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REVIEW

# Searching for sea lice: surveillance to assess environmental infection pressures to model and inform sea lice infestation management

**Berit Rabe[1,*], Alexander G. Murray[1], Stephen C. Ives[1], Meadhbh Moriarty[1], David J. Morris[2]**

[1]Marine Laboratory, Marine Directorate, Aberdeen, AB11 9DB, UK
[2]Salmon and Freshwater Fisheries Laboratory, Marine Directorate, Pitlochry, PH16 5LB, UK

ABSTRACT: The expansion and development of sustainable salmon aquaculture requires research, innovation and, where necessary, regulation to manage environmental impacts. Sea lice are a key concern for marine salmonid fish aquaculture as these parasites adversely affect farmed and wild salmonids. Reducing the risk of harmful infestation levels requires appropriate data to support modelling and inform adaptive management processes. Throughout their life cycle, sea lice occur as either planktonic larvae or as ectoparasites on farmed, wild or sentinel fish host populations. Limited resources require surveillance methodologies and strategies for these stages to be optimized to obtain data that meet the specific needs of control. In this review we assess the different surveillance strategies available to inform the appropriate management of sea lice impacts on wild salmonids. We advocate modelling as the most effective way to use surveillance data, with subsequent model improvements informed by the continued input of collected data. A feedback loop is proposed of identifying/collecting empirical data to improve models, which in turn will direct more focused surveillance for future data collection and so drive adaptive management processes. In the future, surveillance monitoring, as part of an adaptive management regime in Scotland, should build on existing links between stakeholders and policy makers, and use both models and data to help the sustainable development of the aquaculture industry.

KEY WORDS: Sea lice · Monitoring strategies · Surveillance · Aquaculture · Salmon · Sea trout · Management · Feedback loop · Data collection

## 1. INTRODUCTION

### 1.1. Background

Salmon aquaculture is a key economic activity in cool temperate coastal areas, and its sustainable development supports UN goals for the Blue Economy (Lee et al. 2020). However, key risks to sustainability must be controlled. In the case of salmon aquaculture, such a key risk is from sea lice arising from farms impacting on wild salmonid populations (Taranger et al. 2015). Sea lice are also responsible for high economic costs on salmon aquaculture (Abolofia et al. 2017, Boxaspen et al. 2022, Boerlage et al. 2024). As sea lice are identified as a hazard, being a risk to both environmental and economic sustainability, controls must be implemented. The aims of these controls are laid out through various national legislations and the management methods developed through a range of specifically designed regulatory regimes, such as the 'Traffic

*Corresponding author: berit.rabe@gov.scot



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Light System' in Norway (Eliasen et al. 2021), or the 'Sea Lice Risk Assessment Framework' in Scotland (https://consultation.sepa.org.uk/regulatory-services/detailed-proposals-for-protecting-wild-salmon/).

Implementing effective policies to protect wild salmonids requires sustained data collection. These data can provide a direct assessment (e.g. exceeded threshold levels) and/or drive models to evaluate the impacts of policies by providing forcing values and enabling validation. However, the marine environment is large, and resources are generally limited, so surveillance schemes must be devised to maximise the value of collected data. An understanding of sea lice biology and interaction with hosts is required in order to identify what surveillance schemes will provide the most relevant data. The practical efficacy and costs of sampling must also be considered in developing optimal strategies.

The aim of the sampling and monitoring discussed here is to assess the impact of sea lice from salmon farms on wild salmonid fish. Given the life cycle outlined in Section 1.2, key data to monitor are (1) the production of lice from the salmon farms, (2) the distribution of planktonic lice, and hence infection pressure, in the water, and (3) lice abundance on wild fish (Moriarty et al. 2023a). This gives specific areas for surveillance that we explore in this review to identify optimal technical means and strategies, which will aid management. We review existing and new technologies, gaps for improvement, and how these technologies can be implemented. Monitoring data, modelling and management can iteratively inform each strategy, allowing each component to improve with time, thus developing a closer understanding of the true environmental conditions (Lynch et al. 2009) and enabling better knowledge for effective management (Fig. 1).

The scope of this review is restricted to surveillance ('Observations' in Fig. 1) to collect information on sea lice directly. Relevant data on wild and farmed salmonid host populations and their physical environment are also required to assess the extent of sea lice infections and impacts relevant for management, but such data-collections are not covered in this review. An exception is a discussion on monitoring or estimating numbers of fish on farms — but this is in the context of assessing sea lice population. Data on wild salmonid populations, such as smolt migration routes (e.g. Newton et al. 2021), are important for interaction with planktonic sea lice. Estimates of return rates of adult fish (Vollset et al. 2016, Shephard & Gargan 2021) or assessing smolt populations (e.g. by electrofishing in

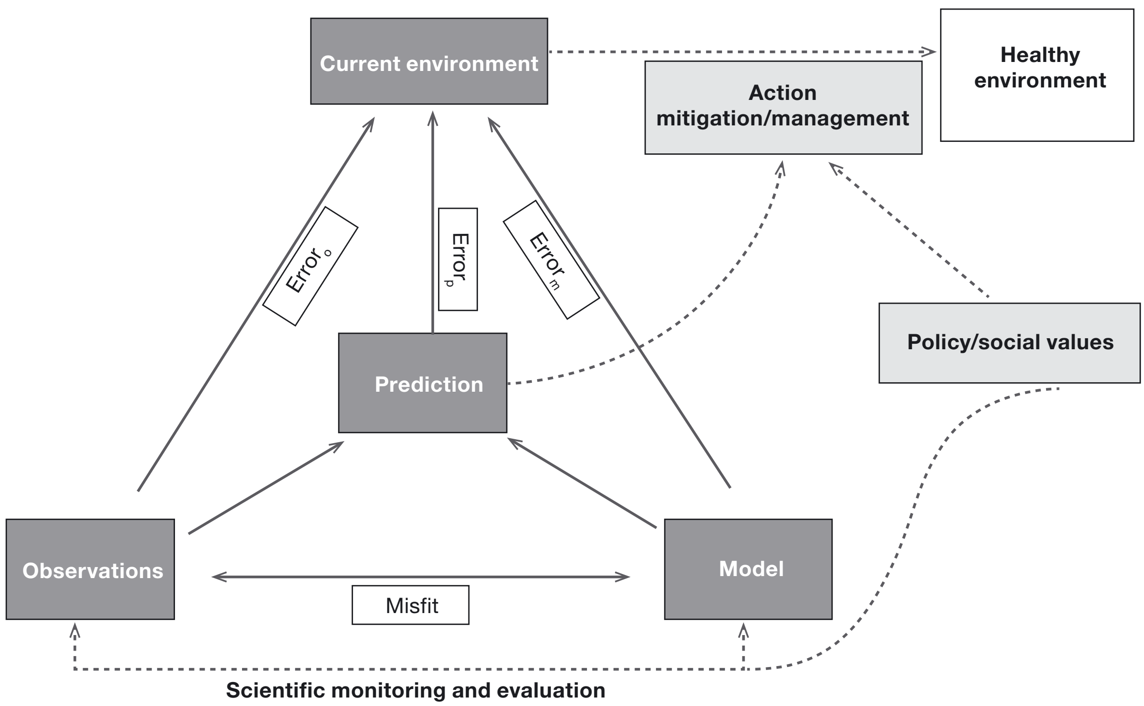


Fig. 1. Conceptual framework showing the interconnected nature of scientific monitoring and evaluation through observations and modelling (leading to predictions), highlighting how it influences actions through management to reach a healthy environment (expanding on the concept of the Observation/Prediction/Model triangle concept from Lynch et al. 2009). Error$_o$: error in observations; Error$_p$: error in predictions; Error$_m$: error in models. Solid arrows between dark grey boxes depict direct links while dashed arrows depict feedback and influences

rivers; Malcolm et al. (2019) are key targets for surveillance regimes for identifying risks to salmonid populations. Similarly, ocean currents and other physical environmental factors are key to sea lice transport and essential to drive dispersal models; examples of oceanographic surveillance programmes can be found in Asplin et al. (2014) and Salama et al. (2018). Finally, sea lice are only one of a multitude of pressures on wild salmonid populations; other pressures or their monitoring, such as climate change, invasive species, and river habitat issues (https://www.gov.scot/publications/scottish-wild-salmon-strategy/), are not discussed here either.

Following a brief review of sea lice biology (Section 1.2), this review is divided into 3 main sections. Section 2 explores the state of the art for sea lice surveillance techniques and methods. Section 3 discusses the application of these techniques, when combined with modelling, how surveillance can be optimised to address management concerns more efficiently, and how data can be used effectively beyond the local area. Section 4 investigates the potential for advancement and refinement of the sea lice management system in Scotland, and how data collection can be improved through iterative development of modelling and surveillance structures underpinning sea lice controls.

### 1.2. Sea lice biology

Sea lice on farmed salmon in the Northern Hemisphere are largely *Lepeophtheirus salmonis*, but several *Caligus* species can also parasitise the fish. *L. salmonis* is a specialist parasite of salmonids (Atlantic salmon *Salmo salar* and sea trout *S. trutta* in the North Atlantic, Arctic char *Salvelinus alpinus* in the far north, and a range of *Oncorhynchus* species in the North Pacific; Pike & Wadsworth 1999). *Caligus* lice are more generalists, although cryptic subspecies may infect different host species. Owing to the scale of aquaculture, the great majority of these salmonids are farmed salmon, and this greatly increased biomass of hosts distorts the dynamics of sea lice epidemiology (Dempster et al. 2021).

Both *L. salmonis* and *Caligus* spp. lice have a multistage life cycle (Hamre et al. 2013). Adult females produce egg strings containing hundreds of eggs, depending on environment and louse age (Brooker et al. 2018). Eggs hatch to produce planktonic nonfeeding nauplii, and after a second nauplii phase the survivors become infectious copepodids. These continue in the plankton until they either die or find a host. Planktonic phases last for a few days dependent on temperature (Samsing et al. 2016), and during this time the larvae may be transported over distances of kilometres by ocean currents (Salama et al. 2016b, Rabe et al. 2020). On infecting a host, the copepodids form a filament with which to attach, becoming parasitic chalimus. After a second chalimus stage the lice become mobile pre-adults and then sexually mature adults; it is these mobile lice that are associated with most impacts on the health and welfare of their hosts (Ives et al. 2023).

## 2. TECHNOLOGIES AND METHODS FOR SEA LICE SURVEILLANCE

### 2.1. Lice on farms: surveillance to estimate viable egg and larval production from farms

The number of adult female sea lice on farms, through the production of viable eggs, determines the number of larval stages that enter the marine environment. The number of nauplii produced at any one time on a farm can be calculated from (1) the number of ovigerous lice per fish (Section 2.1.1), (2) the number of fish on the farm (Section 2.1.2), and (3) the number of viable eggs produced per ovigerous female louse (Section 2.1.3). The accurate estimation of these parameters is critical for assessing salmon lice production by a farm. In addition to sea lice on farms, nauplii are also produced from infected wild salmonids. These hosts can be important in acting as an initial source of infection on farms, following area fallowing. However, for the main salmon farming areas of the Atlantic, such as Canada, the Faroe Islands, Scotland, and Norway, wild salmonids are estimated to account for only a small proportion of total sea lice larval production in coastal waters. In Scotland this is demonstrated by significant correlations reported between lice caught in plankton trawls and quantitiy of gravid *Lepeophtheirus salmonis* on local farmed fish, leading to the conclusion that it is the numbers in the farmed environment that drive numbers in the surrounding sea (Penston & Davies 2009). In Norway farmed hosts are estimated to account for 98% of ovigerous female lice in the coastal environment (Dempster et al. 2021).

#### 2.1.1. Number of lice per fish

The availability and resolution of the lice data reported varies by country. For example, in Scotland, weekly average numbers of adult female lice per farmed salmon (AF) at the farm level have been published since April 2021 on Scotland's aquaculture website (https://aquaculture.scotland.gov.uk/), with monthly averages published between January 2018 and April 2021. Prior to 2018, only area-averaged counts were published by the Scottish Salmon Producers Organisation (now Salmon Scotland), as described in Hall & Murray (2018). These sea lice counts form the most comprehensive monitoring data set available on sea lice for Scotland, and these numbers are used to regulate for farmed fish welfare, as sea lice have detrimental effects on fish health. The Norwegian farm level lice counts (average numbers of female lice per fish) are published weekly online (every 2 wk if water is <4°C) (www.barentswatch.no) (Thorvaldsen et al. 2019). In the Faroe Islands a third party, Firum, carries out lice counts every 2 wk, reporting adult females (mobile and attached sea lice stages).

The count data for lice on farmed fish depend on an accurate sampling regime, based both on biological processes (e.g. louse development time and louse survival depend on temperature and salinity) and a standardised, statistically appropriate sampling design. Currently, farmed fish lice counts are done by catching fish from the cages where they are held and physically counting the lice on them. Bias or inaccuracy in sampling can result from poor techniques or gaps during the sampling procedure. For example, moribund fish may be easier to catch, but may also have higher lice loads, thereby exaggerating counts. During the process of catching and anaesthetising fish, sea lice may become detached. If sea lice detach during netting, they may be lost completely, thus reducing the count. If they detach during anaesthetising, the lice will be retained in the container where the fish are held and so can potentially still be counted; however, any detached lice cannot be attributed to a particular fish unless the fish are held individually. Detachment is not an issue for reporting the averaged sample count but does weaken understanding of the lice distribution on fish within the sample. The requirement to use anaesthetics introduces another problem because the need for a withdrawal period for human food safety reasons means lice counts may not be made in the days immediately prior to harvesting, which itself can occur over an extended period. Therefore, gaps can occur in monitoring; gaps may also be caused by poor weather preventing access to a farm for sampling of lice. Some evidence for bias occurring within sampling comes from reports from Canada that counts of *L. salmonis* were 18% higher in months when inspections were audited (Godwin et al. 2021). Jeong et al. (2023) also noted differences in sea lice counts above treatment thresholds in Norway relative to Canada, although these may relate to multiple factors, including differences in management, fish numbers, environments, or inherent population dynamics arising from frequency of delousing (Sævik & Sandvik 2023).

For all countries there are statistical considerations to address when collecting a sample that can accurately represent the population average of lice per fish on a farm. Sea lice populations are clustered between cages, and so sampling must be designed to account for this clustering (Revie et al. 2005, 2007, Heuch et al. 2011). For these reasons it is important to review routine sampling methodologies and update, if they are found to have a low level of precision, as practises on aquaculture farms change. Sampling methodologies, which require salmon lice to be recorded as adult female, mobile stages and attached stages, are adjusted seasonally and spatially in Norway (https://lovdata.no/dokument/SF/forskrift/2012-12-05-1140). During the wild salmon migration period, regulation requires that salmon lice must be counted on at least 20 random fish from each cage, while outside this period salmon lice must be counted on at least 10 random fish from each cage in the aquaculture facility. In Nord-Trøndelag and in the management areas to the south of this region the higher fish sampling is required from April (start of Week 14) to May (end of Week 21), whereas further north, in Nordland, Troms, and Finnmark, the higher fish sampling is required from mid-May (start of Week 19) to the end of June (end of Week 26). In Scotland, minimum sampling levels are specified under the 'Code of Good Practice for Finfish Production' (CoGP, https://thecodeofgoodpractice.co.uk). The CoGP requires a minimum sample of 25 fish obtained as 5 fish per cage, or 25 distributed evenly across cages, if there are fewer than 5 cages. A 25 fish sample means that a farm on the CoGP treatment threshold of AF = 0.1 has a 7% chance of returning zero lice under a binomial distribution and so may be statistically indistinguishable from a farm that is free of lice. However, this sample size is effective at detecting breaches of the official reporting threshold of AF = 2 lice fish$^{-1}$. At lower prevalence, lice numbers may become negatively binomially distributed (Stien et al. 2005, Heuch et al. 2011), meaning that if sampling the minimum recommended number of fish, there is an increased chance of only sampling unaffected fish, leading to a potential underestimation in the sea lice numbers. In this situation, prevalence may be used as an estimator of sea lice numbers, rather than abundance, therefore increasing the efficiency of the sampling effort (Baillie et al. 2009, Jeong & Revie 2020). In practice, farms often sample more than the minimum number of fish (for example one company's count protocol specifies 10 fish per cage), so lice detection is in practice more powerful than the CoGP minimum standard implies. Reporting only AF is specifically criticised by Jeong et al. (2023) because comparison of AF data with other lice stages provides a test that allows anomalies in these data to be identified.

#### 2.1.2. Number of fish on farms

Data on host numbers are a critical factor for understanding sea lice numbers on the farm. However, data on the numbers of fish on farms are not publicly available in many salmon producing countries, as they can be considered as commercially sensitive (Moriarty et al. 2024). This issue is overcome in Norway by confidential data sharing between farmers and regulators. In Scotland, no such data sharing exists at present; therefore other data must be used to estimate numbers of farmed salmon indirectly, e.g. estimates made from consented biomass (e.g. Moriarty et al. 2023a) for which data are published on Scotland's aquaculture website. This lack of explicit fish number data is identified as a major gap in data required for calculation of viable egg production, and hence source of infection pressure (Murphy et al. 2024). Estimates of biomass are published monthly, in arrears, so mean fish weight would allow an estimate of fish numbers. Producers closely monitor fish weight, as this is valuable information in preparing for harvest, and low weight can indicate poor health. Historically, both numbers and biomass of fish mortalities were reported (Salama et al. 2016a), allowing individual fish weight to be calculated. By assuming that dead fish weight was comparable to average fish weight, it was possible to estimate the number of fish from concurrently reported live biomass; however, fish numbers derived in this way would not be perfect. As numbers of dead fish are no longer reported, such estimations can no longer be currently made.

#### 2.1.3. Production of viable eggs per ovigerous female

Egg production per ovigerous louse is not generally monitored and assumptions are currently made as to the appropriate average number of eggs produced, e.g. 30 eggs $d^{-1}$ (Murray & Moriarty 2021, Moriarty et al. 2023a). However, production of viable eggs varies with temperature, salinity, host factors, and age of the adult female louse (Brooker et al. 2018, Moriarty et al. 2024). Without improved modelling of the relationship between egg production and viability with environmental and maternal factors, monitoring such data would currently be of limited value for assessing viable egg production due to small effort/return ratio. Viable egg production rate per ovigerous female (and risk factors associated with its variation) is therefore more of a gap for research than for monitoring per se.

### 2.2. Lice in the environment: surveillance of planktonic stages and infection pressure

Larval lice interact with migrating salmon smolts, resulting in infection rates assumed to be proportional to the lice concentrations encountered by the fish as they move through the coastal zone. Therefore, if concentrations are known, infection rates can be surmised from the models. Models of this process imply a threshold concentration of larval lice associated with an impact on smolt health (Sandvik et al. 2020, Murray et al. 2022, Moriarty et al. 2023a). Concentration can be predicted from the production of viable larvae (see Section 2.1.3), dispersal processes, and estimated mortality rates of the larvae (Moriarty et al. 2023a), or they can be sampled directly (the focus here). However, for managing and minimizing sea lice dispersal from farms, the fine-scale patchiness of planktonic lice in space and time (á Norði et al. 2015) is not relevant to practical management. Instead, simulating larval lice concentrations at coarser scales is less prone to error, particularly when considering the equally unpredictable movements of wild salmonids (Middlemas et al. 2009, Thorstad et al. 2012). Therefore, surveillance should aim to assess average concentrations or infection pressure over time periods (e.g. the few weeks in spring when salmon smolts migrate to sea) and areas (e.g. fjordic systems or sounds with high farmed salmon densities or high-risk wild salmonid populations) to best support sea lice management modelling. A range of surveillance methods have been used to sample sea lice in the water column and to assess the sea lice infection pressure in the environment (e.g. Penston et al. 2008, Salama et al. 2018, Skarðhamar et al. 2019, Pert et al. 2022). Lice concentrations and infection pressure from the planktonic phases of the sea lice life cycle require different metrics for assessment. Lice concentrations can be assessed by counting larval lice (Section 2.2.1), infection pressure can be assessed via sentinel cages (Pert et al. 2014a) (Section 2.2.2), and proxies for sea lice concentrations can be evaluated by developing sampling technologies, such as environmental DNA (eDNA) (Krolicka et al. 2022) or semiochemicals (Ingvarsdóttir et al. 2002), to improve detection and potentially reduce effort (Section 2.4). The techniques required to implement these methods have been recently described in Pert et al. (2022), and so we will keep discussion of the methods to a minimum and review the issues behind their application to provide surveillance data to assess infection pressure.

#### 2.2.1. Counting planktonic larvae

Sampling of plankton in the marine environment is well established; existing methods include the use of specifically designed nets towed by vessels, raised through the water column or, in shallow water, nets dragged by hand. Samples can be collected from specific point locations (i.e. vertical tows) or along transects (i.e. horizontal tows). Electric pumps can be used to extract plankton from a specific volume of water, forced through a collection net over a given time at specific locations, or by towing by boat. Advantages and disadvantages of plankton sampling overall and of individual sampling techniques are listed in Table 1.

One disadvantage for surveying plankton in the water column is the small area sampled, relative to the environment. Larval sea lice, like most zooplankton, tend to be patchy in both space and time (Haury et al. 1978), requiring sampling at multiple locations and times to provide confidence in population density assessments. Additional complications arise because, while other zooplankton species may be found at densities of 100s ind. $m^{-3}$ or even 1000s ind.$m^{-3}$, densities of sea lice are typically less than 1 ind. $m^{-3}$. In Loch Linnhe (Scotland), total zooplankton densities are typically around 1000 ind. $m^{-3}$ (Heath 1995), but densities can be substantially higher (Thompson et al. 2021). The relative low density of sea lice means volumes of water sampled must be 3 or 4 orders of magnitude larger than for other zooplankton species sampling regimes. Once sampled, identification from the other zooplankton needs to have a specificity >99.9% given their high concentration relative to salmon lice larvae to avoid a high proportion of false positives (Bui et al. 2021). Currently, sea lice collected in plankton samples need to be identified and counted manually under a microscope by experienced staff. This is a labour-intensive process requiring the identification of sea lice (and their life stages, if required) from a complex sample that may contain many other species (and stages) of copepods (Penston et al. 2004, 2011, á Norði et al. 2015, 2016, Skarðhamar et al. 2019). In some locations (e.g. Loch Torridon, Scotland; Penston et al. 2004, 2008) persistent concentrations of sea lice can be found; in other locations, these are transitory, and the samples may contain a high proportion of zero detections.

#### 2.2.2. Sentinel cages

The methodology of deploying anchored or 'fixed' sentinel cages to estimate the infectious pressure experienced by Atlantic salmon residing in a region has been developed and used in Scotland and Norway (e.g. Pert et al. 2014a,b, 2022, Sandvik et al. 2016, 2020, Salama et al. 2018). Published sentinel cage designs (i.e. Pert et al. 2022) are cylindrical (usually 0.8–1.5 m in diameter and 0.9–2 m deep), with each cage being supported by 3 or 4 weighted-down rings made of polyethylene pipe covered with 10–13 mm knotless mesh netting. A weight hung from a bridle under the cage is used to keep the tension in the net. Cages are stocked with salmon smolts (20–30 cm), typically originating from farmed stock (Pert et al. 2014a, 2023, Sandvik et al. 2016, 2020). Cages extend down in the top 3 m of the water column and, in Scotland, the deployments typically last around 1 wk (up to 4 wk in other countries). The length of deployment allows the origin of the population structure of the settled sea lice to be inferred due to the known maturation rates for *L. salmonis* (Johnson & Albright 1991) and *C. elongatus* (Piasecki & MacKinnon 1995) to develop from copepodid (first attachment stage) to mature louse: short deployments of sentinel cages mean that any mobile stages found on the fish would have to have been transported to the sentinel cage, rather than have developed from a resident lice population on the sentinel fish (Pert et al. 2014b). Further instrumentation can be attached to the outside of the cage, for example current meters or conductivity/temperature/depth (CTD) instruments, to provide additional relevant information. After the allocated deployment time, fish are removed from the cages and screened for sea lice (lice numbers, developmental stage, location on host). The anaesthetic water used during fish handling, together with handling nets, should also be examined to count any detached lice.

Sentinel cages directly sample infection rates. However, it should be noted that sea lice impacts are associated with mobile lice stages (Ives et al. 2024) and lice experience mortality between copepodid infection and becoming mobile (Tucker et al. 2002),

Table 1. Advantages and disadvantages of surveying planktonic sea lice in the water column in general and focussing on (1) plankton pumps (fixed deployment), (2) plankton pumps (towed deployment), and (3) plankton tows

| Option | Advantages | Disadvantages |
|---|---|---|
| Surveying planktonic sea lice in the water column in general | • Potentially sampling all planktonic stages<br>• Importance of all plankton stages: it allows age of larvae to be estimated<br>• Fixed area/depth sampling, possibility of programming to allow synchronous sampling strategies<br>• Little to no ethical/conservation considerations relative to other methods where fish welfare is of greater concern | • Catchability unknown<br>• Many counts with zero lice — lots of samples needed (therefore time consuming for analysis)<br>• Labour intensive — laborious processing of samples requiring specialised expertise<br>• Large potential for identification errors depending on analyst expertise<br>• Larval lice decay rapidly (time sensitive)<br>• Potential for lice damage, lice escape after collection<br>• Relatively small area/volume sampled (might miss patches of plankton in time and space)<br>• Nets/pumps can clog, and clogging can go unnoticed during tows or deployment<br>• Sampling is weather dependent<br>• *Caligus* copepodids and naupllii difficult to positively identify without suitable microscopy (i.e. using maxiliped spurs), subtle difference in carapace can be used but requires experienced viewer<br>• Boat sampling (used in all but very shallow and confined locations) is logistically complex and costly |
| (1) Plankton pump, fixed deployment | • Identify depth of lice<br>• Allows targeted measurements in both space and time of specific water volumes<br>• Complementary CTD monitoring possible | • Time and labour-intensive deployment<br>• Potential for retrieval to be delayed by unexpected weather change, leading to spoiled samples<br>• May require frequent cleaning in summer due to biofouling<br>• Clogging issues |
| (2) Plankton pump, towed deployment | • Spatial coverage<br>• Large transects can be achieved and subdivided<br>• Different depths can be examined<br>• Combining techniques of pumping and towing<br>• Complementary CTD possible | • Requires a larger boat with lifting capacity (e.g. derrick)<br>• Need to maintain constant depth which can be challenging<br>• Potentially difficult to deploy and retrieve |
| (3) Plankton tows | • Spatial coverage<br>• Can be deployed on any boat (e.g. commercial, ferries)<br>• Smaller boat is more appropriate due to displacement of water (depending on net deployment)<br>• Can be done from shore in some circumstances<br>• Vertical and horizontal tows possible | • Need to maintain constant depth (for horizontal tows) which can be challenging<br>• Net can clog reducing effective sampling |

so estimates of impact from sentinel cages have to be adjusted for this mortality (Moriarty et al. 2023a). As sea lice in the sentinel cages have not completed their maturation, their mortality is less than mobile lice would have experienced. The infection pressure to which fish in a sentinel cage are exposed is integrated over the deployment period, smoothing out potential effects of short-lived copepodid patchiness (compared to plankton samples at specific points in space and time). This infection pressure is for a specific location, though, and does not account for variability due to behaviour and migration of free-swimming wild fish. In Norway, an experiment was carried out towing a sentinel cage containing Atlantic salmon smolts from the river Vosso along the fjord and towards the open sea to simulate a migration (Vollset et al. 2014), and Vollset et al. (2016) modelled the effect of migration behaviour on mortality. Research in Scotland has examined the feasibility of towing sentinel cages to assess infection pressure on actively migrating fish (Pert et al. 2022, 2023). Table 2 lists advantages and disadvantages of fixed vs. towed sentinel cage methods to assess direct sea lice infection pressure on fish.

### 2.3. Lice on wild fish: surveillance of lice numbers on wild fish to determine exposure levels

Surveillance of sea lice numbers on wild salmonids can be used as a direct assessment of the infection pressure encountered by these fish. Regular surveillance of lice counts on sea trout has been carried out in Scottish coastal waters as an indicator of lice numbers on wild fish (Middlemas et al. 2013, Marine Scotland 2022). It is difficult to statistically link numbers on sea trout, given their migrations and that relatively few trout are sampled, often from 1 location in an area, to

Table 2. Advantages and disadvantages of fixed vs. towed sentinel cage methods for infestation pressure on fish — captured fish in general and focussing on (1) fixed sentinel cages and (2) towed sentinel cages

| Option | Advantages | Disadvantages |
|---|---|---|
| Infestation pressure on fish—captured fish in general | • Samples attached stages<br>• Can attach other instrumentation to sentinel cage for environmental monitoring (e.g. CTD)<br>• Dislodged samples in anaesthesia can be retained and enumerated<br>• Majority of attached stages can be retained and enumerated<br>• PCR can be used to identify small attached | • All parasitic stages missed<br>• Only picks up copepodids<br>• Immune status of fish regarding infection success (consideration)<br>• Negative welfare impacts on fish<br>• Sea state dependent<br>• Fish constrained<br>• Expensive in terms of time and processing<br>• Risk of dislodging infesting animals<br>• Usually only a small number of locations in a system is sampled (may not be representative)<br>• Limited to accessible area<br>• Due to fish welfare issues only a small sampling period permissible<br>• All fish euthanised at point of sampling<br>• Cannot be used in intertidal areas |
| (1) Fixed sentinel cages | • Well-established methods<br>• Provides data on actual infestation pressure at a point<br>• Integrates data over deployment time (e.g. 1 wk) allowing estimation of infestation pressure | • Stationary fish less indicative of typical wild fish<br>• Fixed locations only (indicative of fixed location area plus 'upstream' areas)<br>• Requires larger vessel with lifting capacity to put moorings in place<br>• Requires moorings and permissions<br>• Risk of predator damage<br>• Risk of loss from storm damage / collisions etc. |
| (2) Towed sentinel cages | • Spatial coverage<br>• Fish swimming at reasonable speed<br>• Integrates data over space allowing estimation of infection pressure<br>• Method can be deployed at relatively short notice as logistically simpler<br>• Mirrors experience of migrating fish | • Fixed depth (possibly limited towing distance)<br>• Careful monitoring of natural swimming speed is required<br>• Requires small, manoeuvrable, suitable vessel equipped with navigation equipment to maintain slow speeds<br>• Methodology not fully established<br>• Deployment difficult<br>• Movement of cage must closely follow pre-established migration route, speed of escapement and timing of salmon smolts (if used as a realistic index of infection for actual river populations) |

local farm lice loads. Therefore, these data only provide a valuable metric for sea lice infection on wild fish more generally (Middlemas et al. 2009, 2013). This section evaluates wild fish netting (Section 2.3.1) and smolt trawls (Section 2.3.2), while Table 3 lists advantages and disadvantages for data collection methodologies to assess direct infection pressure on migrating wild fish caused by sea lice, split into (1) sweep netting (sea trout targeted), (2) fixed netting (fyke) (both species), and (3) pelagic trawling (salmon targeted, sea trout sometimes caught).

#### 2.3.1. Wild fish netting

Wild salmon and sea trout can be captured by sweep netting, fyke nets, bag nets or rotary screw traps (e.g. Middlemas et al. 2013, Serra-Llinares et al. 2020), which are types of fixed traps that can be deployed in inshore shallow water. The fixed nets are cylindrical netting bags, mounted on rings or other rigid structures, and anchored to the bottom (https://www.fao.org/fishery/geartype/226/en). Captured fish can then be assessed for sea lice (Urquhart et al. 2008, Thorstad et al. 2015). Gill nets have been used in Norway (Bjørn et al. 2011), but as these result in fish being killed, this method is not suited for examining fish populations under pressure.

Wild sea trout sampling, utilizing the different methods, is well established, and has been used to statistically assess if there is an association between lice on farms and wild fish (Middlemas et al. 2009, 2013, Shephard et al. 2016, Marine Scotland 2022, Vollset et al. 2023, Ives et al. 2024). While standard sample sizes are aimed for, in practice these can vary considerably, even at the same location. Sea trout can move extensively within and between sea lochs (types of fjords) (and in and out of fresh water), so that samples represent an integration over an area of unknown extent, timespan, and location, relative to salmon, which are more likely to display a more directional migration route from natal rivers to the coastal envi-

Table 3. Advantages and disadvantages of data collection methods for infestation pressure on fish — free swimming in general and focussing on (1) sweep netting (sea trout targeted), (2) fixed netting (fyke) (both species), and (3) pelagic trawling (salmon targeted, sea trout sometimes caught)

| Option | Advantages | Disadvantages |
|---|---|---|
| Infestation pressure on fish—free swimming in general | • Samples all attached stages of lice<br>• Locally relevant studies<br>• Integrates infection pressure over time (provided the sampling location is representative)<br>• Well established methods | • All planktonic stages missed<br>• Negative welfare impacts on fish<br>• Can Caligus be easily identified?<br>• Risk of dislodging lice<br>• Handling causes stress |
| (1) Sweep netting | • Wider spatial coverage, long record<br>• Fish health/fish condition can be assessed | • Usually only 1 location in a system is sampled (may not be representative)<br>• Limited to accessible areas<br>• Risk of dislodging lice<br>• Damage to bycatch<br>• Usually requires small boat use and skilled crew<br>• Handling causes stress |
| (2) Fixed netting | • Longer sampling/deployment time (compared to sweep netting)<br>• Fish health/fish condition can be assessed<br>• Can involve local fisheries trusts<br>• Less damage to fish<br>• Lower risk of dislodging lice than alternatives<br>• Methodologies for tidal and marine sampling exist (compared to freshwater) | • Fixed location/low spatial coverage<br>• Limited to accessible areas<br>• Time and spatially dependant<br>• Possibility of resampling same fish, adding unknown bias<br>• History of fish unknown<br>• At risk to predator damage<br>• Net may need to be removed during spates/storms to prevent fish mortality |
| (3) Pelagic trawling | • Large spatial coverage<br>• Collects wild salmon during their natural migration<br>• Can provide information on infestation pressure | • Boat required<br>• Difficult to capture enough salmon<br>• Can result in large wild fish mortality |

ronment. It is possible to constrain the timespan component if fish are found to be infested with early sessile stages of lice, as their development time can be as short as ~3 d at 15°C (Hamre et al. 2019). However, irrespective of the above uncertainties, the information collected on lice infestation of netted sea trout has been useful for comparing among years in relation to the fish farm production cycles and in relation to distance from the nearest salmon farms (Middlemas et al. 2009, 2013, Shephard et al. 2016).

#### 2.3.2. Smolt trawls

Sea lice counts on wild migrating salmon have been collected in Norway by trawling for smolts (Holst et al. 2003) and, more recently, a similar methodology has been trialled in Scotland (https://blogs.gov.scot/marine-scotland/2018/05/11/salmon-smolt-surveys-on-the-sunbeam/). For salmon, returning adults have historically been sampled by commercial salmon fisheries, but the reduction of coastal salmon netting has therefore reduced availability of such data. Lice numbers on returning fish have been assessed for some Scottish east coast rivers, although sea lice numbers attained from these mature fish are unlikely to reflect infestation experienced by smolts during their outmigration through the coastal environment (Todd et al. 2000). Mobile seine and fixed fyke netting (discussed in Section 2.3.1) can be carried out to assess sea lice burdens on wild salmon to inform local environment monitoring, but low numbers of samples have made it difficult to draw any firm conclusions regarding population impacts (e.g. Argyll Fisheries Trust 2021). To minimise potential damage to the sampled migrating salmon smolts, one option is to use a Fish-LIFT device to divert the smolts caught during trawling into an integral floating live box (Holst & McDonald 2000). The practicality of lice counts on smolts using this Fish-LIFT method needs to be evaluated but is recommended, although welfare concerns may arise as fish must be sedated for counting. Other capture methods, such as standard trawls, may cause physical harm by abrading scales and undermine the value of the sample by dislodging lice.

### 2.4. Future and alternative sampling methods

Future and alternative sampling methods have the potential to improve surveillance in terms of, for example, enhanced time and space resolution, efficiency or cost. Migrating salmon smolts are difficult to sample, requiring substantial investment of resource. For sea lice counts on farms, automated counting using camera surveillance and machine learning for identification could be used (Pettersen et al. 2019). Such technology would allow counting under adverse weather conditions and would be standardised, and therefore not be influenced by variation among individuals and teams in counting efficiency and technique; this means that reported values would be expected to have a reduced bias and be less affected by the level of operator experience, although some degree of standardisation (e.g. optical resolution, positioning) would be required for consistency and quality assurance. Camera counting would not require use of anaesthetics on the fish, as manual counting does, and therefore could occur right up to harvest, with no risk of residue present in a product destined for human consumption. Technology for automated image-based lice counting is commercially available (e.g. 'The Stingray System', https://www.stingray.no/delousing-with-laser/?lang=en). The accuracy and reliability of automated counting needs to be established, as estimates could be biased by factors such as water clarity. Currently, manual counting can be a formal, legal, requirement for data collection (Thorvaldsen et al. 2019), limiting the incentive in the short term for the use of automated camera technology. Requirements for manual counting could be relaxed, if automated counting can be confirmed to meet or exceed the standards of such manual counts. Technological advances, such as camera assessment of fish size, and hence weight, could also be a useful development in combination with lice counting cameras (Li et al. 2020).

Alternative methods to manual plankton sample identification, such as eDNA (McBeath et al. 2006, Krolicka et al. 2022) or fluorescence illumination of plankton (Thompson et al. 2021, 2022) and automated counters using image analysis, have the potential to complement identification, so to improve efficiency, if applied effectively. However, studies showing validation of individual automated counting techniques for sea lice are not readily available in the literature. Some examples exist of more general validation of automated plankton counting and identification, where studies using convolutional neural networks show an average precision of 84% (Luo et al. 2018).

One potential area, which may help in monitoring data on egg string length, temperature, or salinity, may be found through utilizing automated systems, such as holocams (taking 3-dimensional images of particles passing through it), image analysis (egg string lengths), and CTD measurements (salinity and temperature), all of which require validation as well.

When combined with laboratory data on viable hatching rates as functions of temperature and salinity, automated egg counting systems might be useful in determining egg production for the future development and refinement of models. Holographic cameras (such as the weeHolocam; Thevar et al. 2023) count sea lice in a volume of water, but currently the volumes of water sampled are small, so the technology is only effective when lice are at high concentrations. The eDNA technique is reviewed by Pert et al. (2022) and is used for sampling environments for the presence of *L. salmonis* DNA. Since *L. salmonis* is almost ubiquitous in marine salmonid populations in the northern hemisphere, DNA detection per se is not particularly useful; what is required is quantification and its relationship to the local population of sea lice, ideally identifying copepodids, so there is a need for additional technological development. Semiochemical and light technologies attract lice into traps, where the concentrated lice can be sampled (Ingvarsdóttir et al. 2002). Such technologies have existed for a considerable time but are not widely applied. One challenge is quantifying the relationship between the numbers trapped and overall concentrations in the environment. As new technologies emerge and refine, their usage within an adaptive surveillance monitoring scheme needs to be investigated.

## 3. OPTIMISING SURVEILLANCE AND EFFECTIVE USAGE OF DATA BEYOND THE LOCAL AREA

Section 2 discussed methods for sea lice surveillance, but the question is how can the data obtained be used to inform managers/stakeholders/researchers about the state of the system and likely impacts on wild fish? Data of different types from multiple sources can be synergised to optimise surveillance, as used in other disease surveillance regimes (Martin et al. 2007). Various types of data can also be used for cross checking. For example, counts of individual lice stages can identify anomalies in adult female lice counts (Jeong et al. 2023), and lice counts on trawled smolts can identify inconsistencies with sentinel cage data (Stige et al. 2022). The use of multiple data sources can both identify anomalies, where there is disagreement, and increase statistical confidence in the results, where different approaches agree.

Surveillance data, even from multiple sources, can never give a complete picture of a system, particularly for a parasite with active behaviour dispersing in a complex and highly variable environment, which can only be sampled in a limited way (Lynch et al. 2009, Skogen et al. 2021). As noted above (Tables 1—3), all current observational data collection methods have limitations and restrictions. Surveillance data must be collected with a specific aim if resources are spent on their collection (Brugere et al. 2017). Surveillance is likely to be most effective when sea lice numbers are high, as the signal to noise ratio is greater. In the case of low lice numbers, even an extensive (and thus expensive) surveillance regime is unlikely to provide a meaningful return. Historically, sea lice numbers tend to be highest in late summer and autumn, when waters are warmest, and not in spring, which happens to be when smolt runs tend to occur (Hall & Murray 2018). Valuable data, e.g. for model validation, can thus be obtained most cost effectively at a time when salmon smolt populations are not at risk, something which may be counterintuitive to some stakeholders.

By combining years of surveillance data, local abundances in lice can be estimated which may compensate for individual sampling periods that are insufficient to give a good estimate of true average sea lice levels for the system. This may be especially true of sweep net data, for which records exist for many years. Year-to-year comparison of these data allows the assessment of trends in lice numbers in a particular system. Understanding of a system based on surveillance data is leveraged using models that interpolate observations into areas where observations are lacking (Fig. 1). Moriarty et al. (2024) provide an overview of the types of models used in various stages of sea lice modelling, their classification and examples of their applications. Here, we explore 3 model types: (1) statistical models of the observations (Section 3.1), (2) simple stochastic models, in this case to assess effectiveness of potential surveillance regimes (Section 3.2), or (3) mechanistic coupled hydrodynamic—particle tracking models, in this case to evaluate surveillance effectiveness (Moriarty et al. 2024) (Section 3.3). The last 2 types are particularly useful given the complicated and non-linear system of sea lice infection transmission.

### 3.1. Statistical models

Regression analysis (generalized additive models) of sea lice counts from farms has been used to assess the regional and national trends in sea lice numbers. These show considerable variation between years in Scotland (Hall & Murray 2018). Although averaging processes across time and regions differ post-2018, sea lice numbers continue to show year-to-year variation but are considerably lower than in the pre-2018 period (Murray et al. 2021) (Fig. 2). This is an important output for assessing the efficacy of sea lice control policies at the larger scale.

At smaller scales, sea lice count surveillance data, accessed directly from producers, has been used historically with other farm level data to investigate sea lice population dynamics and risk factors (Revie et al. 2002, 2003), including providing evidence of the declining efficacy of the anti-lice medicine Slice® (Lees et al. 2008). However, the publicly available data have not been used for such statistical analyses at the farm or local area level to date (in any analyses we are aware of). This is a potentially powerful use of surveillance data, that needs to be exploited in combination with other available data sets in Scotland to maximise understanding of factors influencing sea lice counts. In Norway, where high quality count data are available from farms, farm surveillance data have been used to develop statistical models of kernels of infection pressure, with distance between farms as a key risk factor (Aldrin et al. 2013, Elghafghuf et al. 2020), identifying farms within 30 km as a risk factor for sea lice infestation (Kristoffersen et al. 2013).

In Norway, Scotland and Ireland, regression models (e.g. generalized linear models, generalized linear mixed models, logistic regression) of sea lice count data from sea trout sweep net surveillance have been used to identify risk factors behind elevated sea lice counts (Middlemas et al. 2013, Serra-Llinares et al. 2014, 2016, Helland et al. 2015, Shephard et al. 2016, Vollset et al. 2018, Shephard & Gargan 2021, Bøhn et al. 2022, Ives et al. 2024). These analyses have highlighted a link between farms, especially in the second year of production, and sea lice numbers on neighbouring wild sea trout. They also identify that such risk is affected by environmental factors, being elevated during periods of higher temperatures (Serra-Llinares et al. 2016, Shephard et al. 2016, Vollset et al. 2018) and dry conditions (Shephard et al. 2016).

Statistical modelling (generalized linear mixed model) of sweep netting data has provided strong evidence for the link between environment, farms, and elevated risk of sea lice infection (Ives et al. 2024). However, it is difficult to assign infection pressure to specific farms because of potential interactions between farms in an area, infections being quantified on mobile hosts and a lack, until recently, of sufficiently time-resolved farm level data. The complexity of interactions is better described via detailed coupled hydrodynamic–particle tracking models (Section 3.3).

Similar to sweep netting data analysis, planktonic larval sea lice data obtained in Loch Torridon (Scotland) demonstrated a negative statistical relationship between lice in the environment and distance from farms (Penston et al. 2004, 2008, 2011). Since this modelling described spatial trends across the loch, it allowed for interpolation of likely larval population density conditions at locations where sampling was not available, but such statistical models need further validation. Patchy plankton distributions and samples containing many zero lice counts, together with large numbers of other planktonic organisms, make larval lice difficult to identify, unless relatively large quantities are present in the system (Thompson et al. 2021, Fernandez-Gonzalez et al. 2022).

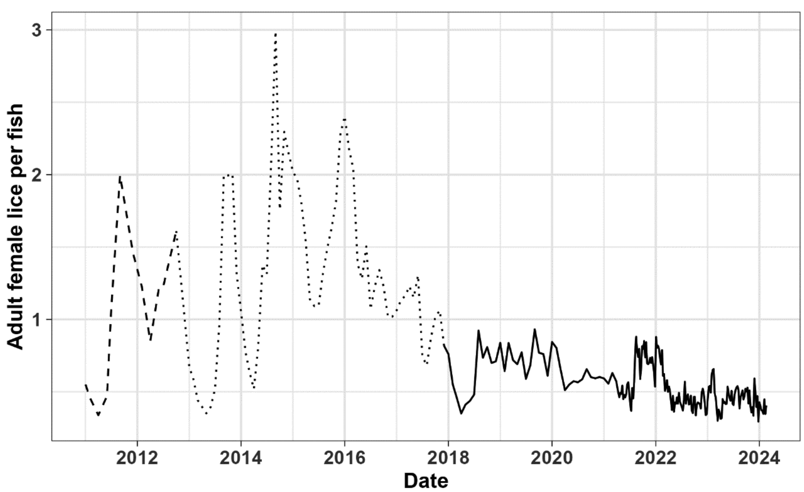


Fig. 2. Average adult sea lice count for December 2010–February 2024. Counts for December 2010–December 2017 are based on regionally averaged data (dashed line) and smaller reporting area averaged data (dotted line) averaged to the national level weighted by area production (methodology from Hall & Murray 2018), while January 2018–February 2024 (solid line) are simple averages across all farms unweighted (source data publicly available: Ives et al. 2021; https://scottishepa.maps.arcgis.com/apps/webappviewer/index.html?id=2218824350e5470e8026076d4138da58)

Sentinel cage infection levels are easier to observe than larval plankton counts and can be used to assess infection rates on fish by dividing the observed numbers of lice by the duration of deployment. Surveillance data collected using sentinel cages in Loch Linnhe, Scotland, from 2011 to 2013 (Pert et al. 2021) were used to estimate the variation in infection rates in time and space. The rate of infection in spring was extremely low in all years, while autumn rates were much higher in 2011 and 2013 (Fig. 3). In 2011, a number of sites had an average infestation rate above 1 louse fish$^{-1}$ d$^{-1}$, and this could be used as an indicator of levels of environmental lice that may be cause for concern.

Results from surveillance (either through plankton trawls or sentinel cages) within a single system (in this example, Loch Linnhe), show that lice concentrations can vary by an order of magnitude or more between times of sampling, and between locations by a factor of 2 at the same sampling time (Salama et al. 2013). This means a single sampling location or time period is unlikely to be representative of a system.

### 3.2. Simple stochastic models

Stochastic processes, like system dynamics models, may be used to design a surveillance regime that could provide a given level of confidence in the true lice concentrations in a system, leading to effective management strategies (e.g. Jeong et al. 2021). These models provide a methodology for studying and managing complex feedback systems, to simplify the problem. These, like other modelling approaches, rely on assumptions and generalisations made about various aspects of the system such as the distribution patterns (e.g. Murray & Moriarty 2021 use a kernel estimate of complex ocean currents). To illustrate the utility of stochastic processes for sea lice surveillance we have produced a simple example for a sentinel cage monitoring regime. As stated in Section 2.2.2, sentinel cages aggregate numbers of lice over time at point locations and hence overcome the issue of highly patchy temporal changes in abundance, making them a useful data set for model validation, if adequate sample locations are included. However, in deciding where and how many sentinel cages need to be deployed to adequately quantify lice densities for modelling purposes, a trade-off has to be made against what is realistically achievable. Increasing the number of sentinel cages decreases uncertainty around an estimate of lice levels, but also increases the cost of deployments and potentially has increased welfare considerations.

We use simple models of distribution (Text A1 in the Appendix) of infectious copepodids in the water to illustrate how confidence ranges on estimated system infection pressure are affected by the number of sentinel cages used. We carried out 1000 simulations, randomly varying the number of notional sentinel cages (1−20), to assess the efficacy of predicting true prevalence of sea lice in the environment (Fig. 4). In Fig. 4a, infection pressure at any particular location in the environment varies randomly between 0 and 1 with a linear distribution, and randomly located sentinel cages detect an infection pressure $p$ in this range. The mean and median observed $p$ is always 0.5, but with small numbers of sentinel cages, the range observed is highly variable. Where there are less than about 6 sampling locations the estimated infection pressure is very poorly constrained. To simulate a patchy distribution of infection pressure (Fig. 4b), a distribution of $p^2$ is used, where $p$ is distributed from 0 to 1. Under this distribution the true mean infection pressure is 0.35, but even the median observed value tends to be an underestimate of true mean prevalence. Variation is larger than for the linearly distributed infection pressure (Fig. 4a), with observations tending to underestimate true prevalence. It should be noted that in a few cases, where sentinel cages lie on simulated 'hot spots', the observations considerably over-estimate the prevalence. This model is intended only as a simple illustration of how variation in distribution of sea lice infection pressure can lead to inaccuracies in estimations based on small numbers of observations.

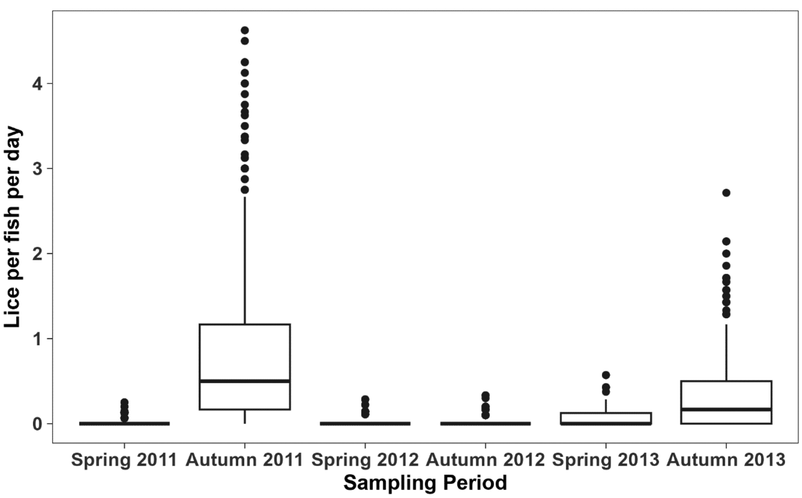


Fig. 3. Infection rates per deployment for the 6 sampling periods. Solid central line represents the median, the box represents the first and third quartiles with the whiskers showing 1.5 × the interquartile range. Outlier values are plotted as solid black circles

### 3.3. Coupled hydrodynamic−particle tracking models

Coupled hydrodynamic−particle tracking models (also known as bio-

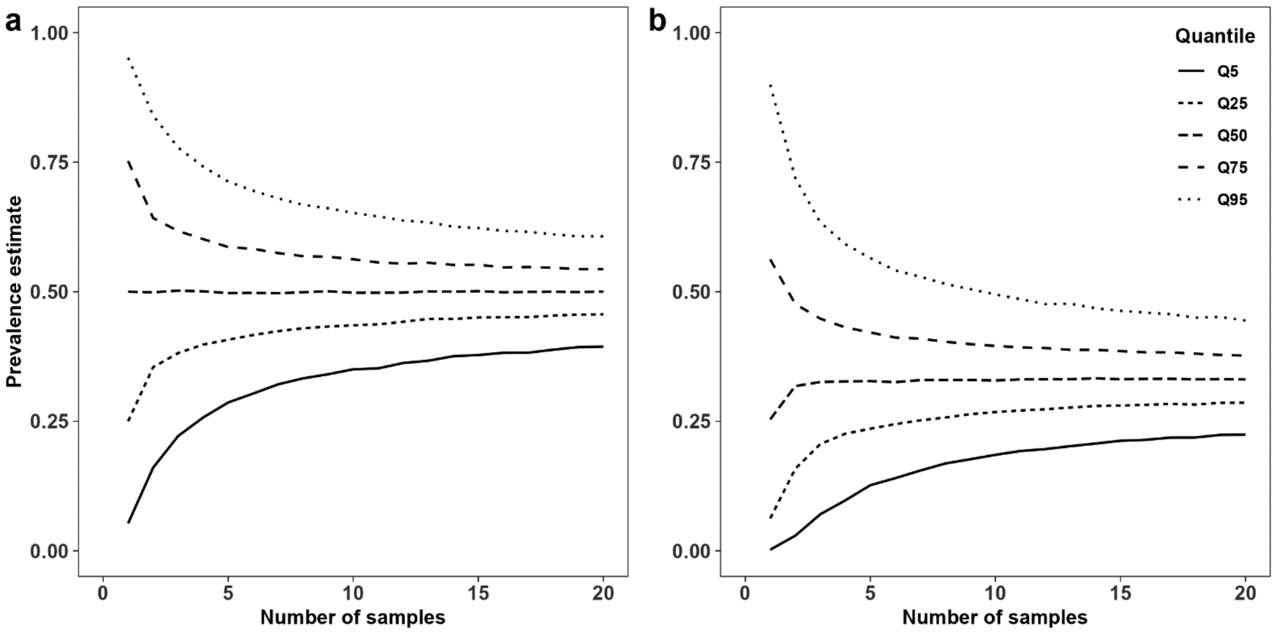


Fig. 4. Prevalence estimates from 2 different modelled population distributions based on the number of samples taken. (a) A population randomly distributed across the system with local prevalence varying uniformly with infection pressure $p$ of 0 to 1. (b) A clustered population where local prevalence varies with $p^2$

physical or physical biological models) are individual-based models which simulate actions and interactions of individual particles within a system (e.g. Myksvoll et al. 2020, Ounsley et al. 2020). These can generate outputs on the distribution of larval sea lice but are computationally more demanding than stochastic models (e.g. Sandvik et al. 2016, 2020, Salama et al. 2018). Outputs can include maps of sea areas where concentration is simulated to be elevated, and therefore identify places that both sentinel cage and plankton sampling surveillance can target. Targeting depends on the purpose of the sampling, for example predicted areas of high and of low concentration to validate models, while in Loch Torridon (Scotland) areas of elevated concentrations near the River Shieldaig have been a target for longer-term surveillance (Penston et al. 2004, 2008) as these strongest signals give the most informative time series of results for assessing variation with time. Even where high concentrations are not persistent, observed infection pressure, especially from sentinel cages, can be compared with model predictions for specific scenarios, and so make optimal usage of the surveillance data (Salama et al. 2018), provided there are sufficient samples to capture likely variation.

The use of sophisticated models can generate new predictions, such as predicted rates of infection generated both by self-infection from the farm site and input from neighbouring farms (Kragesteen et al. 2021). These predictions may introduce opportunities to use new sources of observational data for model validation, for example attached copepodid count data from farms could give new validation data for dispersal models by testing the different self-infection and external infection signals across multiple farms (Kragesteen et al. 2018, 2021). Multiple sources of surveillance data may be able to be used for coupled hydrodynamic model validation, and the use of these multiple data sources in model assessments reduces the vulnerability to bias that could result from relying on a single validation data set.

## 4. USING SURVEILLANCE TO IMPROVE EXISTING SEA LICE MANAGEMENT SYSTEMS

Surveillance data play multiple roles for supporting management: (1) provision of forcing data required to run models, (2) validation of the models, (3) provision of direct values of sea lice numbers to indicate an infection threshold exceedance, and (4) where discrepancies between model results and observations are identified, identification of areas where modelling or surveillance need to be improved. Items 1 to 3 are for day-to-day application of the modelling or management, while item 4 concerns improvement of the modelling as part of an adaptive management strategy (see Section 4.3). These improvements can be in response not only to discrepancies between models results and observations, identified from ongoing surveillance, but also to incorporate new external information, such as data from new scientific studies. Empirical data are necessary for model development and model data are useful to optimise empirical data collection.

### 4.1. Forcing and validation data

Forcing data are the data required for inputs to a model, which drive the outputs, while validation data are needed to assess the model skill; both can be based on surveillance data. Data for local physical forcing of the hydrodynamic model require data collection of key variables, such as wind and freshwater inputs, in that region. For sea lice modelling, the key biological forcing input to a system is the rate of viable egg production. For each farm, this is determined from the surveillance data collected on adult female lice per fish and the estimated number of fish on the farm; this is established practice at the moment but use of lice production models or other types of empirical data (e.g. free-swimming lice larval counts in the water in the cages using optical counters, for example) could be used in the future. Without such surveillance data the model outputs are driven by assumptions, which could lead to spurious results, if inadequate data are used. Fortunately, sea lice count data are now widely available from systematic surveillance (within limits discussed). Unfortunately, in Scotland a lack of reported data on fish numbers requires estimates from consented biomass in assessing this critical factor driving input of larval lice to the system.

For the validation of sea lice dispersal models in Scotland, sentinel cage data have proven the most valuable surveillance data (Salama et al. 2018, Marine Scotland 2023, Moriarty et al. 2023b) despite limited deployments (Pert et al. 2014b, 2023, Salama et al. 2018). The 2 main factors that make sentinel cage data particularly useful for model validation are the known location of the fish in space and time and the relative ease of lice counting and processing. One commonly collected form of data (particularly in Scotland and Norway) is single-site netting of sea trout (i.e. sweep net, fyke net). Despite extensive spatial and temporal coverage (e.g. Middlemas et al. 2013, Serra-Llinares et al. 2020, Ives et al. 2024) these data have not been utilised in dispersal model validation. Here, the main disadvantage (as it is perhaps the core advantage of sentinel cage data) is the unknown location of the sea trout during and after infection with lice, making the potential area covered by the fish and the lice too large to be useful.

Beside sentinel cage and wild sea trout count data, data on planktonic sea lice larval numbers should also have the potential for assisting model validation as planktonic concentrations are the outcome predicted in dispersal models. However, the high level of variability does mean that point-by-point comparability is unlikely to be achieved for transient concentrations. However, averaged concentrations, or comparison of patterns of variation in observed and modelled concentrations, could be very useful for model validation. In the future, new methods of automated collection and counting of larval sea lice could lead to high frequency, even continuous, monitoring and/or at larger spatial scales. This role might also be covered by eDNA sampling, albeit its limitations (Pert et al. 2022). If results are reported rapidly, continuous monitoring might allow for short-term responsiveness, such as emergency treatments, to reduce further outputs from farms, and to adjust management.

### 4.2. Direct indication of salmon lice load threshold exceedance

Sampling can also be used to directly obtain evidence of impacts from sea lice. For example, observation of sea lice loads from sweep net data or trawled smolts can indicate that salmon lice loads are exceeding levels that are likely to cause welfare or mortality problems for the population of sea trout (Middlemas et al. 2013) or salmon smolts (Ives et al. 2023). This is unlikely to be more than indicative because sample sizes are generally small; there is generally only 1 sampling location per area (and this is not usually randomly determined), at least in Scotland (Ives et al. 2024), and the exposure times of the smolts are unknown. Therefore, the data's representativeness of a specific system is very uncertain. Furthermore, elevated lice loads will indicate elevated lice infection rates with the system some week(s) previously, even if data are reported promptly, because they represent the end of the exposure process. This makes it difficult to apply short-term management changes. However, data can be used to identify changes in lice loads associated with specific risk factors, such as farms in the local area being in their second year of production (Middlemas et al. 2013) or trends in lice numbers over time. Areas with persistently elevated lice loads may be identified over years, but as the sampling locations representativeness of the particular system is generally unknown, this is only indicative.

Compared to the delayed information from smolts, lice counts from plankton tows have the potential for a somewhat earlier indication of an emerging problem. Currently, its use is limited by the time and cost of sampling and identification of larval lice. Plankton distribution concentrations are patchy (Haury et al. 1978), so non-detection at a sampling location does not mean an absence of larval lice elsewhere in the immediate area, nor does a detection of an isolated peak confirm a problem. More information on the nature of the patchiness is required, which needs large quantities of surveillance data and sophisticated statistical analysis. Assessing distribution patterns is possible (Penston et al. 2008) but collection of data to accurately assess lice concentrations requires extensive effort, less so at high concentration (Skarðhamar et al. 2019, Fernandez-Gonzalez et al. 2022). Future improved and automated sampling methods of collection and identification are identified as a priority for sea lice research (Murphy et al. 2024) and could make the acquisition of these data more practicable.

At the moment, sentinel cage data are a useful indicator of infection pressure (Pert et al. 2014a, 2022). If sampling effort is sufficient and '$\text{Error}_\text{o}$' is small (Fig. 1), these data can indicate infection pressure over a system, and hence give evidence of infection rates that may be causing problems to smolt health (Ives et al. 2023). It should be noted, however, that if sampling effort is sufficient and '$\text{Error}_\text{o}$' is small, then any type of relevant data could give evidence of a potential problem to smolt health. Collection and reporting of such data take time, and this may limit their use to short-term management. Identification of high sea lice infection pressure directly, however, could indicate potentially high infection pressure without the need for modelling, for example the much higher infection pressure in autumn shown in Fig. 3.

### 4.3. Feedback for adaptive management

If validation data indicate a significant lice infestation pressure (important to management) that the models do not detect, then the models and management strategies should adapt to resolve these issues, i.e. improvement of model skills or measure to be put in place to reduce infestation pressure. As new developments occur in the understanding of sea lice biology, and of their modelling, then — even without the detection of specific anomalies between model predictions and surveillance data — this may also require further modelling adaption. Continuous development of sea lice management and associated improvement in modelling is part of an adaptive management process (Fig. 5). While monitoring results are in satisfactory agreement with the model output, this monitoring information is used to adjust management to keep the sea lice impact within accepted limits (single loop). However, if it becomes apparent that model outputs are deviating from monitoring data, or new scientific knowledge should be incorporated in the model, then the model approach itself needs to be reassessed (main loop). If required, the model design will be updated with the new/modified model/structure in place, and monitoring data continue to be collected and used to evaluate performance.

The accumulation of more information from monitoring data and from developing science means that the system managers continuously acquire more understanding, and therefore the potential to improve practices. This can be applied to acquire more information on where surveillance would be most effectively targeted, either to detect a potentially emerging problem (such as locally persistently elevated infection pressure) or to further evaluate the modelling. Thus, surveillance improves, generating better data to identify where further adaptations to the modelling can be made. Adaptive management allows the man-

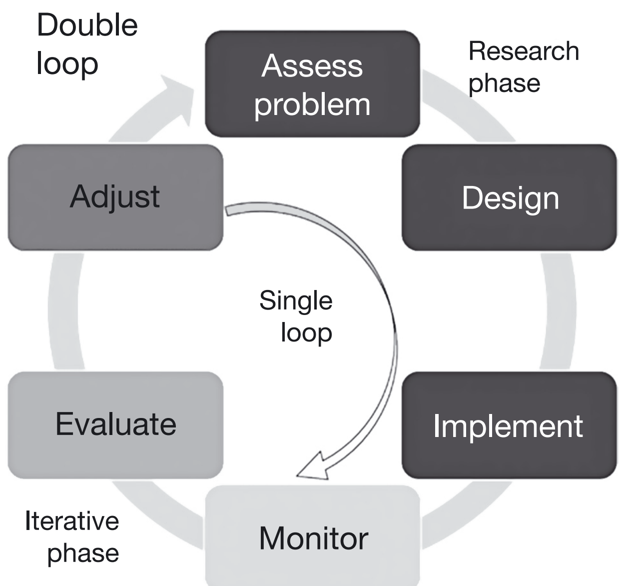


Fig. 5. The continuous cycle diagram shows the high-level process involved in a double looped adaptive monitoring programme (adapted from Williams & Brown (2014, 2018 under the Creative Commons Attribution 4.0 License), proposed to assess and control the risk posed by sea lice from marine fin fish farm developments to wild fish, emphasising the connection between each component in the programme

agement system to incorporate these new data as they become available, and thereafter improve model predictions with the best available data. It is possible that the adaptive process may lead to re-evaluation of key indicators, and thus the elements of a system that are targeted for management intervention. This process also allows managers to adapt to changing production systems, for example the development of larger farms, increased production, the movement of production sites to offshore locations, or climate change.

## 5. DISCUSSION AND CONCLUSIONS

In this review we assessed the efficient use of surveillance in support of management of sea lice impacts on wild salmonids. While improvements can be made in the presentation of these data and assurance of their quality, adult female lice counts per fish are the most reliable and extensive data set available at present. However, the value of this data set is undermined, in some countries (e.g. Scotland), by the absence of explicit data on fish numbers from farms, since a farm's larval lice production depends on the product of lice per fish and number of fish on the farm. These data are already being collated by farmers for the efficient management of their stock's health and productivity, so their absence from published data is a serious obstacle to environmental lice management. Reporting of data on numbers of fish counted, and ideally each individual fish's lice count, broken down by life stage, would allow an assessment of the power of the sampling. In jurisdictions where AF counts are the only life stage reported, shifting from AF to ovigerous lice counts could increase uncertainty in the count due to the smaller number of ovigerous lice (the subset of AF which are currently producing eggs), and the potential for underreporting due to egg strings becoming detached during sampling events. If both counts were reported, this would be informative. Weighing of fish when they were sampled during lice counting would be an alternative to direct data on number of fish on a farm, which could improve accuracy.

The published surveillance data of lice counts on farms also have substantial potential for analysis of sea lice population dynamics (particularly if more life cycle stages are included in counts, such as in the Faroe Islands), and for analysis of regional and national scale trends. These data have been used for assessments at the national and regional levels (Hall & Murray 2018, Murray & Moriarty 2021), and data from privately accessed company records have been used historically (e.g. Revie et al. 2002, 2003). Farm level count data can also be used to assess interactions of infestation between farms, as undertaken in the Faroe Islands (Kragesteen et al. 2021).

Surveillance data obtained directly from sampling sea lice larvae in the water have potential, and, in certain systems, have been effective to understand dispersal dynamics (Penston et al. 2008, á Norði et al. 2015). However, the high costs of collecting and identifying planktonic lice, plus difficult logistics, have limited their application. Developing automated technologies to improve future data collection has the potential to provide details on age (using development stage) as well as vertical distribution of larval lice, depending on which methods are used for model evaluation. The existence of transient patches of larval lice makes it difficult to effectively sample the areas of interest. If sampling is limited, high variability means that samples are unlikely to be representative, and are therefore difficult to use in either management or modelling. Where persistent concentrations are known to exist (i.e. areas where lice accumulate), these may be targets for sampling. These concentrations are not representative but do allow worst cases to be identified and may provide valuable data for model validation (Section 4.1). Intensive or continuous sampling to obtain extensive data sets that can be analysed and averaged to remove the irrelevant high variability may offset the problems caused by the high variability in the data, especially if lice identification can be automated with a high level of precision. If sufficient data were available to quantify lice concentration levels at appropriate scales, then the plankton data could be valuable for model validation, as planktonic concentration is explicitly what models predict. Planktonic larval sampling, if depth-resolved, can inform on lice depth distributions, which is important for dispersal modelling (Garnier et al. 2024), and can characterise nauplii and copepodid distributions — data which can be used to estimate time elapsed since the release of lice and therefore provide additional information for detailed model validation.

Indirect surveillance of lice in plankton through sentinel cages, fixed or towed, has proven the most effective means of surveillance for model evaluation to date (Salama et al. 2018, Pert et al. 2022, Marine Scotland 2023, Moriarty et al. 2023b). The number of cages that can be deployed is limited due to costs and deployment logistics and cages can be lost in adverse weather conditions (Pert et al. 2014a). Another data source is count data from sweep netting of wild sea trout, which has proven useful for evaluation of factors associated with lice risk at the national level. Problems with linking infection pressure to exposure of mobile fish, and the limited potential for sparse and potentially unrepresentative sampling sites, does limit its value for assessment of risk to individual systems. The sea trout data may be supplemented by smolt trawling, which would extend the salmon data, as occurs in Norway. It may be possible to develop a more strategic netting sample strategy, e.g. including randomisation and spatial replication within sampling locations, as more information becomes available on behaviours of sea trout. This could be complemented by, for example, the use of genetics to infer which fish remain in an area or move away, or where they came from, and hence how they were moving. In particular, notable negative impacts on wild fish welfare must be considered when contemplating the use of wild fish sampling, given the various pressures these fish already face (https://www.gov.scot/publications/scottish-wild-salmon-strategy/).

Small numbers of observations are likely to produce results with large levels of variability, and therefore sampling 1 or 2 locations does not provide an accurate assessment of the true status of a system. However, data collected by similar means from different locations and/or times may be pooled for validating a model. This increased confidence in the validation of the model allows increased confidence in prediction at all the sampled locations, and indeed in locations lacking samples. Sampling may be targeting areas of predicted high and low lice counts, identified from a forecast or climatology-based sea lice distribution model, to give the strongest signal to verify the modelling results. Therefore, with validation in one area a model can be applied, with caution, in other areas. This also means that surveillance data from different regions can be used to validate the models, since each piece of surveillance data increases the skill of the fitted model with standardised parameterisation, based on data from different regions. However, such standardised models still require local farm sea lice count data as an input to the model.

Data on sea lice numbers in the environment are most important to management at the time of smolt runs to the sea in spring. However, when the aim of surveillance is to validate models, targeting the times of highest lice loads (typically in the autumn; Hall & Murray 2018) is most likely to provide statistically useful data for this purpose, when the signal to noise ratio is greatest. The models can then be applied in both autumn and spring to assess exposure to sea lice infection, and hence risk to smolts. Validation of models in spring is likely to be more difficult but could still be beneficial to assess confidence in their applicability in the spring smolt run period. In addition, since wild salmon smolts may enter seawater in spring, surveillance to detect problems specifically affecting smolt health would be best targeted to the spring period, if the lice numbers are high enough to resolve a detectable signal.

If alternative models, or modelling approaches, are available then they may identify a better option or strengthen the knowledge to support decision making. The combination of improved model interpolation combined with surveillance data can enhance our understanding of system behaviours (Skogen et al. 2021). In particular, discrepancies between observations and predictions identify areas where less confidence can be placed in the model or possibly the observations. If the difference is large, then this may be evidence for adaptive management to require model updating (or improved observations) (Section 4.3).

Overall, data collated as part of a well-designed surveillance monitoring program are important for the purpose of supporting management decision making. Different factors are important for strategic planning of new locations, or changed production levels, compared to short-term management to avoid specific problems. Models can be improved as more data become available from ongoing surveillance or specific validation exercises. A synergy of improving models as better observational data become available, and better directed surveillance for collection of further data using these models, drives the adaptive management process.

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## Appendix

Text A1. R code for simple model used to generate data for Fig. 4

```
Result<-matrix(nrow=20,ncol=1000)
for(Mfun in 1:20){
Ms<-Mfun
for(run_no in 1:1000){
tot<-0 # total detected
for(Ns in 1:Ms){
# select function for lice runif(1) for uniform population, runif(1)^2 for clustered population
lice_count<- runif(1) #runif(1)^2
tot<-tot+lice_count*1/Ms
} # end set of samples
tot<-tot
Result[Mfun,run_no]<-tot
} # end Ns average for a given number of sample sites
}
```

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