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Ecology of sea lice parasitic on farmed and wild fish

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Abstract

Sea lice, especially *Lepeophtheirus salmonis* and *Caligus* spp., have the greatest economic impact of any parasite in salmonid fish farming and are also a threat to wild salmonids. Here, I review how the biology and ecology of various louse and host species influence their pathogenicity and epidemiology. Recent discoveries of new species and genotypes emphasize the need for more basic research on louse taxonomy and host preferences. Louse development rates are strongly dependent on temperature, and increasing mean sea temperatures are likely to increase infestation pressure on farms and wild fish, as well as affecting the geographical distribution of hosts and parasites. Despite progress in finding *L. salmonis* larvae in the plankton and in modelling louse production in several countries, more data on larval behaviour and distribution are required to develop dispersal and transmission models for both *L. salmonis* and *Caligus* spp. This knowledge could be used to take measures to reduce the risks of lice affecting farmed and wild fish.

Introduction

Sea lice (Copepoda, Caligidae) have been the most widespread pathogenic marine parasite in the 30 year-old Atlantic salmon (*Salmo salar* L.) farming industry, and in the past 15 years pathogenic infestations on other cultured fish and wild salmonids have escalated [1–3]. All but one species of sea lice parasitize bony marine fish (Actinopterygii), and 54% of copepod infestations of farmed fish are caligids [4]. Their impact ranges from mild skin damage to stress induced mortality of individual fish (Figure 1, Box 1), and includes epizootics (see Glossary) in wild fish populations in Europe and British Columbia. Research has concentrated on *Lepeophtheirus salmonis* (Krøyer, 1837) because it has the greatest impact on Atlantic salmon farms (Box 2). However, this research has wider implications because other crustacean ectoparasites, including other caligids and isopods, are pathogenic to salmonids and other cultured finfish [1,4–6]. Four species of *Caligus* occur on farms in British Columbia, Chile, Europe and Japan (Box 2).

Eggs carried by the female louse hatch into non-feeding planktonic larvae that infect a new host (Box 3). How these larvae disperse and find a new host has been one of the most challenging issues, because of its relevance to

Glossary

- Chalimus (plural chalimi):** the four stages of immature lice fixed to the host by a frontal filament around which they feed on host mucus and skin.
- Copepodid:** post-naupliar larvae. In the case of sea lice the term refers only to the free-living, non-feeding, planktonic larva that must find a host to survive, as the next immature life-stage is called the chalimus stage.
- Degree days:** in aquaculture, the sum of temperature degrees experienced daily (e.g. 40 days at 10 °C = 400 °d). It is a useful index of the temperature required for the growth and development of ectotherms within their range of tolerance.
- Diel:** over a 24-hour period of night and day.
- Epizootics:** epidemics in non-human species.
- Fallowing:** the process of leaving cages on a farm site empty of fish so as to interrupt parasite and disease cycles and/or to enable the seabed to recover from waste sedimentation.
- Frontal filament:** an organ attaching chalimi and moulting mobiles of *Lepeophtheirus salmonis* to the host.
- Mobile lice:** pre-adult and adult stages that move freely over the host fish. Commonly referred to as mobiles.
- Nauplius (plural nauplii):** two life-stages of free-living non-feeding planktonic larvae that hatch from the egg and moult to become copepodids.
- Ovigerous female:** a female louse carrying two conspicuous uniseriate egg strings containing a total of 100–1000 eggs.
- Parasiticide:** a chemical or chemotherapeutants used to kill parasites. Can be called a medicine, pesticide, or drug in different countries.
- Pre-adult:** immature mobile louse. There are two pre-adult stages in *Lepeophtheirus* species and there is some debate as to whether they occur in *Caligus* spp.
- Pycnocline:** a zone of rapid change in density in a water body, typically attributable to temperature and/or salinity.
- Sea trout:** sea-running individual of the brown trout *Salmo trutta* L.
- Smolt:** juvenile salmonid fish physiologically adapted for living in seawater. The term is applied to fish immediately prior to their first migration from freshwater to the sea, and can be applied to farm fish within their first year in seawater.
- Uniseriate:** in a single row.



Figure 1. A typical heavy infestation of an Atlantic salmon by the sea louse *Lepeophtheirus salmonis*, showing removal of skin over the head, and female lice bearing paired egg-strings on the back. Reproduced with permission from Alan Pike.

Box 1. Sea louse pathogenicity

Sea lice use rasping mouthparts to graze the host and remove mucus, skin and underlying tissues [1] (Figure 1, main text). They can occur anywhere on the body but often congregate on the head in farmed and wild fish. They grip the host with their second pair of antennae and maxillipeds. Mobile sea lice are designed so that water flow presses them to the host surface over which they swim by jet propulsion. Some salmon leaping behaviour appears to be a response to irritation by sea lice [64] and an attempt to dislodge them [1]; this can attract predators, distract the fish and has energy costs. Impacts on the host skin include epithelium loss, bleeding, increased mucus discharge, altered mucus biochemistry, tissue necrosis and consequent loss of physical and microbial protective function [4,7]. In heavy infestations, chalimi can attach in such numbers that they can be lost from the fins as a result of skin erosion. The attachment of chalimi to the gills appears to be an artefact of laboratory conditions [65] and would explain their absence on the gills of wild fish [7]. However, it might also be due to loss of copepodids from the gills following initial settlement [63].

Host fish have reduced appetite, growth and food-conversion efficiency, and the stress and wounds expose fish to secondary infections [1], to which they are more susceptible [66]. Changes to the host blood include anaemia, reduced lymphocytes, protein, ion imbalance and elevated cortisol [4,7,8]. These changes indicate a stressed and weakened host, with reduced osmoregulatory and respiratory ability and impaired immunocompetence. In Europe, heavily infested sea trout return to fresh water prematurely [67], suggesting that this could reduce osmoregulatory stress and/or help remove lice. Laboratory studies found swimming performance of louse-infested fish improved when transferred from sea to fresh water [68]. Host blood is not an important part of the diet of sea lice, as suggested by some authors, and female lice do not ingest more than males as might be the case for blood-feeding parasites [69]. However, physiologically significant host blood loss can occur with high levels of louse infestation [70]. The risk that sea lice transmit bacterial and viral pathogens is a concern [71]. Although the risk is low for *L. salmonis* [2,7], it is higher for *Caligus* species because they occur on more host species and adults of at least *C. elongatus* occur in the plankton [1].

transfer within and between fish farms and also from farms to wild fish populations. Here, I focus on the patterns of sea louse infestation and the aspects of their biology that influence transmission, because these issues have received least attention in previous reviews [2,4,7,8]. Space limitations require that references given are those published since previous reviews on aspects of this subject [1,2,4,5,7–9]. It should be noted that many observations in the literature have not been replicated across localities, populations or species, and future studies are needed to test the generalizations drawn from previous studies.

Infestation patterns

Although the abundance of sea lice depends on their intrinsic fecundity and rates of growth and development, it could also depend on density-dependant competition within and between species, and on host responses to infestation. Key factors affecting these characteristics and interactions include sea temperature, and host abundance and distribution. The concentration of hosts on salmon farms has increased lice abundance locally, with consequences for lice infestations on farmed and wild hosts.

Louse population dynamics

Sea louse growth is strongly dependent on temperature. In the laboratory, the generation time from egg extrusion to

Box 2. Sea lice in salmon farms

Lepeophtheirus salmonis parasitizes Salmonidae in the northern hemisphere oceans: it has been recorded on 12 species in the genera *Salmo* (North Atlantic salmon and trout), *Salvelinus* (trout and charr) and *Oncorhynchus* (Pacific salmon) [2], and two species of cyprinids in marine waters in and near Japan [9]. In Chile, *Caligus rogercresseyi* Boxshall and Bravo, 2000 is the dominant species on farmed salmonids. In Japan, *L. salmonis* is present on farmed salmonids, but it is *C. orientalis* Gussev, 1951 that is the more pathogenic [9]. *Caligus elongatus* Nordmann, 1832 is common on farmed salmonids in the northern hemisphere and is sometimes pathogenic, and like *C. orientalis* (in Japan), *C. clemensi* Parker and Margolis, 1964 (in British Columbia) and *C. rogercresseyi* and *C. teres* Wilson, 1905 (in Chile), it is not host-specific [8,72]. Although *L. salmonis* is the most pathogenic species on Atlantic farms, probably because of its larger body size, it is also more prevalent and persistent on farmed fish than *C. elongatus*.

Salmonids are probably secondary hosts to the other *Caligus* species recorded on farmed fish, as most are known to occur on one or more wild non-salmonid hosts [8]. Nevertheless, these lice can be pathogenic to their secondary host, and it is crucial that the parasites are correctly identified to understand their origins. One species, *C. rogercresseyi*, was only recently described from farmed salmon in Chile, where it had been mistakenly identified as *C. flexispina*. Genetic analysis indicates that the apparently widespread *C. elongatus* consists of at least two genetically distinct populations in the North Atlantic, both occurring on the same and a variety of hosts [41,72], and that North Atlantic and Pacific populations of *L. salmonis* are distinct [35]. This demonstrates the need for continued taxonomic research on caligids and their hosts and for new identification guides. Louse species have varying environmental tolerances, behaviour as adults and larvae and growth and survival on different hosts, yet species identity has not been well determined in studies aimed to determine whether sea lice spread from farms to wild fish [29,43]. Differences between different host and parasite species, as well as different developmental stages of the host and parasite, must be clarified to prevent confusion in modelling epidemiological impacts of sea lice and developing integrated pest management strategies.

mature adult for *L. salmonis* and *C. elongatus* on Atlantic salmon is ~40 days at 10 °C (i.e. 400 degree days) for males and ~10 days longer for females [1,2,10]. Generation times can be shorter for *C. rogercresseyi* [11], and if derived from monitoring field populations, generation times can appear longer because cohorts are not as synchronized as in the laboratory [11]. In addition, development rates can vary on different hosts [7]. Typically for crustaceans, sea lice live longer and grow larger at colder temperatures, and larger females produce more eggs [2]. Consequently, overwintering females are larger and release more eggs in the spring than summer brooders. Because spring eggs are also larger, spring larvae have greater food reserves and thus they might spend longer in the plankton searching for a suitable host. Laboratory studies could determine larval viability in relation to parent body size and larval size. Although summer generations of females are smaller and have fewer eggs per brood because of the shorter generation time at warmer temperatures, the summer populations can increase exponentially. The different temperature regimes in salmon farming areas (1–14 °C in Atlantic Canada, 6–18 °C in Ireland and 1–20 °C in some Norwegian fjords) are thus likely to result in different sea louse population dynamics. However, further research on different sea louse species and populations is required to explain variation in their development

Box 3. Sea louse life-cycles

Sea louse eggs are carried in a pair of uniseriate strings of ~100 to 1000 eggs extruded from the abdomen of the female [1] (Figure 1). The number of eggs per sea louse varies with time of year, louse size, louse age, host species and population and is affected on farms by the effects of parasiticides [1]. The use of 500 eggs per sea louse on farmed salmon and 1000 on wild fish for modelling louse populations [25] would thus have been conservative in estimating production of sea lice on farms. Further quantitative data on the relationship of egg production to the above variables is important for assessing infestation risks [10,73].

The eggs hatch in sequence from the distal end and the female can produce six to eleven broods [2]. Two nauplius stages of larvae are non-feeding and planktonic for 5–15 days (temperature-dependent) and moult into infective free-living copepodids that attach to a host by their antennae [1]. Eggs manually removed from the female hatch in the laboratory and can be easily reared to copepodids. Evidence suggests that copepodids (i) respond visually to host shadows and flashes from host scales, (ii) use mechanoreceptors on their antennae to respond to vibrations such as those a host creates and (iii) use chemoreceptors to determine host suitability (and later mate detection) [2,11,74]. Recent research also indicates that copepodids and mobile lice could use water-borne chemical cues (semiochemicals) to recognize hosts [75].

The copepodid moults into a chalimus that is attached to the host by a special frontal filament [2]. There are four successive sessile chalimus stages that feed on the host skin around their point of attachment. In *Lepeophtheirus*, but not necessarily in *Caligus* species [5], there are two immature pre-adult stages that move freely over the host skin to feed. These mobile stages attach to the host with a chalimus-like filament when moulting [2]. Although Kabata suggested in 1972 (reviewed in [5]) that all Caligidae have ten life-stages (two nauplius, copepodid, four chalimus, two pre-adult, adult), and that the apparent absence of one or two pre-adult stages in descriptions of some *Caligus* species was an oversight by researchers (including himself), a recent review considers *Caligus* species to have no pre-adult stage [5].

Although direct measurement of individual life-spans is difficult, laboratory studies and the fact that lice over-winter on wild salmon [48] indicate individuals can live for over seven months. The loss of lice from fish in the laboratory cannot be assumed to be natural mortality as sea lice can easily escape from outflow pipes, and where mortality occurs this might reflect suboptimal environmental conditions (e.g. poor water quality).

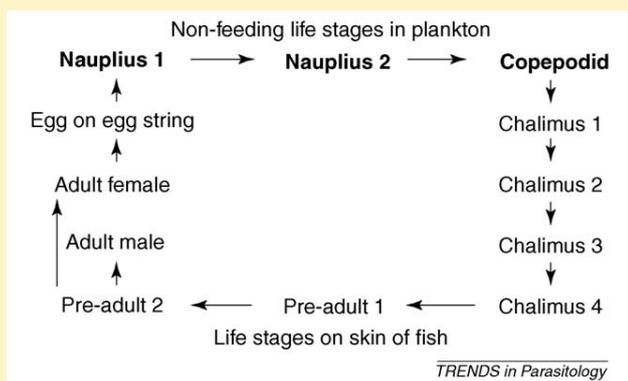


Figure 1. The ten life-stages in the life-cycle of the sea louse *Lepeophtheirus salmonis*. Free-living planktonic stages are shown in bold.

and fecundity with temperature [10]. In addition, how the parasite–host interaction varies with temperature, as well as with the parasite and host species, remains unstudied, despite its implications for fish health management on salmon farms.

Temperature-dependent life-cycle characteristics have important implications for louse control on farms (Box 4).

Box 4. Sea louse control on salmonid farms

The following guidelines give the best practice for sea louse control on salmonid farms [76]:

- To break the population cycle of sea lice, farms should have a fallow period during which no farmed fish are present in an area for 4–6 weeks. This is facilitated by having only one year class of fish per site.
- Cleaner-fish should be stocked into fish cages where they are available.
- In-feed parasiticides should be given to smolts in freshwater tanks before transfer to sea cages and louse abundance should then be monitored to guide future treatment.
- Sick (moribund) fish should be removed from sea cages and net fouling should be minimized to maximize water flow.
- If present, lice should be treated during the winter to remove egg-bearing females before the spring.
- Where parasiticides are used regularly in an area, louse sensitivity (resistance) to them should be monitored.
- The health status of fish stocked into a farm should be made known to neighbouring farms.
- Prevention of escaped salmon will reduce the risks of transfer to other farms and wild fish.
- The potential of transfer of sea lice (and other pathogens) should be considered in the selection of farm sites.

Cleaner-fish were the first successful use of biological control in finfish culture; they include five species of wrasse (Labridae) in Europe [1,77]. Wrasse remove larger lice first, thus eliminating egg-bearing females and do so without stressing the salmon, with consequent benefits in growth and food-conversion efficiency. If wrasse escape or insufficient numbers are available, a parasiticide treatment can be undertaken, even with wrasse in the cage. This practice is well-established in Norway, including the use of novel fisheries and traps and special good husbandry practices [78–80].

Parasiticides against sea lice can be applied as an in-situ ‘bath’ by enclosing the salmon cage in a plastic covering, or they can be mixed with the food pellets as ‘in-feed’ treatments [1]. Bath treatments are generally less effective because it is very difficult to get a uniform concentration within the cage, so some lice are not removed and concentrations can stress the fish [1,81]. In addition, crowding stresses the fish, and it is very difficult to treat all cages on a site on the same day so lice can transfer to re-infest fish previously treated in other cages. However, in-feed treatments cannot be used when fish are not feeding. Furthermore, because they are systemic, it takes longer for levels in the fish to be reduced to those permissible for human consumption; which might delay harvest. The initial parasiticides used against sea lice were baths of the organophosphates trichlorvos and dichlorvos, now replaced by azamethiphos (also an organophosphate), cypermethrin and deltamethrin (permethrins) and hydrogen peroxide. The in-feed treatments are the chitin synthesis inhibitors diflubenzuron and teflubenzuron and the most popular sea louse parasiticide emamectin benzoate. Resistance to organophosphates, permethrins and hydrogen peroxide has been recorded [82–84].

Increased average sea temperatures, whether due to annual variation or as predicted by climate change scenarios for future decades (<http://www.ipcc.ch>), are likely to increase louse abundance on wild and farmed fish as a result of shorter generation times. In addition, they are likely to affect the geographical distribution of sea lice and their wild hosts, potentially bringing new sea louse species into contact with wild and farmed fish. Moreover, locally increased maximum temperatures might stress sea lice and/or their hosts.

Treatments that remove egg-bearing females during the winter or early spring could prevent the release of many larvae during the spring, leading to lower infestations on farmed and possibly wild salmon in the vicinity (Box 4). If a

farm is exposed to infestations (from other farms or from wild fish) during the summer, parasiticide treatments are required more frequently to interrupt the life cycle and prevent exponential population growth. If a treatment affects only mobile stages, then repeat treatments are necessary when the chalimus stages moult to pre-adults, perhaps only every one or two weeks at summer temperatures.

Intra- and interspecific competition

Competition for mates and avoidance interactions can affect the distribution of lice on the host. Adult male lice actively compete for and guard females before mating. Although the male transfers a spermatophore that blocks the female from further mating [12,13] for a time, females can mate again and polyandry is common [14]. Sperm storage reduces the need for mating at low parasite densities.

The fact that the first infestations on farms are often *C. elongatus*, later replaced by *L. salmonis*, which thereafter remains the dominant species [15], suggests density-dependent inter-specific competition. Schram *et al.* [16] rejected competitive exclusion between these species, but the intensity of infestation on the wild sea trout (*Salmo trutta* L.) that they analysed was low (< 0.04 lice g^{-1}), so it is possible that no competition had occurred. Variation in the abundance of *C. elongatus* over time is greater than might be expected from population growth and mortality on wild sea trout [16] and on farmed Atlantic salmon [17] and suggests that mobile stages might infest and leave their hosts. Although in the past *L. salmonis* has typically increased in abundance on farms despite anti-parasite 'bath' treatments [17], *C. elongatus* abundance is similar on farmed salmon in their first and second sea-years. This suggests re-infestation from wild sources, which could explain the lack of benefit of parasiticide treatments for *C. elongatus* on Scottish farms [17].

The prevalence and intensity (i.e. abundance on infected fish only) of sea lice generally increases with the age of wild Pacific salmon and with fish size. However, louse intensity per unit area of fish surface does not increase with fish size [18,19], suggesting a maximum intensity of lice per host. This could be a consequence of antagonistic interactions (interference competition) between sea lice jockeying for the best positions or competing for mates and/or the host being able to shed parasites by physically dislodging them. Immunological factors might be involved whereby an increased host response offsets the increase in the sea louse population. For example, if the host developed significant immunity with age or duration of infestation, decreased louse intensity would be expected, as occurs for other ectoparasites [1]. One study found that repeated laboratory infections of Atlantic salmon with *L. salmonis* do not predict later levels [20], but another suggested that prior louse infestation stimulates genetically based resistance of Atlantic salmon to *L. salmonis* [21]. Thus, before it can be concluded that no long-term immune protection develops in individual fish, such experiments need to be repeated at different louse intensities on fish of varying age, size, genotype and physical condition.

Louse productivity

Most sea louse larval production in Ireland [22,23], Scotland [24] and Norway [25] is currently from salmon farms, because there are far more farmed than wild Atlantic salmon in coastal waters and farmed salmon are present all year around. By contrast, wild salmonids migrate from their natal freshwaters to the sea annually, and some species move away from coastal waters during their marine residence. In Norway, there are 100 times more farmed than wild salmon, and escaped farm salmon have 10 times more lice than wild salmon [26]. Thus, escaped fish could be a significant reservoir of sea lice and could bring sea lice into close proximity to wild fish. Significant numbers of escaped farmed salmon also occur in the lower Bay of Fundy, Canada, and their louse burdens are similar to levels on wild fish and on nearby farms [27], suggesting a common infestation pool. More significant reservoirs of lice occur on wild salmonids in the northern Pacific Ocean than in the Atlantic Ocean because more species of salmonids occur there and these fish are more abundant. This exposure to infestation from wild fish is a concern for Pacific farms, but transfer of lice from farms to wild fish could also be locally significant [28,29].

Aggregation of lice on hosts

On wild fish and during the early stages of farm infestations, the frequency of occurrence of lice on the host population is highly aggregated and the numbers of chalimus are fewer than of mobile stages [1,30], reflecting the longer duration of the mobile life stage. This aggregated distribution is typical of most parasites, with most hosts having few or no sea lice. By contrast, when pathogenicity occurs on farmed and wild fish, all or almost all hosts are infested, and the abundance of lice increases (Figure 2). Concomitantly, the frequency distribution of parasites changes from highly dispersed to normal [1], a pattern generally considered to indicate parasite-induced mortality [31]. Epizootics on wild sea trout smolts [1] and wild juvenile Pacific salmon [28] are characterized by the dominance of chalimus stages. Laboratory infections typically have a normal distribution, probably related to more homogenous experimental infestations, but also perhaps the result of lower genetic variation in farmed fish [18].

Abundance of pathogenic lice

The prevalence (% population infested) and the abundance of lice on hosts increase in concert and show similar patterns for wild Pacific and Atlantic salmon and for sea trout in areas without salmon farms (Figure 2). Sea trout in areas with salmon farms generally have more sea lice at all levels of prevalence, reflecting the higher proportions of chalimi. Epizootics recorded on sea trout in Europe and Pacific salmon in British Columbia tended to have over 60% prevalence and more than five lice per fish. Such louse levels have occurred on wild fish (Figure 2), and more heavily infested fish might not live to be sampled. Although this suggests that lice are pathogenic to more wild populations than previously appreciated, it should be noted that Pacific salmon are less impacted by *L. salmonis* than *Salmo* spp., and larger fish can support more sea lice. Levels of infection of < 0.1 mobile lice g^{-1} (i.e. ten lice on

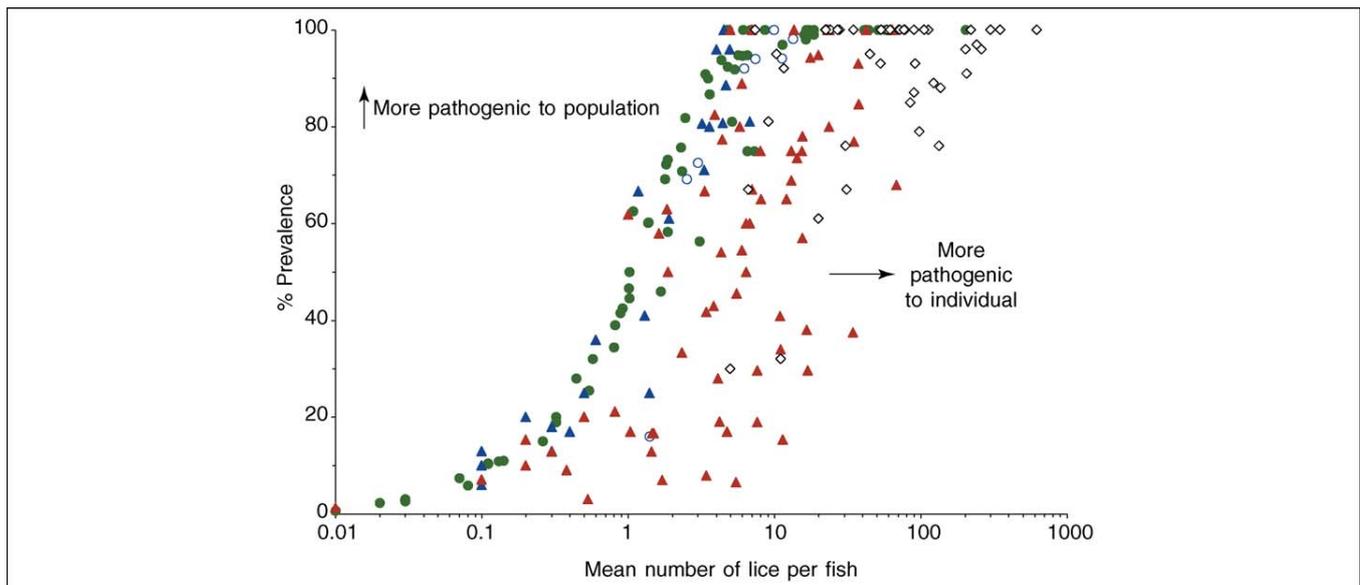


Figure 2. Relationship of mean *L. salmonis* abundance to prevalence on samples from wild salmonids. Solid green circles, Pacific salmon; open blue circles, Atlantic salmon; blue triangles, sea trout outside areas with salmon farms; red triangles, sea trout within areas with salmon farms; open black diamonds, samples from epizootics on wild sea trout and sockeye salmon that represent known pathogenic infestations. Numbers include pre-adult, adult and chalimus stages, but the chalimus stages might have been underestimated in some samples. Sample sizes and host body size varied. The occurrence of some wild fish data within the area encompassed by the epizootic data, and the higher abundance on sea trout in areas near salmon farms, suggest that levels on wild fish above 60% prevalence and five lice per fish were pathogenic. The data and sources used to compile the figure are detailed in the Online Supplementary Material.

100 g fish) in experimental infections caused changes in host physiology, biochemistry and immunology, in both the presence and absence of a host stress response [7,8]. Farm observations suggest that more than ten mobile lice per fish reduce the appetite of a 3–4 kg Atlantic salmon [32,33], and five per fish (~ 0.05 to 0.1 mobile lice g^{-1}) generally trigger treatment of smolts on farms. Thus, experimental infections of individual fish, farm experience and patterns across populations indicate that more than 5–10 lice per fish (> 0.1 lice g^{-1}) can or will become pathogenic.

Transmission

How copepodids increase their chances of intercepting a host has been one of the most challenging questions for researchers. The diversity of caligids, many specific to certain species, genera or families of marine fish, demonstrates effective host-specific transmission. Microsatellite [34] and mitochondrial [35] DNA analysis showed that *L. salmonis* is a single population in the North Atlantic, but Atlantic and Pacific populations were distinct, reflecting dispersal by their migratory hosts and planktonic larvae. Although genetics cannot discriminate between populations of sea lice on wild and/or farmed fish [36–38], measures influenced by diet such as carbon–nitrogen stable isotope ratios [39], and by diet, environment and genes such as elemental signatures [40], can do so. Furthermore, genetic analyses of other louse species have found sub-populations or cryptic species, illustrating the need for caution in generalizing between populations and species [41].

Distribution of louse larvae

Epizootics of sea lice on wild fish consist almost entirely of chalimus stages [1,28] (Figure 2), indicating that the fish simultaneously encounter high concentrations of the

infective planktonic copepodids. Plankton sampling in sea inlets in the mid-west of Ireland revealed that louse larvae, especially infective copepodids, are most abundant in shallow estuarine areas, ideal locations to intercept migratory salmonids [42]. These studies revealed a rapid decrease in sea louse nauplius concentrations away from fish farms, but no such trends for copepodids. Sampling programmes in two Scottish lochs repeatedly produced the highest concentrations of copepodids in shallow water near the estuary mouth [43,44]. Indeed, the highest concentrations of these larvae were caught with hand-nets by researchers wading along the shore, rather than from nets towed by boats. It thus seems that *L. salmonis* larvae not only move vertically in the water column, but are transported horizontally towards shallow waters, where salmonids are more abundant. An alternative hypothesis to explain estuarine concentrations of copepodids is that ovigerous lice detach from salmonids that are migrating up rivers and the eggs survive and hatch in the estuary [42]. This hypothesis was proposed in part because the observed gradient of decreasing concentrations of nauplii 2 km from a fish farm was interpreted as requiring an alternative source of louse infestation in the estuary. However, the same study found no such gradient for copepodids, and all other evidence suggests that larvae with a planktonic life span of several days disperse over much greater distances than 2 km (see below). Furthermore, *L. salmonis* do not fall off their host until in fresh water for some days and their eggs do not hatch in fresh water [1].

Larval dispersal

Lepeophtheirus salmonis do not find their hosts only in estuaries. The presence of chalimi on wild salmon in the

offshore Atlantic and Pacific oceans indicate they receive low levels of *L. salmonis* infestation when away from the coast [9,46–48]. The typical development of infestations on farmed salmon indicate that many larvae are available to re-infest their parent's hosts, and plankton sampling has shown that not all copepodids disperse away from the cages [42]. A study on *C. elongatus* infesting haddock (*Melanogrammus aeglefinus* L.) suggested that louse larvae are distributed in a mid-water layer and intercept haddock that swim through this zone [1]. Salmonids typically feed at the surface in farm cages and also come near the surface to feed in the wild. Thus vertical movement of sea louse larvae or their hosts could increase opportunity for parasite–host contact.

Significant correlations between *L. salmonis* abundance on salmon in farms and on wild sea trout in Ireland has been found up to 30 km from the farms [7,22]. Salmon on Norwegian farms that are > 10 km apart seem to have fewer lice [49], as do pristine areas where farms were absent [46]. A field and modelling study in British Columbia found that larval dispersal and infestation on wild salmonids extends 30 km from a farm and that secondary production of lice from infested migrating wild fish is detectable up to 75 km from the farm [29]. Sea louse larvae could disperse in a concentration gradient that depends on tidal currents and prevailing wind patterns [43,44,50].

Studies on other marine organisms that disperse in the plankton have demonstrated passive transport of 2–23 km in one 6 hour tide for seagrass [45], and mussel larvae can disperse an average of 20–30 km and have a population range of 60 km [51]. Decapod and cirripede crustaceans can invade new areas at a rate of 33–160 km per year [52]. From known larval survival data and dispersal distance it is possible to predict that louse larvae could disperse an average of 27 km (range 11–45 km) over 5–15 days [53]. Predicted average dispersal of sea louse larvae ranges from 12 km (range 5–17 km) in low currents ($\sim 5 \text{ cm s}^{-1}$) to 47 km (range 23–70 km) in higher currents ($\sim 20 \text{ cm s}^{-1}$) (B. Kinlan, personal communication). This suggests that sea louse larvae can typically disperse 10–50 km. However, the interaction between larval behaviour and local hydrographic conditions can vary locally and could lead to larval retention within some areas [23]. Simple diffusion models predicted dispersal of louse larvae from a farm in British Columbia and subsequent infestation of juvenile wild fish [29]. The species of sea lice infesting the farm was not reported, but 53 of the 65 ovigerous lice on juvenile wild fish were *C. clemensi*, a species found to infest returning wild Pacific salmon in these coastal waters [54]. The dispersion model could apply to this species or both it and *L. salmonis*. The abundance of *L. salmonis* on wild fish has also been linked to farms in the area [28].

Behaviour of Lepeophtheirus salmonis larvae

Larvae of many species, including crustaceans and molluscs, migrate vertically with diel and tidal periodicities, with consequent transport into or out of estuaries and thus settlement in their preferred habitats [55–57]. Copepodids of the copepod parasite *Lernaenicus sprattae* (Sowerby, 1806), and their juvenile fish hosts, concentrate at the sea

surface at night [1]. Some populations of scallop larvae have vertical migration adapted to local hydrographic conditions [55]. The evidence suggests that *L. salmonis* behaviour facilitates interception of salmonids migrating through estuaries. The fact that it survives much longer in fresh water than *C. elongatus* [1], up to 14 days when attached to its host [58], could be an adaptation to survive on hosts that frequent brackish waters.

Both active and passive mechanisms to aid host interception are probably involved. The larvae might have endogenous tidal rhythms, respond to sunlight, moonlight, salinity or water pressure, or detect turbulence associated with high current velocities to stimulate upward swimming and thus position themselves to be passively transported in tidal currents as other larvae do [7,55,56,59,60,61]. The larvae of many species concentrate along pycnoclines [61], and vertical migration and reaction to salinity gradients is known for *L. salmonis* larvae [62]. In laboratory flumes, copepodid attachment to hosts was greatest in conditions of medium light (300 lux), full salinity (35 parts per thousand) and low velocity (0.2 cm s^{-1}) [63].

Sea louse infestations have been observed to arrive in pulses. This could be a passive consequence of lunar periodicity of the tides; the difference between spring and neap tides can result in concentration or dilution of sea louse larvae through changes of 25–30% of the tidal seawater volume in a bay. The risk of dilution could be offset by larvae concentrating in surface waters and against haloclines. Further research into these mechanisms will enable more spatially explicit estimates of the risk of infestation on farmed and wild fish.

A transmission model for L. salmonis

The following process could explain how sea louse larvae of *L. salmonis* are transported and concentrated into shallow coastal and estuarine waters that salmonids frequent. Nauplii swim upwards during the day but do not actively swim downwards. They are thus likely to concentrate in surface waters. During the day, onshore winds generated by thermo-convection from warmer land drive surface waters containing the sea lice towards the shore and towards estuaries (as these are further inland). Where fresh water lies on the surface, sea louse larvae can congregate along the halocline. Thus larvae can concentrate at the surface and/or the marine–freshwater interface, which salmon smolts migrate through to enter ocean waters. Tidal currents increase in estuaries as the tidal volume is forced into a narrow channel. This increase in current velocity increases the likelihood of copepodids being close to a potential host, although host attachment might be more difficult in stronger currents [63]. These options for the transmission model could be tested by giving particles a daily vertical migration behaviour in a previously validated 3D hydrographic model that includes wind direction. A consequence of this transmission mechanism is that the risk of infestation could be at least as high near the shore and in estuaries as at an infested fish cage. This was the pattern observed on salmon in experimental cages in Killary Harbour, Ireland [42].

Future research

The most abundant and pathogenic sea lice on farmed fish in Chile was recently found to be a species new to science, and the commonest species in the North Atlantic, *C. elongatus*, has at least two genotypes. These findings emphasise the need for more basic research on sea louse taxonomy and natural hosts.

Research indicates roles for both the host immune response in reducing sea lice impacts and the parasite in suppressing such responses [8]. The former could reduce louse development, fecundity and/or survival and be heritable. Further research integrating selective breeding and fish health management, including dietary and immune stimulants, might produce new methods of reducing louse abundance and impacts on farmed fish that complement existing control measures.

The rate of development of sea louse species has been shown to be strongly temperature-dependent. However, how the parasite–host interaction varies with temperature has not been studied, and the effects of extreme temperatures on sea louse development and fecundity, and on host sensitivity, are largely unknown. The interaction between temperature and female body size on sea louse development and viability of planktonic larvae is important in estimating louse production, and is amenable to laboratory experiments.

Experiments to determine whether competition within or between mobile stages of louse species on their host limits abundance on hosts will help us to understand whether densities observed on wild fish are kept below pathogenic levels by parasite interactions or a host response. If neither is the case, then high louse prevalence and abundance could indicate mortality of more heavily parasitized fish.

Sea lice are widespread on wild fish, but pathogenic infestations take at least months to develop in salmon farm cages. Thus, by fallowing and locating cages away from where wild hosts and louse larvae congregate and distant from neighbouring farms, the risk of infestation can be reduced. However, further laboratory and field studies on louse behaviour and sensory biology are required to elucidate larval dispersal and host-location mechanisms, especially for *Caligus* species. The mechanism proposed here, with *L. salmonis* larvae concentrating in shallow surface waters and estuaries, should be modelled and tested. This knowledge of louse transmission is crucial for farms to estimate the likelihood of transmission of lice from other farms and between farm and wild fish populations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.pt.2006.08.006](https://doi.org/10.1016/j.pt.2006.08.006).

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