine growth and increased marine mortality will reduce the benefit of marine migrations for individuals in anadromous populations, and may thereby result in selection against anadromy in areas with high lice levels (see chapter 10). In the extreme, this could result in the loss of anadromous sea trout populations, particularly in catchments with conditions unsuitable for brown trout during some periods of the year. Large rivers and catchments with suitable year-round conditions may not face a risk of total loss of brown trout, but a severe reduction or loss of the anadromous life history strategy may result in altered genetic composition of a population, establishment of populations characterised by freshwater residency, and perhaps reduced overall genetic diversity and less variable life-history characteristics. The loss of the enhanced growth opportunities offered by the marine environment also may lead to a lower total abundance of brown trout, altered life-history traits, lowered recruitment and loss of the large veteran migrants popular among fishers. These large multiple-spawner fish may make a disproportionate contribution to overall population egg deposition and perhaps should be a focus of conservation strategies. Some ecological changes may have occurred already for some sea trout populations and catchments in farm-intensive areas, as suggested by some monitoring studies (see chapter 10); but a general lack of long-term monitoring of sea trout populations and comprehensive population effect studies makes it difficult to make specific judgements.

- **Impact factors other than salmon lice**

Factors other than salmon lice can affect sea trout populations negatively, and there is local and regional variation in the incidence and relative importance of those impact factors. The status of sea trout stocks and fisheries varies across the distribution range according to the influence of such local and regional factors. These include climate change effects, pollution, overfishing, diseases (caused by viruses, bacteria, fungi and parasites and perhaps attributable to the increased occurrence of fish farming), hydropower development and other river flow regulation, migration obstacles and habitat alterations. Some factors, such as hydropower development, are identifiably specific to a given watershed or catchment, whereas others (such as freshwater acidification, salmon lice and climate change) are pervasive and can influence marine survival over large geographical areas and collectively multiple populations. Often, several anthropogenic factors can be identified as impacting sea trout populations simultaneously. The interactive effects of two or more impact factors may be complex, non-linear and unpredictable, and their overall outcome may not be clear from predictions based upon knowledge of the effects of those single factors in isolation. Climate change inevitably is a particularly important impact factor that interacts with other anthropogenic influences, including salmon lice. Negative effects of salmon lice might become more severe in northern populations due to climate change. Sea trout populations with reduced population size, genetic variation and variation in life history traits due to other impact factors are expected to be less robust in adapting to climate change.

- **Need for co-ordinated mitigation measures**

For sea trout populations experiencing negative anthropogenic impacts, both in freshwater and in the marine environment, there is need for co-ordinated mitigation measures to sustain and enhance populations. If, for example, the risks of salmon lice infestations could be reduced, the sea trout population may still be reduced below its maximum production potential if unrelated impact factors in freshwater reduce smolt production to levels below the maximum potential for that catchment. Conversely, if negative freshwater pressures are removed or reduced, so that the maximum potential for smolt production is reached, a sea trout population may still be reduced in terms of number of returning spawners proportional to the additional mortality encountered at sea, whether this is salmon lice-induced or caused by other marine impacts. The difference between the effects of freshwater and marine impact factors is accountable by density-related regulation of some phases of the freshwater life cycle, and freshwater impacts will affect sea trout population size only if recruitment in terms of smolt output is reduced below the maximum potential of the catchment. By contrast, additional mortality at sea always will have a proportional negative effect on stock size in terms of the number of spawners. Hence, any increase in marine mortality can have considerable consequences for sea trout in terms of (1) reduced or eliminated harvestable surplus for fisheries, and (2) reduced future recruitment of the population if the added mortality reduces stock size to a level below that needed to achieve the maximum production potential.

13 Knowledge gaps and research needs

From the wider perspective, the effect of salmon lice on sea trout is a relatively well-studied subject, with a large number of published studies available, as shown in this review. The effects of salmon lice on individual sea trout also are relatively well documented both through laboratory and field studies. Knowledge gaps and research needs are specifically outlined for each chapter in this report, and we refer to these sub-chapters for details. The main knowledge gaps that we would elect to emphasize are related to:

- Effects of salmon lice at the host population level.
- Quantifying the reduction in wild sea trout populations as a result of increased mortality and reduced growth, and the consequential effects on life history traits including anadromous behaviour.
- Information on sea trout marine migration behaviour and foraging areas for both first-time and veteran migrants.

The most important knowledge gaps are related to effects at the population level and in quantifying the reduction in wild sea trout populations as a result of increased mortality and reduced growth caused by salmon lice. The effects of salmon lice on life history traits – especially trout population age structure and size at maturation – and selection against anadromous behaviour in favour of permanent freshwater residence also are not well understood. More knowledge regarding how salmon lice may act in concert with other impact factors to regulate or reduce the wild stocks, both in freshwater and in the sea, is also required.

Specifically, the report highlights the need for more comprehensive and robust data to facilitate our understanding of, and to adjust and more finely define, the threshold classifications for salmon lice-related mortality estimates derived from laboratory studies and to be applied to field data and wild populations. More detailed, comprehensive and consistently acquired monitoring data of salmon lice levels on wild sea trout populations also is required. Such data would facilitate more inclusive analyses of the various factors likely to contribute to the variation in salmon lice levels noted for areas impacted by fish farms.

For robust and informed evaluation of the effects of salmon lice on sea trout populations, more field experiments comparing survival and growth of fish released to the environment following prophylactic treatment against salmon lice should be undertaken. These experimental releases need to incorporate large numbers of fish, with suitable control (untreated) groups released in parallel, and experiments should be repeated across multiple rivers and years in order to account for temporal and spatial environmental variation. A primary consideration in planning the feasibility of such experiments is to ensure an effective means of ultimately retrieving the maximum number of tagged fish. Natural mortality rates of salmon and sea trout at sea generally are high and this underscores the need to release very large numbers of fish in order to permit the retrieval of an appropriately high number of tags for data analytical purposes. Given these high mortality rates, the reliability, robustness and applicability of any comparative estimates of salmon lice impacts on free-ranging salmonids is determined by the absolute numbers and proportions of tags retrieved. Ideally, and as included in some of the studies reviewed in this report, these release experiments would include also groups of treated and untreated wild fish (rather than hatchery-reared smolts), quality-control assays of uptake of the prophylactic chemical treatment by sub-samples of the experimental fish, and confirmation of the osmoregulatory status of fish at release. These latter data are of especial importance in instances where percent survivorship at the cohort or population level is a specific research objective and where, perhaps, the observer is comparing impacts over multiple years or different locations. Individual-based, and dynamic state-variable, models offer a powerful and informative means of obtaining clear insights relating to the effects of salmon lice on sea trout populations and the expression of variation in life history traits. In order to effectively pursue that modeling strategy, there is a need for concerted efforts to parameterize these models with suitably comprehensive empirical data, both from field and laboratory studies.

More detailed quantitative information is needed on how salmon lice planktonic larval stages may spread and be dispersed in coastal areas, and which environmental factors ultimately determine the resultant salmon lice level on wild sea trout in a given area. Numerical models and their data basis on production and distribution of infective salmon lice larvae from farms to wild sea trout need to be improved. Such information is necessary both to evaluate and optimise mitigation measures, such as the identification or delineation of protective areas lacking salmon farming, to evaluate existing and potential future farm sites for development, and to predict their likely impact on wild sea trout populations. For example, and despite local and geographic differences in hydrography, salinity and wind-driven circulation of coastal waters, suitably parameterised particle dispersion models − aimed at predicting the spread of larval salmon lice from point sources − might allow their transferability across regions and countries and thereby improve advice on mitigation measures.

In contrast to Atlantic salmon, wild sea trout populations generally have been rather poorly studied, monitored and mapped, although there is variation in this respect among catchments, regions and countries. Even the status of sea trout populations and a basic understanding of putative anthropogenic factors potentially impacting them are not well known for many localities. With specific regard to the marine environment, the behaviour and survival of sea trout is less well understood than for many other salmonid species. More information is required on sea trout marine migration paths and trajectories, and the foraging areas they may exploit, relative to marine salmon aquaculture. The migration distances and routes taken by sea trout emigrating from home rivers and through coastal waters is poorly understood and more information is required to be able to assess the potential impact of salmon lice from marine salmon aquaculture on sea trout stocks from rivers close to and more distant from such installations. This information is critical in assessing whether sea trout from rivers remote from salmon farms undertake migrations which may yet expose them to the influence of salmon lice produced by farms. Such information is essential when interpreting salmon lice monitoring data on farmed and wild fish, in evaluating the likely efficacy of any adopted mitigation measures and in permitting the formulation of appropriate and relevant scientific advice on possible mitigation measures.

Sea trout individuals and populations often are characterised by much variability in their behaviour and ecology: thus, stock structure and life-history strategies often vary considerably among river systems and within geographical regions and the proximate drivers of this variability often is poorly understood. Many sea trout studies are undertaken on already impacted and reduced populations, and there is a general lack of reference data from more pristine areas.

Long-term studies, and comprehensive longitudinal data sets from consistent monitoring, are especially valuable but are available for only few catchments and populations. Whilst the maintenance of time series should be viewed as a priority, investment in such programmes should not preclude new research themes which can provide empirical data for the development of general mathematical and statistical models that might offer transferability across countries and thereby an improved robustness of management advice.

Glossary

Abundance – Mean number of parasites calculated for all the fish in a sample, i.e., including individuals lacking parasites in the calculation. Abundance can also be calculated as prevalence multiplied by intensity and divided by 100.

Anadromous fishes – Fishes that migrate between spawning habitats in freshwater and feeding habitats at sea.

Disease – Broadly refers to any condition that impairs normal function, and is therefore associated with dysfunction of normal homeostasis. Commonly, the term disease is used to refer specifically to infectious diseases, which are clinically evident diseases that result from the presence of pathogens. An infection that does not, and will not, produce clinically evident impairment of normal functioning is not considered a disease.

Epizootic – an outbreak of disease affecting many animals of one kind at the same time.

Fish physiology – The scientific study of how the biochemical, metabolic and physical attributes of the fish function together in the living animal.

Freshwater resident – Trout that remain in freshwater their entire life, but which may undertake migrations within freshwater, for example between spawning areas in a river and feeding areas in a lake.

Infestation – State of being invaded by parasites. Refers to animal parasites s such as mites, ticks, lice and worms and excludes those caused by protozoa, fungi and bacteria, which are termed infections.

Intensity – Mean or median number of parasites per infested fish of a sample, i.e., excluding individuals without parasites in the calculation.

Iteroparous – Organisms which can have produce offspring several times in different seasons or years over the course of their lives are termed iteroparous, as opposed to semelparous organisms which undergo a single reproductive event and then die.

Kelt – Life stage of sea trout or salmon after spawning and until such time as the fish re-enters saltwater.

Mobile lice – Preadult and adult life stages of the salmon lice.

Moribund – State of near-death.

Parasite – A species that benefits at the expense of another species, called the host. In this case salmon lice are the parasites and sea trout the hosts.

Parr – Juvenile stage of anadromous salmonids, including sea trout, in the river after they have dispersed from the spawning redds but before they undergo smoltification and migration to sea.

Pathogen, also called *infectious agent* – A microorganism that causes disease in its host. Can in its widest sense be a virus, bacterium, prion, fungus or parasite.

Pathological effects – Effects caused by a disease, and especially a description of structural and functional changes in organs, tissue and cells.

Physiological effects – Disturbances to the body functions, or to the fish homeostasis (equilibrium). Functions can be mechanisms such as metabolism, salt regulation, blood and lymph circulation, immune defence and control systems (nerves and hormones).

Post-smolt – Marine life stage of anadromous salmonids after the smolt stage, when they have departed from the river and entered the sea. Salmonids are termed post-smolts usually between the day of first entry to seawater up until end of the first winter at sea.

Prevalence – Percentage of parasite infested fish in a sample.

Resident trout – Trout that remain in the same (e.g. freshwater) habitat throughout their entire life and do not undertake migrations.

Salmonid – Fish of the fish family Salmonidae. This fish family includes Atlantic salmon, brown trout and Pacific salmon species, among others.

Sea loch – A Scottish term to describe an enclosed or elongate sea inlet, comparable to a Scandinavian fjord. Sea lochs are quite distinct from freshwater lochs in being brackish or marine embayments.

Smolt – Freshwater life stage of anadromous salmonids, including sea trout, at which point the juvenile phase in the river has accomplished the smoltification process and the fish is migrating downstream to enter the sea.

Smoltification process – The preparatory process prior to seaward migration: this involves the morphological, biochemical, physiological and behavioural changes that pre-adapt anadromous salmonids for life in high salinity water. The physiological changes prepare salmonids to control body salt levels in the marine environment. The morphological changes include a slimmer body form and alterations in body coloration (darkened fins, dark back, white belly and silver sides) that help to conceal the fish in the pelagic environment.

Veteran migrant – Trout that migrate to sea and that have undertaken one or more previous sea migrations.

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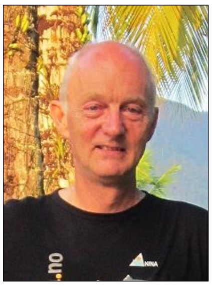

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