Vol. 13: 377–388, 2021
https://doi.org/10.3354/aei00413
AQUACULTURE ENVIRONMENT INTERACTIONS
Aquacult Environ Interact
Published September 23

System-specific salmon louse infestation thresholds for salmon farms to minimize impacts on wild sea trout populations

Samuel Shephard*, Patrick Gargan

Inland Fisheries Ireland, 3044 Lake Drive, CityWest Business Campus, Dublin 24 Y265, Ireland

ABSTRACT: Salmon lice *Lepeophtheirus salmonis* from aquaculture can cause negative impacts on sea trout *Salmo trutta* and other wild salmonids. Long-term records from 5 Irish rivers were used to explore relationships between annual sea trout runs and estimated total number of lice on nearby salmon farms. It was hypothesised that local environmental conditions may result in system-specific differences in realised louse pressure on sea trout. Louse count was thus tested as an absolute number and as a relative pressure, i.e. standardised by farm. When the standardised total number of mobile lice on a given salmon farm in April was above baseline level (50th percentile of observed annual values on that farm), there was a high probability of a below-average sea trout run in the local river. Absolute louse counts did not show an important effect on runs. This finding suggests that salmon farm louse production in spring can have a strong system-specific regulating effect on wild sea trout populations. Total number of lice on a farm was most strongly driven by changes in individual infestation rate, with a lesser effect of stocking density. Thresholds for number of mobile lice per farmed salmon required to maintain total louse count below the baseline varied with stocking density and among systems: greater density required lower infestation rate. Regulations relying on a generic louse threshold to trigger treatment are not sufficient to protect sea trout populations — stocking density and site characteristics must be considered to evaluate system-specific infestation pressure and impacts on wild salmonids.

KEY WORDS: Salmon louse thresholds · *Salmo trutta* · Salmon aquaculture · West of Ireland rivers

1. INTRODUCTION

Salmon lice *Lepeophtheirus salmonis* impose widely reported negative impacts on wild sea trout *Salmo trutta* populations in areas with Atlantic salmon *Salmo salar* aquaculture (Taranger et al. 2015, Thorstad et al. 2015). Sea trout are known to inhabit inshore areas for considerable periods, often in the vicinity of salmon farms (Pemberton 1976, Thorstad et al. 2007, Middlemas et al. 2009). This behaviour imposes sustained vulnerability to infection, with potential for trout to encounter lice of farm origin over an extended period (Thorstad et al. 2015).

Most free swimming non-infective nauplii salmon lice in spring arise from farmed salmon sources (Tully & Whelan 1993, Heuch & Mo 2001, Butler 2002, Gargan et al. 2003), and sea trout post-smolts have been shown to harbour substantial louse infestation in salmon farming areas (Mackenzie et al. 1998, Tully et al. 1999, Grimnes et al. 2000, Butler 2002). There is significant exchange of lice between farmed and wild hosts in Norway, and salmon louse populations on wild fish in salmon farming areas are largely driven by aquaculture (Fjørtoft et al. 2017). The heaviest infestations and greatest variation in infestation are seen on sea trout captured close to salmon

*Corresponding author: sam.shephard@fisheriesireland.ie

Publisher: Inter-Research · www.int-res.com

farms (Birkeland & Jakobsen 1997, Bjørn et al. 2001, Gargan et al. 2003, Serra-Llinares et al. 2014). Annual production of the Irish salmon farming industry (~20 000 t) is very small in comparison to Scotland (200 000 t) and Norway (1.3 mt), but studies of sea trout in Ireland have demonstrated serious louse infestation (Tully et al. 1993, Gargan et al. 2003), at rates (mean louse intensity 31.5 fish^{-1}) similar to those recorded elsewhere (Birkeland & Jakobsen 1997, Bjørn et al. 2001, Butler 2002, Butler & Watt 2003, Thorstad et al. 2015).

Laboratory and field studies have demonstrated the effects of salmon lice on individual sea trout (McVicar et al. 1993, Tully et al. 1993, Bjørn & Finstad 1998, Dawson et al. 1998). However, the most important knowledge gaps relate to louse impacts at the population level (Thorstad et al. 2015). Previous studies in salmon aquaculture areas have shown increased louse infestations on sea trout and reduced returns to rivers (Poole et al. 1996, 2006, Bjørn et al. 2001, Gargan et al. 2006, 2016, Skaala et al. 2014). Wild migrating salmon and sea trout smolts show moderate to high likelihood of mortality close to salmon farms along the Norwegian coastline (Taranger et al. 2015). Sea trout have exhibited reduced growth and increased marine mortality in salmon aquaculture areas (Thorstad et al. 2015), and sea lice from salmon aquaculture are believed to be a major factor in sea trout stock collapses recorded in Ireland (Tully & Whelan 1993, Tully et al. 1999, Gargan et al. 2003).

In this study, counts of mobile salmon lice (pre-adult and adult male and female lice that have developed beyond the attached larval stage) on farms in April were used as an index of louse pressure on out-migrated sea trout smolts in May. This timing was selected because peak sea trout smolt runs are known to occur from late April to mid-May in the monitored Erriff river (Gargan et al. 2016), and similar timing of sea trout smolt out-migration occurs on other rivers in the current study. Sea trout smolts are typically exposed to infective juvenile salmon lice soon after sea entry. Most sea trout in the study areas are 0-group sea age fish known as finnock, and are expected to return to their native rivers in the summer of their out-migrating year. Numerous studies in Ireland demonstrate that sea trout develop louse infestation soon after sea entry (Tully et al. 1993, Gargan et al. 2003), and very large mortality can occur, with marine survival as low as 1–2% (Gargan et al. 2006, Poole et al. 2006). In cases of heavy louse infestation, surviving sea trout can return to rivers prematurely, i.e. within a few weeks of migrating to sea (Gargan et al. 2003). Laboratory experiments have shown that louse-induced mortality of hatchery-reared and wild sea trout post-smolts tends to commence between 10 and 20 d following exposure to salmon lice (Bjørn & Finstad 1997, 1998, Wells et al. 2006, 2007). The louse infestation pressure experienced by sea trout soon after arriving at sea is thus critical in determining survival due to louse impact(s). Using an estimate of pre-adult and adult louse numbers on salmon farms in April provides an index of initial louse infestation pressure in May, when sea trout enter the sea.

Long-term field experiments and monitoring are required to assess the effect of salmon lice on sea trout populations and to estimate sustainable infestation pressure (Heuch et al. 2005). Data series from 5 Irish rivers were used here to develop statistical models directly relating observed annual returns of wild sea trout to estimated total louse numbers on nearby salmon farms. A subsequent brief analysis explored how observed values of total louse count on a given salmon farm reflected changes in salmon stocking density and individual louse infestation rate. This exercise aimed to inform appropriate (and possibly system-specific) louse infestation thresholds for farmed salmon at differing stocking densities to minimise negative impacts on associated wild sea trout populations.

2. METHODS

Statistical models were first developed to relate observed annual sea trout runs in given study rivers to the corresponding total louse count on active salmon farms in the local estuary/bay. This process revealed a strong negative correlation, with impaired sea trout runs in years when the estimated total number of salmon lice on a farm in April exceeded a baseline level (the 50th percentile of observed annual values on that farm).

The annual total number of lice on a given salmon farm was calculated by multiplying the estimated number of salmon stocked on that farm by the estimated individual louse infestation rate (see Section 2.1). An important practical question is which of these components is most important in driving overall realized louse load on the farms, and thus might be most responsive to management intervention. A brief second analysis explored this issue and found that individual infestation rates varied much more than salmon stocking density. The louse infestation rates at which total louse count on a given farm site remained below the 50th percentile baseline of observed annual values in that system were then predicted as candidate system-specific louse thresholds for specified salmon stocking densities.

2.1. Data

This study considered annual sea trout runs estimated from fish counters in 5 rivers in western Ireland that enter bays with salmon aquaculture (Fig. 1). Runs occurred predominately in June and July. Sea trout runs and corresponding records of louse levels on salmon farms covered the following rivers and time periods: Erriff (1998–2019), Eany and Eske (2010–2018), Dawros (2010–2019) and Ballynahinch (2005–2019). Four rivers had a fish counter capable of accurately recording the annual sea trout run, while annual sea trout rod catch was used as an estimate of sea trout run for the Ballynahinch river. The typical number of sea trout returning varied considerably among rivers, and so returns were standardised (subtract mean and divide by SD) by river. This created a normally distributed continuous variable with positive and negative values, i.e. years of better or worse than average returns for a given system.

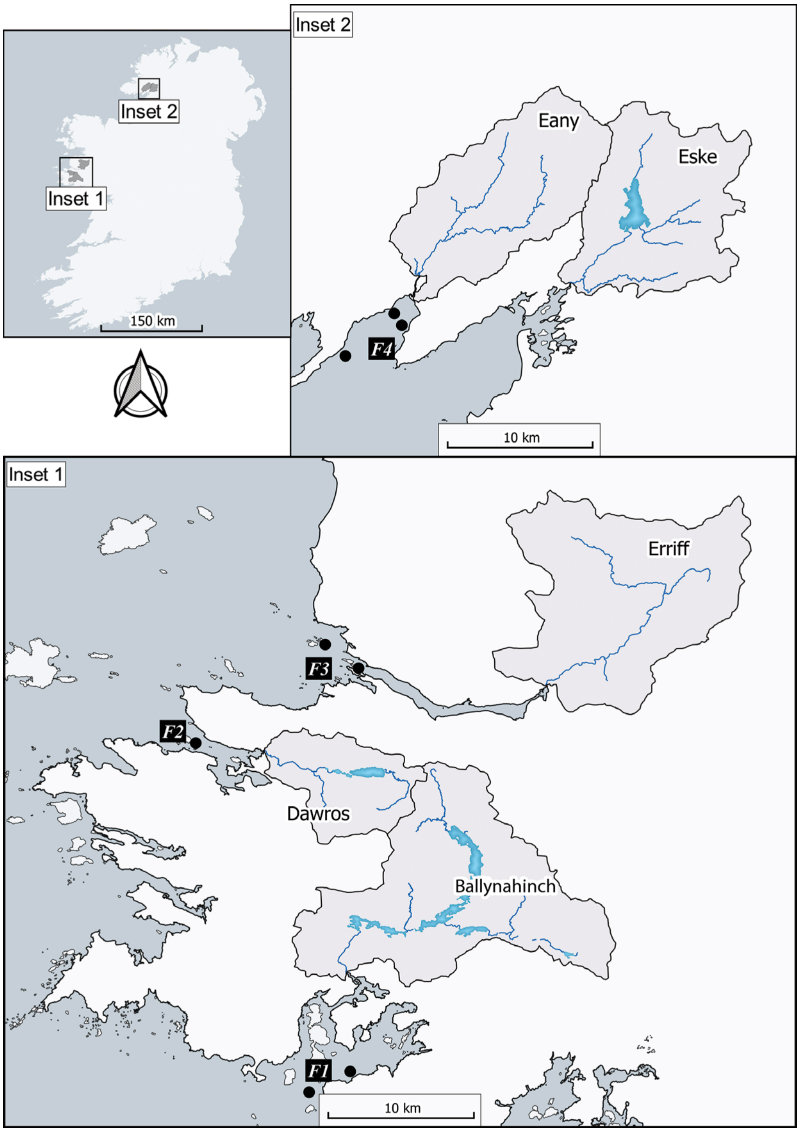

Fig. 1. Map of the study river systems on the west coast of Ireland. Salmon farm sites are shown as F1 to F4. The black dots are individual farms at each site. All the farms at a given site are not typically active every year

Aquaculture records comprised average number of mobile (pre-adult and adult) lice per fish on salmon on-growing (>1 sea winter) and smolt sites in April (www.marine.ie/Home/site-area/areas-activity/aquaculture/sea-lice) and the number of salmon stocked by site as estimated from data provided by the Irish Marine Institute and from the Department of Agriculture, Food & the Marine (www.agriculture.gov.ie) inspection reports of marine finfish farms in Ireland (see also Shephard & Gargan 2021). Estimated total number of lice per study farm site in April was then derived by multiplying reported number of lice per fish by estimated total number of salmon at each site (Fig. 2).

It is likely that local environmental conditions, e.g. hydrodynamics, influence how number of lice on a farm propagates into realized louse pressure on nearby wild sea trout populations. This scenario would mean that a given absolute number of lice on a salmon farm in one location might impose a different degree of pressure on wild sea trout as the same number of lice on a farm in a different location. To explore this possibility, absolute estimated louse numbers were also standardised by farm site (F1 to F4) to represent a relative annual louse pressure in each study system. Note that this provides the same louse pressure series for the Eany and Eske rivers, which have the same nearest salmon farm site (Table 1, Figs. 1 & 2). The candidate model set (see Section 2.2 and Table 2) was duplicated for these 2 specifications of louse pressure, i.e. fit to annual sea trout runs using both absolute and standardised louse numbers as the louse pressure explanatory variable to see which specification provided better fit.

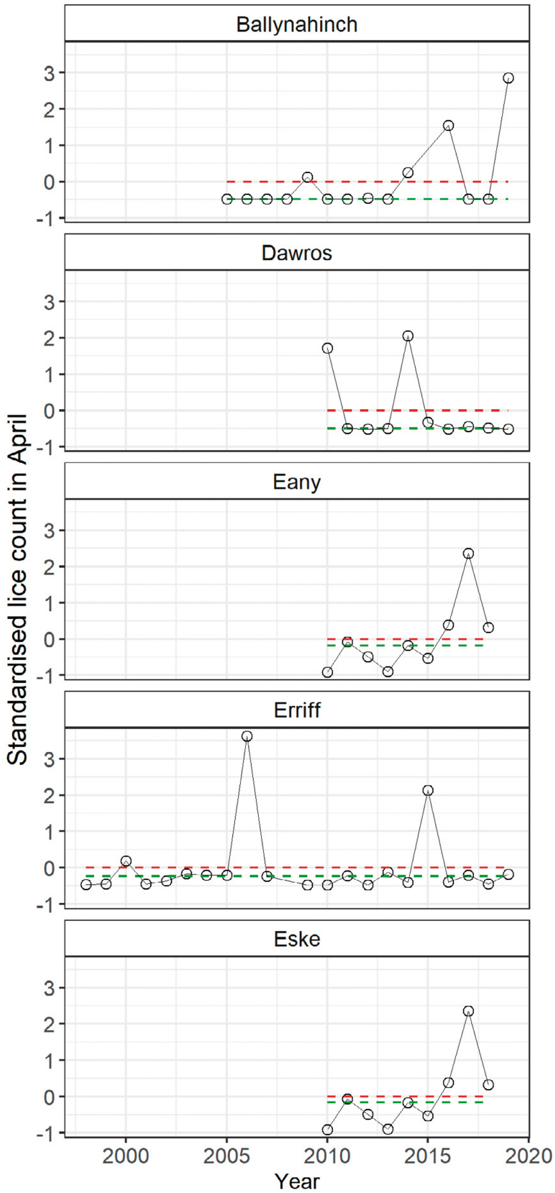

Fig. 2. Time series of the standardised total number of mobile lice counted on the salmon farms nearest to study rivers in April (open circles). Note that this provides the same series for the Eany and Eske rivers, which have the same nearest salmon farm site (F4; see Fig. 1). Red dashed line is the average louse pressure value for each system; green is the 50th percentile of this variable

Sea trout runs and salmon louse production from salmon farms in estuaries are both affected by local temperature and river flow regimes, and so these factors merit consideration. Annual rainfall and temperature were summarized for the study catchments, following Shephard & Gargan (2017). The Irish weather service (Met Éireann) produces spatial datasets that interpolate climatological parameters for Ireland on a 1 km grid using point data from over 500 rainfall recording stations and over 80 temperature recording stations. Using ArcMap, a polygon layer comprised of the Ballynahinch, Dawros, Eany, Erriff and Eske river catchments was spatially intersected with climatological datasets which contained monthly rainfall (mm) and mean daily maximum air temperature (°C). For each river catchment, monthly rainfall was summed, and monthly mean maximum daily temperature was averaged, across the months February to May (the period approaching and during smolt migration) to produce a single rainfall and temperature value for each year from 1998 to 2019.

Table 1. Mean, 50th percentile and SD of absolute louse numbers on the salmon farms closest to study rivers over the whole recording period for each system (Fig. 2)

River	50th percentile	Mean	SD
Ballynahinch	0	86226	163452
Dawros	24977	1200630	2374471
Eany	1656200	2014341	2071382
Erriff	415500	822375	1747273
Eske	1656200	2014341	2071382

2.2. Relationships between annual total louse infestation on salmon farms and corresponding sea trout runs

The data consisted of the parameters S_{ij}, L_{ij}, P_{ij}, T_{ij}, R_j and Y_i, where S_{ij} is the standardised number of sea trout returning to river j in sampling year i. L_{ij} is the estimated total number of salmon lice on the salmon farm site nearest to river j in year i (tested as both a standardised and absolute count). This louse variable was fit as a quadratic curve because number of returning sea trout showed a curvilinear response along the observed gradient of louse pressure, with a steep initial decline followed by some levelling out at the highest louse levels (although there were relatively few data in this upper region). P_{ij} and T_{ij} are the summed total precipitation (rainfall) and mean daily maximum temperature respectively in spring (February to May) in year i proximate to river j. River was modelled as a categorical random effect, R_j, with 5 levels. Year was used to fit a random walk smoother to temporal trend Y_{ij} in the number of sea trout returning to river j in year i, thus incorporating interannual fluctuation (reflecting unexplained environmental forcing) and any sustained underlying shift (e.g. long-term decline) in returns to a given system.

A set of 15 candidate models of sea trout returns was defined (Table 2) and duplicated for absolute and standardised louse counts. These models were specified to test possible interactions between covariates, as well as simpler scenarios. The response variable (standardised annual sea trout runs) was assumed to have normally distributed (Gaussian) errors. The Watanabe Akaike information criterion (WAIC) was used to select the best-fitting model(s). WAIC was used because AIC is less informative when fitting models with informative priors, and the current models were specified with priors for the random effects. Models within 2 WAIC points were deemed to have similar fit, but similar models that included additional 'unimportant' variables (where the posterior distribution of estimated betas included zero) were not retained. The selected model (Model 9, see Table 2) for sea trout run S to river j in year i was specified as:

$$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + Y_{ij} + R_j + \varepsilon_{ij} \quad (1)$$

$$Y_{ij} = Y_{i-1,j} + v_{ij} \quad (2)$$

$$\varepsilon_{ij} \sim N(\mu, \sigma^2_{\varepsilon}) \; v_{ij} \sim N(\mu_j, \sigma^2_{vj}) \quad (3)$$

$$R_j \sim N(0, \sigma^2_{River}) \quad (4)$$

where the trend Y_{ij} in returns to river j in year i was modelled as the trend from year i–1 in river j plus error v_{ij}; the initial value for Y_{ij} was selected as Y_{0j} = 0. The model thus estimates an individual error term σ^2_{vj} for the trends in sea trout returns in each of the 5 study rivers j. R_j is the random effect on the intercept of river.

Models were fit in a Bayesian statistical framework using the R package INLA (Rue et al. 2016), where statistically important results were considered where 95% credible intervals for the betas (estimates of the slope) of a given covariate did not contain zero (i.e. the possibility of no slope). Model validation used residual plots to check the assumptions of linearity and homogeneity of residuals. The predicted effect of farm site total louse count on associated sea trout runs was plotted in relation to the observed returns for each river.

2.3. Values of salmon stocking density and individual louse infestation rate contributing to total louse infestation on Irish salmon farms

Total number of lice per farm j in year i (L_{ij}), was estimated as the product of number of mobile salmon lice per farmed salmon (infestation rate M_{ij}) and estimated total number of salmon on the farm site (N_{ij}). It may be useful to understand which of these 2 components tends to vary most on Irish salmon farms and hence may be the most influential management lever. The observed relationship between individual louse infestation rate and total number of lice on the farm site was plotted for 3 observed levels of salmon farm stocking density. A statistical model was then fit to illustrate system-specific louse thresholds expected to keep total number of lice below the 50th percentile baseline level.

Table 2. Tested statistical models (see Section 2.2. for description of parameters) of salmon louse pressure (total number of lice on a farm site) and associated sea trout runs to nearby rivers. The model set was duplicated for standardised louse numbers (Std: relative annual louse pressure by river) and absolute (Abs) annual louse numbers. Models had different numbers of parameters (Pars), and were compared using the Watanabe Akaike information criterion (WAIC). Note that models estimate an individual error parameter σ^2_{vj} for the temporal trend in sea trout returns in each of the 5 study rivers j (see Fig. 5). Reported models are shown in **bold**

	Model	Pars (Std)	WAIC (Std)	Pars (Abs)	WAIC (Abs)
1	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \beta_3 P_{ij} + \beta_4 T_{ij} + \beta_5 L_{ij}^2 \times P_{ij} + \beta_6 L_{ij}^2 \times T_{ij} + Y_{ij} + R_j + \varepsilon_{ij}$	14	179.87	14	185.02
2	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \beta_3 P_{ij} + \beta_4 T_{ij} + \beta_5 L_{ij}^2 \times P_{ij} + Y_{ij} + R_j + \varepsilon_{ij}$	13	178.36	13	183.89
3	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \beta_3 P_{ij} + \beta_4 T_{ij} + \beta_5 L_{ij}^2 \times T_{ij} + Y_{ij} + R_j + \varepsilon_{ij}$	13	178.35	13	183.17
4	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \beta_3 P_{ij} + \beta_4 L_{ij}^2 \times P_{ij} + Y_{ij} + R_j + \varepsilon_{ij}$	12	177.25	12	182.07
5	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \beta_3 T_{ij} + \beta_4 L_{ij}^2 \times T_{ij} + Y_{ij} + R_j + \varepsilon_{ij}$	12	176.84	12	181.23
6	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \beta_3 P_{ij} + \beta_4 T_{ij} + Y_{ij} + R_j + \varepsilon_{ij}$	12	176.71	12	182.16
7	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \beta_3 P_{ij} + Y_{ij} + R_j + \varepsilon_{ij}$	11	175.59	11	180.39
8	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \beta_3 T_{ij} + Y_{ij} + R_j + \varepsilon_{ij}$	11	175.22	11	180.29
9	$\boldsymbol{S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + Y_{ij} + R_j + \varepsilon_{ij}}$	**10**	**174.30**	**10**	**178.65**
10	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + Y_{ij} + \varepsilon_{ij}$	9	174.31	9	178.68
11	$S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + R_j + \varepsilon_{ij}$	5	166.76	5	175.90
12	$\boldsymbol{S_{ij} = \alpha + \beta_1 L_{ij} + \beta_2 L_{ij}^2 + \varepsilon_{ij}}$	**4**	**166.75**	**4**	**175.93**
13	$S_{ij} = \alpha + Y_{ij} + R_j + \varepsilon_{ij}$	8	181.48	8	181.48
14	$S_{ij} = \alpha + R_j + \varepsilon_{ij}$	3	181.19	3	181.19
15	$S_{ij} = \alpha + Y_{ij} + \varepsilon_{ij}$	7	181.50	7	181.50

3. RESULTS

3.1. Relationships between annual total louse infestation on a salmon farm site and corresponding sea trout runs

Louse numbers standardised by river provided generally better fit than absolute louse numbers in models of annual sea trout returns (Table 2). The simplest tested model to include standardised louse pressure as a covariate (Model 12) had the lowest WAIC overall, with the corresponding model for absolute numbers having close to lowest WAIC in that set (Table 2). We report results for standardised louse pressure from Model 12 and Model 9, which included informative river and year effects on sea trout returns (Table 3). The squared (quadratic) louse term was not statistically important in any of the reported models, but examination of model residuals revealed that including this term provided better fit to years with the greatest number of sea trout, where the simpler louse variable resulted in model underfit. Model residuals indicated good fit to the data for both these reported models (Fig. 3).

Model outputs showed a strong negative impact on annual sea trout runs of standardised total number of salmon lice on nearby salmon farm sites, but not of absolute louse numbers (Table 3, Fig. 4). None of the more complex tested models had statistically important additional variables (e.g. temperature and/or rainfall). Average or above average sea trout runs tended to occur at salmon farm louse levels at or below the 50th percentile baseline. Louse levels above the baseline were associated with a high probability of impaired sea trout runs (Fig. 4). This result was exemplified by the empirical data, which showed that large sea trout runs occurred almost exclusively in years of low louse infestation, notably on the Erriff and Eany rivers (Fig. 4). For all rivers except the Dawros, observed and fitted sea trout returns fell below the mean run size (shown as a dashed red horizontal line) at louse levels at or very close to the 50th percentile of louse pressure on the local farm site (Fig. 4). Fitted smoothers indicated that, after accounting for the louse effect, there were no obvious temporal trends in sea trout returns to the study rivers, but there was considerable unexplained interannual variability (Fig. 5).

Table 3. 95% credible intervals for parameters of the selected models of salmon louse pressure and associated sea trout runs. Results are shown for the models including sea louse pressure standardised by river (Std) and absolute (Abs) numbers (see Table 2). Statistically important covariates are shown in **bold**

	Mean	SD	0.025	0.975
Model 9 (Std)				
(Intercept)	−0.096	0.176	−0.441	0.249
Mobile lice	**−0.702**	**0.265**	**−1.225**	**−0.179**
Mobile lice^2	0.143	0.112	−0.078	0.363
Model 9 (Abs)				
(Intercept)	−0.089	0.200	−0.483	0.304
Mobile lice	−0.563	0.320	−1.193	0.067
Mobile lice^2	0.103	0.123	−0.141	0.346
Model 12 (Std)				
(Intercept)	−0.126	0.143	−0.408	0.157
Mobile lice	**−0.778**	**0.238**	**−1.247**	**−0.308**
Mobile lice^2	0.149	0.104	−0.056	0.353
Model 12 (Abs)				
(Intercept)	−0.044	0.162	−0.363	0.274
Mobile lice	−0.467	0.280	−1.018	0.084
Mobile lice^2	0.056	0.115	−0.171	0.283

3.2. Values of salmon stocking density and individual louse infestation rate contributing to total louse infestation on Irish salmon farms

Observed total number of lice on a given salmon farm site was most strongly driven by changes in individual infestation rate, while there was also an effect of farm stocking density (Fig. 6). The observed range of total louse counts varied among systems, such that the individual louse infestation rate re-

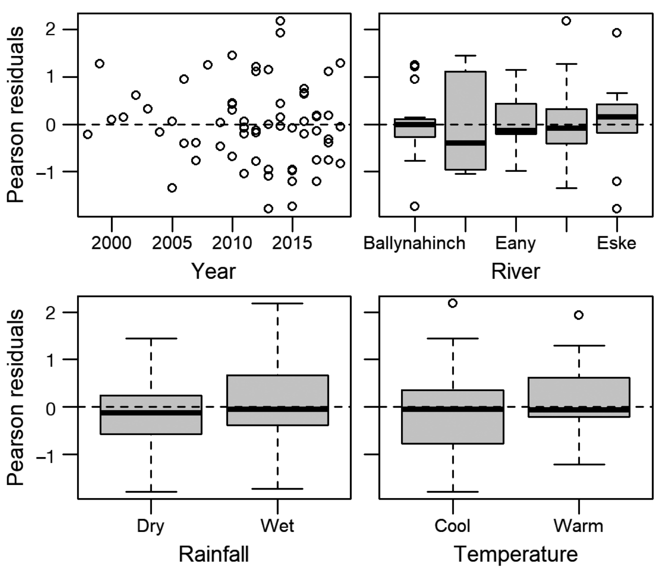

Fig. 3. Residuals for Model 12 of salmon louse pressure and associated sea trout runs (see Tables 2 & 3) plotted against some variables not included in this model

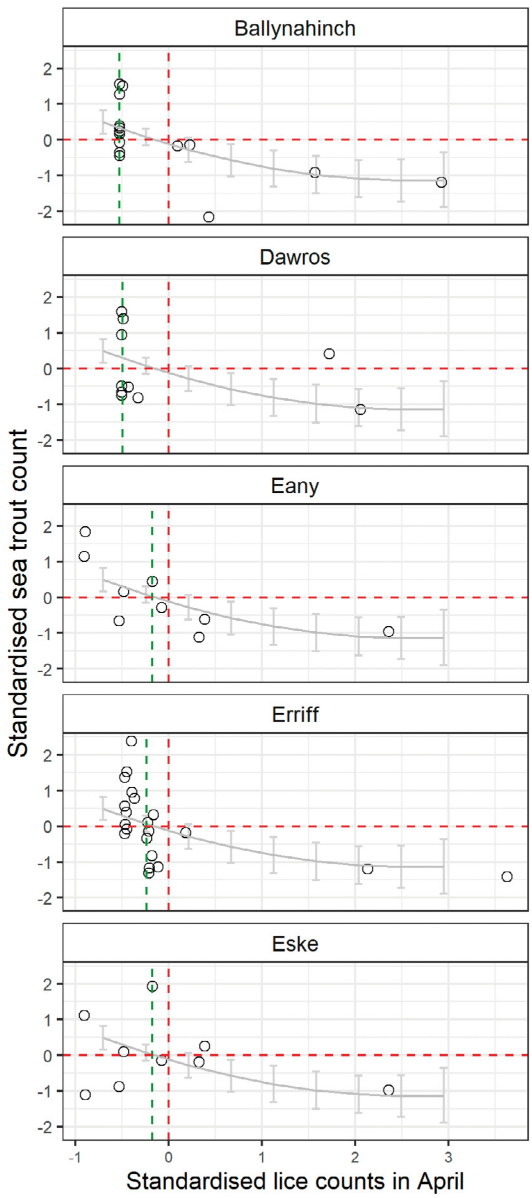

Fig. 4. Standardised annual counts of sea trout (open circles) for each study river in relation to standardised louse counts on the nearby salmon farm site in April. Grey solid line is predicted sea trout runs from Model 12 (see Tables 2 & 3), with 95% credible intervals. The louse count thresholds (dashed green vertical line: 50th percentile; dashed red vertical line: mean) are shown for each river to illustrate how observed and predicted sea trout runs decline across the observed louse pressure gradient. The red dashed horizontal zero line represents the mean standardised annual return to each river

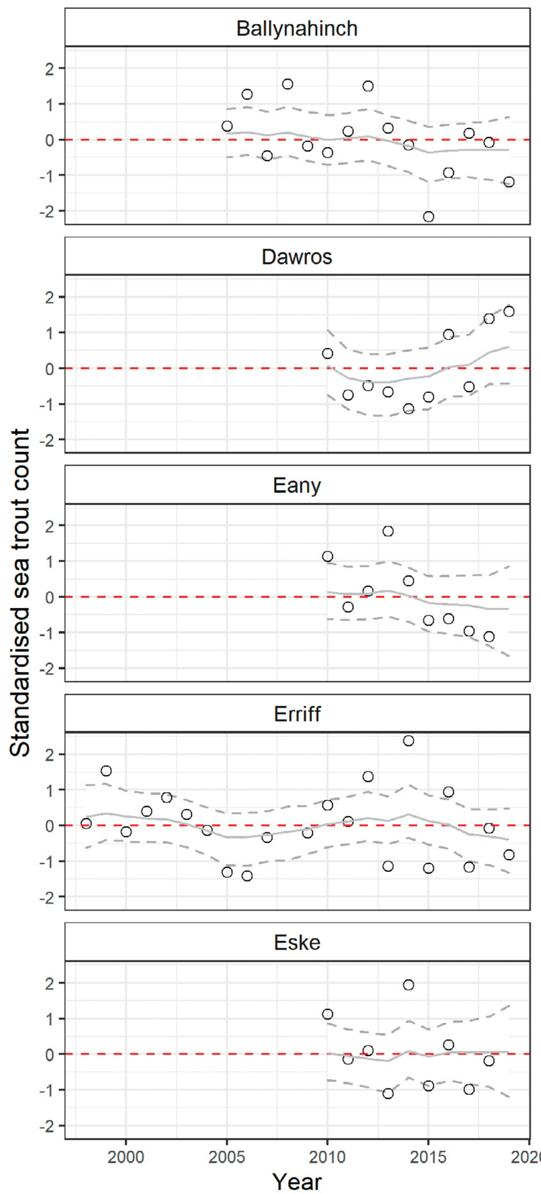

Fig. 5. Standardised annual number of sea trout returning to each of the study rivers, with a fitted random walk smoother with 95% credible intervals. Red dashed horizontal zero line represents the mean standardised annual return to each river

quired to keep total number of lice on the farm below baseline also differed. A notable case was the Ballynahinch, where the observed April louse count was zero in 9 of 15 study years, with a maximum annual value of 0.98 lice per fish. This situation meant that the 50th percentile baseline was zero lice. Other systems appeared somewhat more resilient regarding louse impact, with the 50th percentile representing greater louse numbers. For the farm near the Erriff river, the louse infestation rate required to maintain total number of lice below the baseline may be 0.5 lice per fish at high stocking density, but 2.0 lice per fish at low stocking density (see high and low stocking densities [Farm_num] in Fig. 6). Corresponding numbers of ovigerous lice can be estimated using a linear regression with mobile lice (Fig. 6). Medium

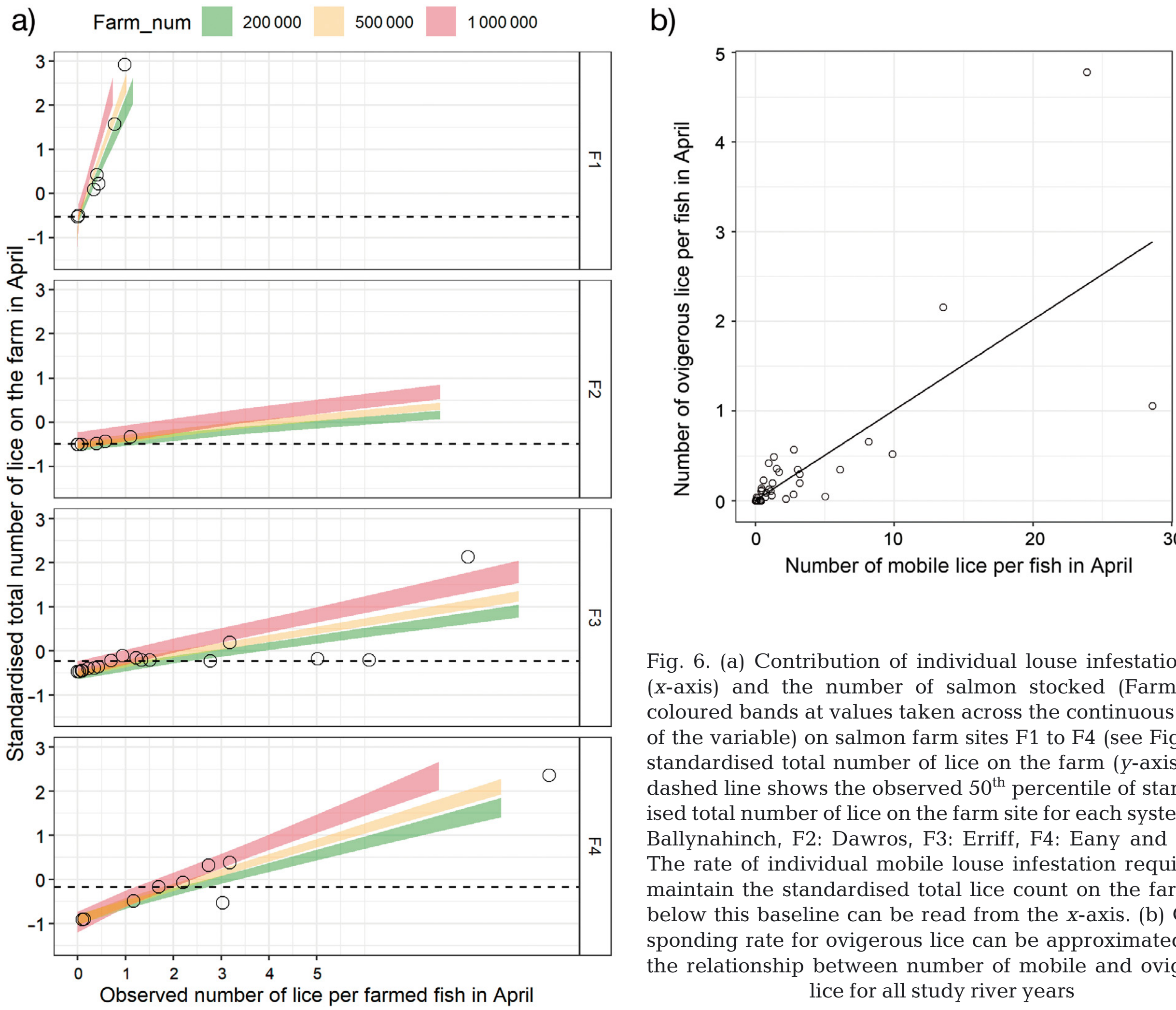

Fig. 6. (a) Contribution of individual louse infestation rate (*x*-axis) and the number of salmon stocked (Farm_num: coloured bands at values taken across the continuous range of the variable) on salmon farm sites F1 to F4 (see Fig. 1) to standardised total number of lice on the farm (*y*-axis). The dashed line shows the observed 50th percentile of standardised total number of lice on the farm site for each system (F1: Ballynahinch, F2: Dawros, F3: Erriff, F4: Eany and Eske). The rate of individual mobile louse infestation required to maintain the standardised total lice count on the farm site below this baseline can be read from the *x*-axis. (b) Corresponding rate for ovigerous lice can be approximated from the relationship between number of mobile and ovigerous lice for all study river years

and high stocking density consistently required lower louse infestation rates to keep overall louse loads below the 50th percentile at all locations (Fig. 6).

4. DISCUSSION

Infestation with salmon lice from coastal salmon farms is known to impose negative impacts on wild sea trout. Annual returns of sea trout to the study rivers fluctuated around average when standardised louse infestation was below a system-specific baseline level (<50th percentile of observed annual values) at local farm sites. Greater louse levels were associated with a high probability of impaired returns. Importantly, annual sea trout returns were more strongly predicted by louse pressure standardised by river than by absolute louse pressure. This result indicates that pressure-state relationships between lice on farmed salmon and the health of wild salmonids may vary among systems.

The observed total louse load on a given farm site was shown to depend predominately on changes in individual infestation rate, with some effect of farm stock size. The infestation rate required to maintain overall louse numbers below the 50th percentile, and thus minimise impacts on wild sea trout, varied among systems. Maintaining louse infestation on salmon farms at or below baseline will very likely help minimise impacts of salmon lice from aquaculture on wild sea trout populations. However, this approach implies that management should consider system-specific louse thresholds rather than a single regional value.

High louse levels on salmon farms are likely to drive increased infestation on sea trout (Tully et al. 1993, Gargan et al. 2003, Serra-Llinares et al. 2014, Thorstad et al. 2015) and result in strong reductions in rod catch (Walker 1994, Northcott & Walker 1996, Gargan et al.

2006). Greater louse infestation is evident on sea trout captured closer to salmon farms (Bjørn et al. 2001, Gargan et al. 2003, Middlemas et al. 2013, Serra-Llinares et al. 2014, Shephard et al. 2016), with a corresponding reduction in marine survival (Poole et al. 1996, Butler & Walker 2006, Gargan et al. 2006, Skaala et al. 2014, Serra-Llinares et al. 2020). Previous studies generally used proximity to a salmon farm as a proxy for louse pressure on local sea trout populations (Butler & Walker 2006, Taranger et al. 2015, Gargan et al. 2017), although Marty et al. (2010) examined the relationship between sea louse production on salmon farms and pink salmon *Oncorhynchus gorbuscha* productivity in the Broughton Archipelago region of western Canada. The current study may be the first to show a quantified negative relationship between estimated total louse production on salmon farms in spring and recorded annual sea trout return to local rivers. This relationship represents direct and system-specific population-level pressure on wild sea trout.

The infestation rate required to maintain total number of lice below baseline differed among the study systems, but was consistently very low at greater farm stocking densities. The 50th percentile baseline is proposed here as a threshold because years where the standardised total number of lice on a given farm was below this level tended to show healthy sea trout runs in nearby rivers. This baseline will probably need to be interpreted for individual cases. An example is the Ballynahinch system, where the 50th percentile of standardised total louse numbers was zero and a more pragmatic threshold would be appropriate.

Kristoffersen et al. (2014) found that louse transmission from external sources was the prime determinant of efforts needed to keep louse levels within legal limits around local networks of salmon farms in Norway. In the present study region, salmon farms are operated as single smolt and grower sites in individual bays. Louse transmission from more distant farm sources is expected to be minimal, implying that louse infestation pressure is governed by individual farm dynamics and local topography.

Most countries with Atlantic salmon farming have a salmon louse threshold level as part of their strategy to protect wild salmonid stocks and (to a lesser extent) to avoid cross-farm louse infestation (Kristoffersen et al. 2014, Kragesteen et al. 2019). This threshold is typically specified as an ovigerous louse level in spring varying from 0.2 to 0.5 lice per fish. If this level is breached, farmers are instructed to implement some form of anti-louse treatment to reduce the potential threat to migrating salmonid smolts. The statutory threshold in Ireland is between 0.3 and 0.5 (depending on licence conditions) ovigerous lice per fish during the period from March to May, and a regulatory notice to treat is issued if this level is breached. A mandatory accelerated harvest can be ordered by the licence authority if the threshold is breached in successive months, but this outcome has occurred very infrequently over the past decade. Results from the current analysis indicate that a general salmon louse threshold level is not appropriate, because the number of mobile lice in April that results in an acceptable total number of lice on a salmon farm site increases with increasing individual infestation rate and farm stocking density, and may differ strongly with site location. Even if the statutory salmon louse threshold is achieved on a given farm, realized infestation pressure shaped by farm location hydrodynamics and stocking density may still result in serious impacts on sea trout.

Louse infestation pressure from fish farms is important in determining salmon louse infestations on wild sea trout (Vollset et al. 2018). The number of farmed salmon hosts present is related to the rate of salmon louse infection in a population (Heuch et al. 2005) and to host density (Anderson 1993). Kristoffersen et al. (2018) quantified the risk of louse-induced mortality of salmon smolts along the Norwegian coast and found that salmon louse egg production was significantly correlated with local biomass density of farmed fish. They found that local louse infestation pressure will be greater in large salmon farm production areas, resulting in increased infestation of wild fish and increased mortality from louse infestation.

In Norway, salmon louse thresholds are set on farms to reduce the potential impact of sea lice, but these thresholds do not account for the density of salmon farm hosts, which Jansen et al. (2012) found to be the primary driver of louse abundance. As the density of salmon farming increases, use of mean numbers of sea lice per fish as a threshold on salmon farms is likely to increase salmon louse infection pressure from aquaculture. Jansen et al. (2012) therefore recommend that sea louse thresholds should be based on the spatial density of sea lice and not on mean louse abundance on farms. Such a concept has been recently recommended by Larsen & Vormedal (2021), who evaluated the environmental effectiveness of sea louse thresholds in Norway. They found that adherence to thresholds does not decrease the louse infestation pressure on wild salmonids. They concluded that other issues such as total salmon biomass in an area, the spatial distribution of sites, the number and size of sites and environmental variables also affect sea louse infestation pressure. Their results indicate that compliance with strict louse thresholds alone will not prevent lice impact on wild fish, and other measures need to be considered. In this context, the current study finds that relationships between louse pressure and sea trout population state are system-specific. This result points to the likely importance of local conditions in shaping how number of lice on a salmon farm propagates into a negative effect on local sea trout populations.

Local (e.g. bay-level) thresholds for louse pressure (farm infestation rate multiplied by stocking density) may be a more appropriate management measure to ensure sustainability of wild salmonids. Sandvik et al. (2016) developed a new system to predict louse infestation pressure on wild salmonids in Norway. Their model uses data on adult female lice, temperature and the density of farmed salmon. A hydrodynamic model is then coupled to a particle tracking model for spatiotemporal estimation of pelagic lice numbers. The model provides information to identify areas of elevated infestation pressure and provides advice to managers on the potential impact of lice from salmon farm sites on wild salmonids all along the Norwegian coast (Svåsand et al. 2015, Taranger et al. 2015). The model provides an opportunity for more sustainable growth of the aquaculture industry in Norway (Sandvik et al. 2016).

This spatial-temporal modeling concept has been further developed in Myksvoll et al. (2018), where an operational salmon louse model has been developed to include both hydrodynamics and lice behaviour. Modelled louse dispersion correlates with louse counts from sampled wild salmonids. By using data on louse infestation pressure from salmon farms, and data on louse loads on wild fish in near real-time, this approach provides an improved assessment of high-risk areas for wild fish, which will help the sustainable development of salmon farming (Sandvik et al. 2016, Myksvoll et al. 2018).

Statistical models of individual louse infestation rate, the number of stocked farm salmon and the estimated total number of lice on farms provided direct evidence of system-specific impacts of salmon lice on sea trout returns to 5 Irish rivers. These findings support the concept of defining local louse infestation pressure as a means of assessing likely impacts on wild salmonid populations. Current salmon louse thresholds used to trigger treatment do not incorporate information on local louse pressure-state dynamics, individual site characteristics or salmon farm stocking density, and hence are not appropriate in efforts to reduce the impacts on wild salmonids of lice from salmon farms.

Acknowledgements. Padraic O'Malley and Lindsey Clarke (Inland Fisheries Ireland) are gratefully acknowledged for the provision of fish counter data from the studied rivers.

LITERATURE CITED

Anderson RM (1993) Epidemiology. In: Cox FEG (ed) Modern parasitology. Blackwell Scientific Publications, Oxford, p 75–116

Birkeland K, Jakobsen PJ (1997) Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. Environ Biol Fishes 49:129–137

Bjørn PA, Finstad B (1997) The physiological effects of salmon lice infection on sea trout post smolts. Nord J Freshw Res 73:60–72

Bjørn PA, Finstad B (1998) The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected post smolts of sea trout (*Salmo trutta*). Can J Zool 76:970–977

Bjørn PA, Finstad B, Kristoffersen R (2001) Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. Aquacult Res 32: 947–962

Butler JRA (2002) Wild salmonids and sea louse infestations on the west coast of Scotland: sources of infection and implications for the management of marine salmon farms. Pest Manag Sci 58:595–608

Butler JRA, Walker AF (2006) Characteristics of the sea trout *Salmo trutta* (L.) stock collapse in the River Ewe (Wester Ross, Scotland), in 1988–2001. In: Harris G, Milner N (eds) Sea trout: biology, conservation and management. Blackwell, Oxford, p 45–59

Butler JRA, Watt J (2003) Assessing and managing the impacts of marine salmon farms on wild Atlantic salmon in western Scotland: identifying priority rivers for conservation. In: Mills D (ed) Salmon at the edge. Proc 6th Int Atlantic Salmon Symp. Atlantic Salmon Trust/Atlantic Salmon Federation, Blackwell Science, Oxford, p 93–118

Dawson LHJ (1998) The physiological effects of salmon lice (*Lepeophtheirus salmonis*) infections on returning post-smolt sea trout (*Salmo trutta* L.) in western Ireland, 1996. ICES J Mar Sci 55:193–200

Fjørtoft HB, Besnier F, Stene A. Nilsen F, Bjørn PA and others (2017) The Phe362Tyr mutation conveying resistance to organophosphates occurs in high frequencies in salmon lice collected from wild salmon and trout. Sci Rep 7:14258

Gargan PG, Tully O, Poole WR (2003) The relationship between sea lice infestation, sea lice production and sea trout survival in Ireland, 1992–2001. In: Mills D (ed) Salmon at the edge. Proc 6th Int Atlantic Salmon Symp. Atlantic Salmon Trust/Atlantic Salmon Federation, Blackwell Science, Oxford, p 119–135

Gargan PG, Roche WK, Forde GP, Ferguson A (2006) Characteristics of the sea trout (*Salmo trutta* L.) stocks from the Owengowla and Invermore fisheries, Connemara, western Ireland, and recent trends in marine survival. In: Harris G, Milner N (eds) Sea trout: biology, conservation and management. Blackwell Publishing, Oxford, p 60–75

Gargan PG, Kelly FL, Shephard S, Whelan KF (2016) Temporal variation in sea trout (*Salmo trutta* L.) life history traits in the Erriff river, Western Ireland. Aquacult Environ Interact 8:675–689

Gargan PG, Shephard S, MacIntyre C (2017) Assessment of the increased mortality risk and population regulating effect of sea lice (*Lepeophtheirus salmonis*) from marine salmon farms on wild sea trout in Ireland and Scotland. In: Harris G (ed) Sea trout: science & management. Proc 2nd Int Sea Trout Symp. Matador Publishing, Leicester, p 507–522

Grimnes A, Finstad B, Bjorn PA (2000) Registrations of salmon lice on Atlantic salmon, sea trout and charr in 1999. NINA Assign Rep 634:1–34 (in Norwegian with English Abstract)

Heuch PA, Mo TA (2001) A model of salmon louse production in Norway: effects of increasing salmon production and public management measures. Dis Aquat Org 45:145–152

Heuch PA, Bjørn PA, Finstad B, Holst JC, Asplin L, Nilsen F (2005) A review of the Norwegian 'National Action Plan Against Salmon Lice on Salmonids': the effect on wild salmonids. Aquaculture 246:79–92

Jansen PA, Kristoffersen AB, Viljugrein H, Jimenez D, Aldrin M, Stien A (2012) Sea lice as a density-dependent constraint to salmonid farming. Proc R Soc B 279:2330–2338

Kragesteen TJ, Simonsen K, Visser AW, Andersen KH (2019) Optimal salmon lice treatment threshold and tragedy of the commons in salmon farm networks. Aquaculture 512: 734329

Kristoffersen AB, Jimenez D, Viljugrein H, Grontvedt R, Stien A, Jansen PA (2014) Large scale modelling of salmon lice (*Lepeophtheirus salmonis*) infection pressure based on lice monitoring data from Norwegian salmonid farms. Epidemics 9:31–39

Kristoffersen AB, Qviller L, Helgesen KO, Vollset KW, Viljugrein H, Jansen PA (2018) Quantitative risk assessment of salmon louse-induced mortality of seaward migrating post-smolt Atlantic salmon. Epidemics 23:19–33

Larsen ML, Vormedal I (2021) The environmental effectiveness of sea lice regulation: compliance and consequences for farmed and wild salmon. Aquaculture 532:736000

Mackenzie K, Longshaw M, Begg GS, McVicar AH (1998) Sea lice (Copepoda: Caligidae) on wild sea trout (*Salmo trutta* L.) in Scotland. ICES J Mar Sci 55:151–162

Marty GD, Saksida SM, Quinn TJ (2010) Relationship of farm salmon, sea lice, and wild salmon populations. Proc Natl Acad Sci USA 107:22599–22604

McVicar AH, Sharp LA, Walker AF, Pike AW (1993) Diseases of wild sea trout in Scotland in relation to fish population decline. Fish Res 17:175–185

Middlemas SJ, Stewart DC, Mackay S, Armstrong JD (2009) Habitat use and dispersal of post-smolt sea trout *Salmo trutta* in a Scottish sea loch system. J Fish Biol 74:639–651

Middlemas SJ, Fryer RJ, Tulett D, Armstrong JD (2013) Relationship between sea lice levels on sea trout and fish farm activity in western Scotland. Fish Manag Ecol 20:68–74

Myksvoll MS, Sandvik AD, Albretsen J, Asplin L and others (2018) Evaluation of a national operational salmon lice monitoring system — from physics to fish. PLOS ONE 13: e0201338

Northcott SJ, Walker AF (1996) Farming salmon, saving sea trout; a cool look at a hot issue. In: Black KD (ed) Aquaculture and sea lochs. Proc Scottish Ass Mar Sci and the Challenger Society, Dunstaffnage Marine Laboratory. Oban, p 72–81

Pemberton R (1976) Sea trout in North Argyll sea lochs, population, distribution and movements. J Fish Biol 9:157–179

Poole WR, Whelan KF, Dillane MG, Cooke DJ, Matthews M (1996) The performance of sea trout, *Salmo trutta* L., stocks from the Burrishoole system western Ireland, 1970–1994. Fish Manag Ecol 3:73–92

Poole WR, Dillane M, DeEyto E, Rogan G, McGinnity P, Whelan K (2006) Characteristics of the Burrishoole sea trout population: census, marine survival, enhancement and stock-recruitment relationship, 1971–2003. In: Harris G, Milner N (eds) Sea trout: biology, conservation and management. Blackwell Publishing, Oxford, p 107–114

Rue H, Riebler A, Sigrunn HS, Illian JB, Simpson DP, Lindgren FK (2016) Bayesian computing with INLA: a review. Ann Rev of Statistics and its Application. 4:395–421

Sandvik AD, Bjørn PA, Ådlandsvik B, Asplin L and others (2016) Toward a model-based prediction system for salmon lice infestation pressure. Aquacult Environ Interact 8:527–542

Serra-Llinares RM, Bjørn PA, Finstad B, Nilsen R, Harbitz A, Berg M, Asplin L (2014) Salmon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. Aquacult Environ Interact 5:1–16

Serra-Llinares RM, Bøhn T, Karlsen Ø, Nilsen R and others (2020) Impacts of salmon lice on mortality, marine migration distance and premature return in sea trout. Mar Ecol Prog Ser 635:151–168

Shephard S, Gargan PG (2017) Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. Aquacult Environ Interact 9:181–192

Shephard S, Gargan PG (2021) Wild Atlantic salmon exposed to sea lice from aquaculture show reduced marine survival and modified response to ocean climate. ICES J Mar Sci 78:368–376

Shephard S, MacIntyre C, Gargan PG (2016) Aquaculture and environmental drivers of salmon lice *Lepeophtheirus salmonis* infestation and body condition in sea trout (*Salmo trutta* L.). Aquacult Environ Interact 8:597–610

Skaala Ø, Kålås S, Borgstrøm R (2014) Evidence of salmon lice-induced mortality of anadromous brown trout (*Salmo trutta*) in the Hardangerfjord, Norway. Mar Biol Res 10: 279–288

Svåsand T, Boxaspen KK, Karlsen Ø, Kvamme BO, Stien LH, Taranger GL (2015) Risikovurdering norsk fiskeoppdrett 2014. Fisken Havet 2-2015. Institute of Marine Research, Bergen. http://hdl.handle.net/11250/281780

Taranger GL, Karlsen Ø, Bannister RJ, Glover KA and others (2015) Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES J Mar Sci 72: 997–1021

Thorstad EB, Økland F, Finstad B, Sivertsgård R, Plantalech N, Bjørn PA, McKinley RS (2007) Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. Hydrobiologia 582:99–107

Thorstad E, Todd CD, Uglem I, Bjorn PA and others (2015) Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta*–a literature review. Aquacult Environ Interact 7:91–113

Tully O, Whelan KF (1993) Production of nauplii of *Lepeophtheirus salmonis* (Krøyer) (Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (*Salmo trutta* L.) off the west coast of Ireland in 1991. Fish Res 17:187–200

Tully O, Poole WR, Whelan KF (1993) Infestation parameters for *Lepeophtheirus salmonis* (Krøyer) (Copepoda: Caligidae) parasitic on sea trout, *Salmo trutta* L., off the west coast of Ireland during 1990 and 1991. Aquacult Fish Manage 24:545–557

Tully O, Gargan P, Poole WR, Whelan KF (1999) Spatial and temporal variation in the infestation of sea trout (*Salmo trutta* L.) by the caligid copepod *Lepeophtheirus salmo-*

nis (Krøyer) in relation to sources of infection in Ireland. Parasitology 119:41–51

Vollset KW, Qviller L, Skår B, Barlaup BT, Dohoo I (2018) Parasitic sea louse infestations on wild sea trout: separating the roles of fish farms and temperature. Parasit Vectors 11:609

Walker AF (1994) Sea trout and salmon stocks in the Western Highlands. In: Problems with sea trout and salmon in the Western Highlands. Atlantic Salmon Trust, Pitlochry, p 6–18

Wells A, Grierson CE, MacKenzie M, Russon IJ, and others (2006) Physiological effects of simultaneous, abrupt seawater entry and sea lice (*Lepeophtheirus salmonis*) infestation of wild, sea-run brown trout (*Salmo trutta*) smolts. Can J Fish Aquat Sci 63:2809–2821

Wells A, Grierson CE, Marshall L, MacKenzie M, and others (2007) Physiological consequences of 'premature freshwater return' for wild sea-run brown trout (*Salmo trutta*) postsmolts infested with sea lice (*Lepeophtheirus salmonis*). Can J Fish Aquat Sci 64:1360–1369

Editorial responsibility: Bengt Finstad, Trondheim, Norway
Reviewed by: 3 anonymous referees

Submitted: November 20, 2020
Accepted: June 17, 2021
Proofs received from author(s): September 6, 2021