

Review

Controlling salmon lice on farmed salmon and implications for wild salmon

Simon R.M. Jones*

Address: Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia, V9T 6N7, Canada.

***Correspondence:** Email: simon.jones@dfo-mpo.gc.ca

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Abstract

This review documents the extent to which management of salmon lice (*Lepeophtheirus salmonis*) on farms has a measurable impact on the health of wild salmon. The salmon louse is a persistent and often severe parasite of farmed salmon throughout the Northern Hemisphere. High farm densities in some areas have led to lice levels within adjacent wild salmon populations that are higher than occur naturally. To minimize the additional infection pressure of the parasite on wild salmon, aquaculture industries adopt strategies of integrated pest management that include systematic monitoring, treatment, locating farms to minimize exposure to lice and maintaining optimal stock densities and single year-classes. Often these management activities are coordinated among farms within a region. A number of national or regional programmes collect and publicize salmon louse infection data from farmed and wild salmon. Some but not all management programmes show evidence of reducing infection levels on wild salmon; however, the available data are not yet sufficient to make firm conclusions regarding population effects. The local management and conservation of wild salmon populations should continue to be coordinated and integrated as the abundance of these fish is influenced by climatic, oceanographic and anthropogenic factors, including but not limited to salmon aquaculture.

Keywords: *Lepeophtheirus salmonis*, Aquaculture, Management, Transmission, Wild salmon

Review Methodology: This review considered information available from *Scopus* and *Web of Science* up to 15 May 2009, using keywords: aquaculture, *Lepeophtheirus salmonis*, salmon lice, treatment, management, wild salmon and population. In addition, colleagues were contacted for access to unpublished observations and/or analyses.

Introduction

The production of farmed salmon in open marine net-pens has risen steadily from 37 000 tonnes in 1985 to 1.3 million tonnes in 2006 [1], and ranges widely among countries. In 2006, production in Norway was 626 000 tonnes while that in Scotland was 132 000 tonnes and in the Irish Republic, 11 200 tonnes. Annual production in Canada was 102 000 tonnes, of which about 54 000 tonnes was produced in British Columbia (BC). Regionally, the Hardangerfjord in Norway produced ~60 000 tonnes in 2007 [2], whereas production in the Broughton Archipelago (BA) region of BC is ~20 000 tonnes [3]. The ability of salmon aquaculture to meet an increasing global demand [1] is based on improved feed composition and conversion ratios, improved disease diagnostics and

prevention through vaccination, enhanced biosecurity and related husbandry measures. Despite these improvements, infectious diseases continue to impose costs to the industry. Among these, the salmon louse *Lepeophtheirus salmonis* has gained particular notoriety, having received the attention of scientists, policy-makers, the media and general public in all countries in which salmon are farmed in the Northern Hemisphere.

L. salmonis is a common parasite of wild adult Atlantic (*Salmo salar*) and Pacific (*Oncorhynchus* spp.) salmon and sea trout (*Salmo trutta*) throughout their natural oceanic range [4–8]. The parasite is not new to science; it was formally described in 1838 but previously had been well known among fishers and naturalists [9]. Despite this long awareness, a scientific basis for understanding the impact of the parasite is relatively new, coinciding with the advent

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of intensive salmon aquaculture. The parasite was one of the earliest pests to be recorded on farmed salmon [10, 11] and after several decades of scientific enquiry and technological innovations, the influence it still exerts is a testimony to the challenges of prevention or treatment [12]. In addition to the direct costs incurred by aquaculture, there are concerns that salmon lice infections on farmed Atlantic salmon give rise to infections that may be harmful to wild salmon populations [13, 14]. Furthermore, documented cases of reduced sensitivity to commonly used salmon louse medications raise the possibility of drug resistance within parasite populations.

The large body of salmon louse literature is reflected in a series of recent reviews focusing on the ecology, host-parasite relations, genetics, reproductive biology and economic impact of the parasite [12, 15–20]. The purpose of the present paper is to review the control and management of sea lice on farmed salmon and to discuss the extent to which these practises have had measurable benefits to the health of wild salmon populations. Reflecting the available information, this review will focus mainly on salmon populations occurring in the Northern Hemisphere.

The Biology and Pathological Consequences of Salmon Lice Infections

Parasitic adult female salmon lice release first-stage nauplii into the water column, where they develop through second nauplius and infective copepodid stages [15]. These stages subsist entirely on endogenous lipids during dispersal with the seston and their developmental rate, infectivity and survival depends strongly on temperature and salinity [21], and ultimately on successfully finding and settling onto a suitable host. While the larval parasite displays diurnal vertical movement, evidently in response to visual cues, horizontal dispersal primarily relies on the magnitude and direction of advective processes occurring in surface and near-surface waters. Having settled onto an appropriate host, the copepodid produces a frontal filament with which it and the subsequent four chalimus stages are attached to the host. The life cycle is completed as the parasite develops through preadult and adult stages that are unattached and mobile on the host [15]. Another mode of transmission, favoured under conditions of high host proximity, is the direct transfer of mobile *L. salmonis* stages among hosts [22, 23]. The broader ecological implications of this host switching behaviour require further research, particularly in the context of highly prevalent infections that occasionally occur among sympatric non-salmonid hosts [24].

The maintenance of large numbers of salmon in relatively dense populations on farms provides an environment more suited for parasite proliferation and dispersal than typically is found within wild host populations. Therefore, opportunities to systematically investigate the

pathological potential of *L. salmonis* were first provided by salmon aquaculture in marine netpens as platforms for effective and ongoing observation and quantification. Epizootics first occurred in farmed salmon in Norway in the late 1960s [11], in Scotland in the mid-1970s [25] and in eastern Canada in the mid-1990s [26]. Damage caused by *L. salmonis* is principally the result of its feeding behaviour, particularly that of the larger, mobile preadult and adult stages. When left untreated, high-intensity infections cause skin erosion with varying degrees of invasiveness and associated haemorrhage [27–29]. The combined effects of the parasite on farmed salmon include reduced growth and loss of scales, thus providing an opportunity for secondary pathogens to become established and more severely damage the fish, further reducing its marketability [30]. It is now clear that sub-lethal effects in Atlantic salmon including increased stress and reduced swim performance are also important consequences of *L. salmonis* infection [31].

The pathological consequences of *L. salmonis* infections on wild adult Atlantic and Pacific salmon are less well understood but have been described in two cases in eastern and western Canada [32, 33]. In both, the high prevalence of parasites and the cutaneous lesions were associated with high densities of fish occupying suboptimal water conditions and possibly exacerbated by environmental stressors that rendered the salmon less able to resist the infection. Indirect evidence comes from the relatively higher recapture rate of returning adult Atlantic salmon that had been treated for salmon lice before release as smolts, compared with untreated salmon [13, 34]. Sea trout post-smolts may be at greater risk of exposure to the parasite because they spend more time in nearshore waters compared with the salmon post-smolt. The infected sea trout may return prematurely to freshwater resulting in reduced growth compared with individuals that remain in seawater [35, 36]. In addition to host pathology, very little is known about variations in pathogenicity among louse populations. A recent study found that, genetically, the forms of *L. salmonis* inhabiting the Pacific and Atlantic Oceans were sufficiently distinct to be considered separate species [37]. It will be important to determine whether this distinction is associated with differences in pathogenicity. The generally poor understanding of disease associated with *L. salmonis* or other pathogens in wild populations reflects fundamental difficulties in systematic observation.

Controlled laboratory exposure of otherwise healthy fish for the purpose of characterizing and quantifying the causes and effects of infectious disease is an important research tool. A consistent feature of laboratory studies of salmon lice has been the use of post-smolts which, because of their small size, are compatible with the constraints of tank-based investigations thus permitting the use of statistically significant sample sizes. An unfortunate consequence is that well-controlled data from sub-adult, adult and sexually mature salmon are underrepresented.

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Wagner *et al.* [19] reviewed the earlier literature and summarized the concepts and methods used to understand the interactions between the sea louse and its hosts. Some key findings of the early studies include a significant effect of host species in susceptibility, confirmation that low level infections affect host physiology, increased clinical consequences associated with the development to preadult and adult parasites and the role of bioactive modulators in the salmon louse saliva. More recent laboratory studies have focused on the unique processes associated with resistance to *L. salmonis* in juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon, which may be exposed to sea lice at body masses less than 1 g [38–40]. As a result of rapid growth following entry into the ocean [41], juvenile pink salmon develop natural resistance to *L. salmonis* after 4 to 6 weeks [40]. Unlike the earlier studies conducted on Atlantic salmon and sea trout, the mortality observed among the small pink salmon occurs while infections consist mainly of chalimus stages. Incomplete skin development during early ocean rearing appears to put juvenile pink salmon at elevated risk to a wide range of environmental effects related to water quality, predation and ectoparasite infection [42, 43]. Generally, controlled exposure studies have provided the basis for understanding and quantifying the risks to wild salmon associated with *L. salmonis* infections.

The effects of *L. salmonis* on survival of juvenile pink and chum salmon have also been investigated by holding wild-caught fish in captivity [44–46]. While providing a unique opportunity to observe natural sea lice infections on the juvenile salmon, the absence of controls to determine the cause of mortality combined with difficulties in identifying early sea lice developmental stages raise concerns about the interpretation of susceptibility data from holding trials [47].

It is clear that susceptibility to *L. salmonis* varies significantly among host species belonging to the genera *Oncorhynchus* and *Salmo*, and factors affecting the resistance mechanisms are beginning to be understood [19]. However, the health and abundance of aquatic animal populations are multifactorial and the extent to which even well-controlled laboratory trials can explain this complexity is uncertain. Jones and Hargreaves [42] discuss the limitations of extrapolating from laboratory studies to explain population effects of salmon lice. Understanding the impact of salmon-farm-derived sea lice will require input from laboratory and field observations combined with region-specific formulae for risk management.

Treatment of Salmon for the Control of Salmon Lice

It is apparent from the outbreaks of salmon lice on farms in the early 1970s that a need for control had arisen before the availability of reliable epizootiological

information. The epizootiology of *L. salmonis* infections on farmed salmon has since formed a considerable body of knowledge [3, 25, 48–56], helping to form a rational basis for control strategies. Practical and theoretical control methods for salmon lice include the topical application of therapeutants, in-feed medicines, alternative husbandry strategies (fallowing, single year-class stocking at sites or among sites within an area), biological control, vaccination and selective breeding. Boxshall and DeFaye [57] provide an historical perspective on salmon louse control measures.

A history of applying pesticides for the treatment of ectoparasitic copepods on freshwater fishes provided the basis for early attempts to treat salmon lice on seawater-reared Atlantic salmon [27, 28, 58]. The number of treatment options has since increased through the availability of new classes of therapeutants: organophosphates, pyrethroids, disinfectants, insect growth regulators and avermectins. The recent demonstration that methylene blue (MB) or a cocktail of MB and Nuclear Fast Red were toxic to a free-living copepod following photoactivation may indicate a novel but as yet unproven treatment strategy for *L. salmonis* [59].

Organophosphates are synthetic acetylcholinesterase inhibitors topically administered to salmon by bath application. They were among the first compounds used to treat sea lice and are only effective against mobile parasitic stages [60]. Dichlorvos was used in Scotland and the Irish Republic from the late 1970s. Metrophinate, a related compound, preceded the use of dichlorvos in Norway until the mid-1980s [61]. Application of azamethiphos, a new-generation, less-toxic organophosphate, began in Scotland and Norway in the mid-1990s. Azamethiphos is authorized for use in Scotland, Norway, the Faeroes and Chile [62–64].

Pyrethroids are synthetic compounds that cause a loss of function in arthropod neuronal sodium channels leading to paralysis [65]. They are less toxic than the naturally occurring pyrethrins and have greater solubility in water [66]. Pyrethroids are broad-spectrum pesticides affecting both attached and mobile sea lice stages. Cypermethrin, high-*cis*-cypermethrin and deltamethrin have been used as a topical treatment for sea lice since the mid-1990s. Cypermethrin is used in Scotland [61], while the latter two compounds are used in Norway [67]. Deltamethrin was licensed for use in Chile in late 2007 [54].

Hydrogen peroxide (H_2O_2) has been used topically to treat sea lice infections in Norway, Scotland and Canada [65, 66, 68]. Its mode of action may be related to the formation of oxygen emboli in the haemolymph of the parasite [69] and the compound is only efficacious against mobile parasitic stages [63]. H_2O_2 has a narrow therapeutic margin and is not recommended for use above 14°C [65]. Application is further limited by the difficulty of establishing an efficacious concentration in tarpaulin-lined netpens, combined with the tendency of lice to recover after treatment.

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The insect growth regulators diflubenzuron and teflubenzuron inhibit chitin synthesis in the copepod exoskeleton and have been used to treat sea lice since the mid-1990s. Teflubenzuron is authorized for use in salmon in Scotland, Norway, the Irish Republic, Canada and the Faeroes [63, 70] and diflubenzuron has been used in Norway [68, 71]. Both compounds are delivered in-feed and are effective against actively moulting early developmental stages. Although the therapeutic margin in fish is high [63], chitin inhibitors begin to lose efficacy 7 days after treatment [72].

Avermectins including ivermectin and emamectin benzoate (EB) interfere with neuronal GABA- and glutamate-gated chloride channels [65]. Limited off-label use of ivermectin as an in-feed treatment of sea lice has occurred in the Irish Republic, Scotland and Canada [61, 73–76]; however, the therapeutic margin of this compound is narrow [65, 77, 78]. In contrast, therapeutic doses of EB are non-toxic to salmon and licensed for use in Norway, Scotland and Chile. The drug is available in the USA under the provisional status of an investigational new animal drug [79] and in Canada under the emergency drug release process [80]. EB appears to combine ease of administration, virtual absence of toxicity to salmon [81] and efficacy against all lice stages persisting from 10 weeks to five months [3, 82]. In Chile, EB has been used against the sea louse *Caligus rogercresceyi* since 2000 [83].

Evidence for Resistance to Therapeutants

Usage trends from Norway show an early predominance of organophosphates followed by that of pyrethroids after which EB usage increased [68]. Similar trends may be inferred to have occurred in Scotland and the Irish Republic. EB has been used exclusively since 2002 in the State of Maine, USA [84]. More recently in Norway, Scotland and Chile, the alternating use of EB and pyrethroids is becoming more common [85]. These trends relate to the changing availability of products with improved therapeutic margins, efficacy and ease of delivery. Differences in treatment strategies [68] and in regulations affecting the availability of chemotherapeutants [63] also contributed to usage trends regionally and nationally. Insect growth regulators and disinfectants have been less frequently used in all regions. A pattern of repeated usage of compounds with the same or similar mechanisms of activity has created theoretical opportunities for the development of increased tolerance or resistance within lice populations. Indeed, changes in efficacy over time are suggested from reports of increased tolerance to organophosphate, H_2O_2 and pyrethroids in Norway, Scotland and Canada [63]. While these infection trend data may not discriminate between true resistance and apparent resistance, in which treatment failure is the result of causes other than increased drug tolerance, there are several confirmed accounts of increased tolerance to organophosphates

[86–88] and pyrethroids [67, 89]. Similarly, resistance of *L. salmonis* to H_2O_2 has been demonstrated [90]. In contrast, Westcott *et al.* [70] found no bioassay evidence of increased tolerance to EB in sea lice in the Bay of Fundy, Canada, although seasonal or temperature associated trends were noted. Lees *et al.* [54] modelled pre- and post-treatment farm data and found evidence that not all EB treatments were effective and that efficacy varied spatially and tended to decline over time. There have been recent reports, confirmed with bioassays, of increased tolerance to EB among *L. salmonis* in Norway (T. Horsberg, personal communication). Bioassay was used to describe increased tolerance to EB among *C. rogercresceyi* from 18 salmon farms in Chile [83]. Given the diversity of environmental conditions and husbandry practises within which salmon louse treatments are administered globally, bioassay or similar controlled sensitivity tests are required to discriminate between true and apparent increased tolerance to medication [67, 70].

Optimizing Husbandry Practises for the Control of Salmon Lice

Pharmacological, clinical and epizootiological evidence strongly support the efficacy of chemotherapeutic intervention in the control of salmon lice. Until recently however, there have been few scientific data to support claims that salmon louse infections on farmed salmon may also be reduced through the optimization of husbandry practises [15, 29, 91]. Mathematical analysis of the data obtained from approximately 40 Scottish salmon farms over a four-year period identified level and type of treatment, cage volume, current speed, local tidal flushing time and recent sea lice infections to be statistically significant predictors of sea lice on farmed salmon [92]. The latter study found stocking density, site biomass, water temperature, the presence of independent neighbouring farms or length of fallow to be statistically insignificant predictors of lice levels. It is also recognized that epizootiological patterns of *L. salmonis* infection differ significantly between Scotland and Norway [49] and that there are apparent contradictions regarding the effectiveness of fallowing [93]. Within regions, year and location are significant sources of variation in salmon louse infection patterns on farms in Norway, Scotland, the Irish Republic and Canada [13, 48, 53, 56, 94]. Together, these reports indicate the importance of local environmental conditions, particularly salinity and water currents, in regulating the abundance of the parasite. The diversity of husbandry and environmental variables influencing parasite abundance have led some salmon-farming organizations to adopt integrated pest management (IPM) strategies, in which the tendency towards local environmental uniformity within an embayment is recognized and combined with coordinated treatments and/or optimized husbandry practises among the local farms [30, 91]. It has

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been recognized that IPM strategies must be tailored to fit each salmon-producing region [95].

Other husbandry practices aimed at mitigating salmon louse infections include the application of a variety of wrasse species (Pisces: Labridae) by cohabitation with the farmed salmon. The wrasse preferentially grazes on adult and preadult sea lice [18, 91, 96, 97] and the practice is now mainly employed in Norway [96].

A vaccine against salmon lice has been described as a 'Holy Grail' [98]. Despite the promise of early efforts to characterize potential candidate *L. salmonis* antigens [99–101] there is no indication that a commercially viable vaccine will be available soon [17]. However, recent applications of microarray technology to understand gene expression [102] and the descriptions of *L. salmonis* proteins [103, 104] suggest genomic and proteomic methods have potential in providing novel approaches for vaccine development.

The Atlantic salmon is relatively susceptible to *L. salmonis* infection. However, significant variation in the levels of *L. salmonis* infection observed among three wild stocks of Atlantic salmon suggested the possibility of genetic variability in susceptibility [105]. Thus, a number of studies have explored the possibility that the frequency of resistance traits occasionally observed among full-sibling families of Atlantic salmon may be increased through breeding programmes [106–110]. There is a need for further research, perhaps applying a broader suite of resistance-associated traits, to determine the usefulness of breeding programmes for the selection of enhanced resistance to *L. salmonis*, relative to selection for other desirable production traits [108].

The absence of a vaccine, acquired resistance among salmon louse populations to existing therapeutants, an apparent absence of the commercialization of novel classes of compounds and concerns about impacts to non-target species among existing and novel therapeutants together indicate that for the foreseeable future, control of salmon lice in localized coastal areas will emphasize IPM strategies.

Assessing the Effectiveness of Controlling Farm-derived *L. salmonis* Infections

In considering the potential impacts to wild populations of sea lice derived from farmed salmon it is necessary to discuss the extent to which lice movements may be tracked among salmon populations. Unfortunately, the numerous analytical methods applied to date, including morphometry, elemental structure, carotenoid pigments, allozymes, stable isotopes and genetic markers have not proven useful in tracking populations of the parasite between farmed and wild salmon [111–116]. However, recent genetic evidence suggests a detectable structure among *L. salmonis* populations in Western Canada based on the relative frequencies of cytochrome oxidase

haplotypes [117]. Similar results were obtained in another study [118], in which evidence of *L. salmonis* population structure was determined from four microsatellite loci, observed among Irish salmon farms. If local patterns of genetic structure within parasite populations are found to be temporally and spatially consistent, they may form the basis of methods to track louse populations at an appropriate scale of resolution.

Alternative methods to assess the magnitude and timing of the louse transfer between farmed and wild salmon have also been examined. For example, estimates of parasite egg and larval production have been based on counts of adult female or gravid *L. salmonis* on farmed salmon in an area, with or without indexing for stock size [119–123]. Unfortunately there are few reliable estimates of the early survival and infectivity of *L. salmonis* from field observations and the number of eggs per egg string, the hatch rate and the survival through to the infective copepodid stage are estimated from laboratory data. Comparative sea lice counts on wild salmon collected at varying distances from salmon farms have also been used to estimate farm-associated infection pressure [13, 119, 120, 124–127]. This approach is based on the premise that risk to wild salmon is greater in proportion to proximity to the farm [128], often resulting from the siting of farms along salmon migratory routes [129]. In some coastal zones of Scotland, the Irish Republic and Norway the appropriateness of this assumption is further supported by a depressed abundance of wild salmonids such that the number of farmed salmon is greater than that of wild salmon [13, 119, 122, 128, 130]. For example, the reproductive output of *L. salmonis* from farmed salmon along the west coast of Norway is estimated to be two orders of magnitude over natural production [121]. The design of collection programmes to adequately assess the significance of infections in wild populations must also consider the presence of *L. salmonis* infections in areas without salmon farms [4, 131]. In addition, season and host age can be important determinants of infection level on wild salmon [5, 132].

In the BA of Canada's west coast, where the number of wild salmon is relatively high, the role of salmon farms as the sole significant source of infection is not clear. As many as seven species of anadromous salmon occur along the coast of BC, all serving as natural hosts to *L. salmonis* [133, 134]. The three-spine stickleback (*Gasterosteus aculeatus*) also hosts *L. salmonis* in BC [24]. Although the parasite rarely develops beyond the preadult stage on this host, the ability of mobile stages to switch hosts, as discussed earlier, further add to the uncertainty concerning farms as sole significant sources of infection. Estimates of the salmon farm contribution to infection pressure in the BA have been obtained from a series of mathematical advection – diffusion – decay models, developed from spatially and temporally segregated *L. salmonis* counts on migrating juvenile pink and chum salmon [45, 135]. Observed infection patterns within the

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migratory populations are consistent with infection pressure associated with salmon farms up to five orders of magnitude greater than the background louse infection pressure [135]. Descriptive analysis of *L. salmonis* infections within the same populations of migrating juvenile salmon between 2003 and 2008 also showed evidence of significant spatial and temporal trends in parasite abundance [42, 136–138]. Linear regression analysis identified host size and month of capture to be significant predictors of *L. salmonis* numbers [137]. However, these studies [42, 45, 135–138] did not include coincident data from salmon farms and there remain uncertainties regarding conclusions relating to salmon farm effects. Association of the observed infections with point sources of infection were further limited by the absence of detailed knowledge of hydrographic processes in the area. Thus, while modelling and descriptive methods are useful in tracking spatial and temporal trends in the abundance of free larvae or infection levels, the absence of oceanographic and farm data continues to render associations with farmed salmon speculative.

Researchers have become increasingly aware of the need to integrate data from salmon farms, plankton investigations, larval behavioural studies and environmental monitoring through the use of mathematical modelling to understand the dispersal of sea lice larvae from point sources. A series of studies conducted in Loch Torridon, a fjordic sea loch on the Scottish west coast, has demonstrated the value of a multidisciplinary approach in understanding the dispersal of sea lice larvae. Loch Torridon is the largest fjord system on the Scottish west coast [139]; however, the volume of freshwater flow into the sea loch is relatively low and the two major rivers entering the sea loch support small populations of sea trout and Atlantic salmon [140, 141]. In addition, Atlantic salmon are farmed in open netpens in Loch Torridon. Circulation was described in detail by Gillibrand and Amundrud [139] and found to be mainly forced by wind and tides. Murray and Gillibrand [142] studied the simulated distribution of 'sea lice' particles from point sources within Loch Torridon under a variety of wind forcing scenarios using a tracking model driven by the output of the hydrodynamic circulation model. Later, Gillibrand and Willis [143] improved the predictive capacity of these coupled models in mapping copepodid dispersal by incorporating the combined effects of wind forcing and the diurnal migratory behaviour of larval lice. The coupled models have been further refined through the incorporation of louse maturation and mortality parameters [144]. Coincident with the improved understanding of the hydrography of the sea loch, direct counts of larvae in waters surrounding the salmon farms were obtained using surface or near-surface plankton tows [145, 146], as pioneered in the Irish Republic [147]. These surveys are highly labour-intensive and require considerable skill in plankton taxonomy. However, real-time polymerase chain reaction was shown to be rapid and sensitive in detecting

and quantifying larval *L. salmonis* in plankton samples [148]. A tendency for copepodids to aggregate along the windward shores of Loch Shielraig within the Loch Torridon system [145, 146] was consistent with models forced by westerly winds (which prevail in the area). In addition to larval distribution, the plankton tow research suggested a correlative link between the abundance of *L. salmonis* in the water column and the number of lice on salmon in adjacent farms. A possible association between planktonic stages of *L. salmonis* and sea louse management practises on the salmon farms was further strengthened through spatial and temporal analysis of the abundance of nauplii and copepodids in Loch Torridon [149, 150]. The highest densities of nauplii were located near the salmon farms whereas the copepodids tended to be more widespread, suggesting water-borne advection during development of the larvae to the infective stage [149]. While the authors point out that the principles learnt from the Loch Torridon effort may be generally applicable in other coastal areas [144], verification will require additional research in proportion to the physical and biological complexities involved. Similar efforts to integrate salmon farm and environmental data to predict the distribution and abundance of sea lice larvae in the surrounding water column have been initiated in the Hardangerfjord in Norway [56, 151] and in the BA in western Canada [152, 153]. Knowledge of the processes governing the distribution of sea lice larvae in coastal zones occupied by salmon aquaculture may readily be transferred to the epizootiology of other pathogens of fish [154].

Through observation and mathematical modelling there is evidence that farmed salmon, despite the significant effects of proactive management activities remain a quantifiable source of *L. salmonis* larvae. However, given uncertainties surrounding the extent of population-level impacts of this enhanced infection pressure, a balanced perspective must be adopted in the development of national and regional mitigation policies.

National and Regional Salmon Louse Mitigation Strategies and Implications for Wild Salmon

While it is recognized that threats to wild salmon on the high seas are caused by oceanographic and climatic effects as well as those of anthropogenic origin, national sea lice management programmes tend to reflect a pragmatic approach in which salmon aquaculture plays a central role. Regulation of salmon aquaculture activities in coastal zones must consider that the *L. salmonis* infection pressure from salmon farms may occasionally be sufficient to cause host population effects that are measurable against the variation in population abundance that results from other causes. Quantitative tools, such as thresholds of lethal infection that are host-specific, may provide some assistance in establishing management policies [42, 155], but as indicated by Heuch *et al.* [13], much more work is

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required to establish relative impacts of sea lice in wild populations.

Geographic variation in the scale or density of salmon aquaculture, in the strategies employed for the control of salmon lice and in the biological properties of the relationship between the salmon and the parasite indicates a need for region-specific mitigation strategies. Recognizing the significant risk to wild salmon posed by high density salmon aquaculture, Norwegian authorities implemented in 1997 a National Action Plan (NAP), the rationale and objectives of which have been reviewed [13]. By implementing systematic monitoring and treatment triggers on farmed fish combined with surveillance of lice levels within wild populations, the long-term goal of the NAP is to minimize harmful effects of salmon lice in wild and farmed salmon. While Norwegian national treatment trigger levels are 0.5 adult females or 3 mobile lice per fish year round, these are not linked to production and it is possible that appropriate thresholds should be 10-fold lower, particularly in the zones of high density farming [121]. The creation of National Salmon Fjords, within which salmon farming is not permitted, aims at improving survival of salmon and sea trout smolts [2]. Evidently, an ongoing and long-term reassessment of farm siting and density criteria that are fjord-specific or region-specific is required, in addition to the optimization of treatment and other husbandry practises on farms.

In 2003, the province of BC, Canada implemented the Sea Lice Management Strategy, which included mandatory industry monitoring of lice levels on farmed salmon combined with a government audit [3]. Management triggers were established at three mobile lice per fish based on monthly monitoring. Lice levels above the threshold between March and July, coincident with the migration of juvenile salmon, triggered either treatment or harvest. Recent coordinated area management agreements in the BA region of BC now include the proactive treatment of all farms between December and February to ensure the virtual absence of lice during the spring migration. Concurrently, in 2003 Fisheries and Oceans Canada implemented the Pink Salmon Action Plan that included an annual synoptic assessment of lice on juvenile salmon and other species in the BA throughout the nearshore spring migration [136]. Concurrent with these monitoring efforts, the British Columbia Pacific Salmon Forum was commissioned to coordinate a multi-year research programme addressing the BA ecosystem with an emphasis on sea lice.

A national sea lice monitoring programme was implemented in the Irish Republic in 1994. The Irish programme includes bi-weekly monitoring of farmed salmon in March, April and May to ensure the treatment trigger level of between 0.3 and 0.5 ovigerous lice per fish is met [156].

Throughout the north and west coasts of Scotland, the Tripartite Working Group concept provides a framework for cooperation among governments, wild salmon

stakeholders and salmon farmers in the form of area management agreements [91, 130].

The results of some of these national or regional programmes are in the public domain, and available on-line (http://www.marineharvestcanada.com/farming_farm_locations.php; http://www.al.gov.bc.ca/ahc/fish_health/sealice_monitoring_results.htm; <http://www.lusedata.no/default.aspx>; <http://www.pac.dfo-mpo.gc.ca/science/aquaculture/pinksalmon-saumonrose/findings-resultats-eng.htm>; www.marine.ie), providing an opportunity for scientific analysis, as recommended earlier as well as demonstrating corporate accountability and transparency.

It is probably too early to assess the full impact of these strategies although some data are beginning to emerge. More recently in Norway, lice levels on wild salmon in some heavily farmed fjords remain high, although there are indications that lice numbers are reduced in some of the larger protected areas [2]. Between 2004 and 2009, the average annual louse settlement on sentinel salmon in the Hardangerfjord has ranged from 0.5 up to 20 per fish. While many farms in the fjord have adopted a treatment trigger that is more stringent than the national trigger level (0.25 adult females and 2.5 mobile lice), more work is required to understand the role of environmental factors, such as reduced winter seawater temperatures, in facilitating treatment efficacy (K. Boxaspen, personal communication). In western Canada, the overall abundance of *L. salmonis* on migrating pink and chum salmon has continuously decreased between 2004 and 2008 [42, 138] to levels approximating those reported from northern BC [157, 158], where there are no salmon farms. These findings appear to contradict the conclusion that local populations of pink salmon face extinction due to mortality from sea lice [14]. The controversy surrounding the latter conclusion [47, 159, 160] may be related to the absence of a long-term series of data that includes sea lice.

Conclusion

The concerns that salmon lice diminish wild salmon populations are based on the knowledge that sea lice can have significant adverse impact on individual salmon. Alternatively, the contentiousness of this relationship is caused by knowledge gaps in our understanding of the early marine ecology of anadromous salmonids. It is not trivial that despite the many years of study in the North Pacific and Atlantic Oceans, processes contributing to the high mortality of juvenile Atlantic and Pacific salmon between ocean entry and the first winter at sea remain poorly understood [161, 162]. Although it is beyond the scope of this review to summarize the latter body of research, an objective assessment of the role of salmon lice in the early marine mortality of juvenile salmon will require a comprehensive knowledge of the ecology of juvenile salmon. In the face of this uncertainty, efforts to

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mitigate the impacts of farm-derived salmon lice on wild salmon have been implemented. In some regions, localized indications of reduced infection levels on wild salmon are evident. However, the development of resistance to the widely used therapeutant EB is an obvious consequence of the increased frequency of treatments in these areas, particularly since the implementation of stringent treatment triggers. With a growing emphasis on IPM, there is an ongoing need to better understand coastal ecosystems to provide a more rational approach to the co-management of aquaculture and wild salmon fisheries. Furthermore, the benefits derived from the long-term awareness and actions surrounding sea lice transmission between farmed and wild salmon are those associated with the integrated and coordinated activities of all shareholders in coastal communities.

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12 Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources

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