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FEATURE ARTICLE

Aquaculture and environmental drivers of salmon lice infestation and body condition in sea trout

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ABSTRACT: Infestation of sea trout *Salmo trutta* L. by salmon lice *Lepeophtheirus salmonis* is associated with increased mortality risk and possible sub-lethal effects. Separating anthropogenic causes of infestation from background ecological variability has proved difficult. A unique 25 yr dataset was collated comprising lice counts from >20 000 sea trout sampled from 94 separate river and lake systems in Ireland and Scotland at varying distances from marine salmon farms. Statistical models were developed to explore the potential effects of distance to a salmon farm, rainfall and ambient temperature on sea trout lice infestation and body condition (weight at length). These models indicated that sea trout captured closer to salmon farms had significantly higher levels of lice infestation, and that this effect was exacerbated in warmer years. Sea trout sampled closer to salmon farms also had significantly reduced weight at length (impaired condition), with the strongest impact in dry years. The study dataset covers a broad geographic area over multiple years, and accounts for variability in temperature and rainfall. Our results imply a rather general impact of salmon farming on lice infestation and body condition of sea trout. This finding has implications for current lice control management strategies, coastal zone planning, recovery of sea trout stocks in aquaculture areas and the scale of aquaculture-free zones.

KEY WORDS: Salmon farming · Sea lice · *Lepeophtheirus salmonis* · Fish parasites · *Salmo trutta* · Marine mortality

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Salmon farm at the mouth of Killary fjord, western Ireland and example of a lice *Lepeophtheirus salmonis* infested sea trout *Salmo trutta* L. taken from the nearby river Erriff.

Photos: P. Gargan IFI

INTRODUCTION

Marine salmon farming is often associated with high levels of the sea lice parasite *Lepeophtheirus salmonis.* Significantly increased salmon farm production since the 1980s has raised concerns regarding the potential impact of sea lice larvae from farms on local wild salmonid populations. In salmon aquaculture bays in spring, the majority of caligid copepod nauplii derive from ovigerous sea lice infesting farmed salmon (Tully & Whelan 1993, Heuch & Mo 2001, Butler 2002). Ectoparasites are capable of seriously impairing the fitness of their host (e.g. Lehmann 1993) and increasing mortality risk (e.g. Rousset et al. 1996). Mortality of wild salmonids at-

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tributable to sea lice infestation is widely documented (Costello 2009) and observed population declines have often been associated with infestation (Frazer 2009). Revie et al. (2009) concluded that the weight of evidence suggests that sea lice of farm origin can present, in some locations and for some host populations, a significant threat to wild salmonid stocks.

Sea trout *Salmo trutta* L. normally remain for extended periods in near-coastal waters (Pemberton 1976, Thorstad et al. 2007, Middlemas et al. 2009) where the majority of salmon farms are located. This fish is therefore particularly vulnerable to sea lice impact, having the potential to encounter lice of farm origin throughout much of its marine phase. Studies in Ireland, Scotland and Norway show a relationship between lice infestation of sea trout and distance to the nearest salmon farm, with greatest infestation levels and variation in infestation seen close to farms (Anon 1997, Birkeland & Jakobsen 1997, Mackenzie et al. 1998, Bjørn et al. 2001, Butler & Watt 2003, Gargan et al. 2003). The collapse in sea trout rod catches in western Ireland during the mid-1980s coincided with the development of salmon aquaculture in inshore bays, and is linked to infestation of lice from salmon farms (Tully & Whelan 1993, Tully et al. 1999, Gargan et al. 2003). An extensive review of the impacts of sea lice on sea trout (Thorstad et al. 2015) concluded that salmon farming increases the abundance of salmon lice in the marine habitat and that salmon lice in intensively farmed areas have negatively impacted wild sea trout populations by increasing marine mortality, changing migratory behaviour, reducing marine growth and depleting populations.

Middlemas et al. (2010) commented that an important step in examining the contribution of salmon farming to levels of sea lice on wild salmonids was to establish how closely, and over what spatial scale, lice infestation of wild sea trout related to salmon farming practices. Anon (1995) demonstrated that there was a relationship between the level of lice infestation on sea trout post-smolts and the proximity of salmon farms in Ireland (1992 to 1994), and developed a physical (dilution and dispersal) and biological (larval behaviour, longevity) rationale to explain this effect. Gargan et al. (2003) demonstrated that lice infestation on sea trout in western Ireland was related to distance to the nearest salmon farm, with greatest infestation and variation in infestation seen close to farms. Gillibrand & Willis (2007) later produced a general sea lice dispersal model showing that infective sea lice levels peaked 7 to 12 km seawards of the source. Serra-Llinares et al. (2014) also found that the distance to surrounding fish farms plays a key role in the success of the protected salmon fjords in Norway; sea lice levels recorded on wild sea trout caught inside large protected areas (i.e. where the distance to the closest fish farm was >30 km) were consistently low over time, presumably having little effect on local populations of wild salmonids.

Sea lice infestation can have lethal (e.g. Grimnes & Jakobsen 1996) and sub-lethal (e.g. Wagner & McKinley 2004) impacts, and it is important to characterize infestation levels associated with physiologically significant impacts on a salmonid host. Bjørn & Finstad (1997) found that a threshold of 0.7 lice larvae per gram of fish weight was associated with physiological problems and osmoregulatory disturbances in sea trout. Middlemas et al. (2010) developed a critical threshold model to examine the spatial range of effect on sea trout of lice from salmon farms on the west coast of Scotland (2003 to 2009); they used a threshold of 13 mobile lice per fish derived from laboratory studies (Wells et al. 2006) to indicate the proportion of trout subject to physiological stress and potential death from sea lice infestation. Taranger et al. (2015) specified a range of infestation rates causing physiological stress in sea trout, and developed an index that estimates increased sea trout mortality risk due to sea lice infestation. Levels of lice infestation associated with salmon farms are likely to change across gradients of external stressors (e.g. Lafferty & Kuris 1999) such as temperature and rainfall (Helland et al. 2015). The present study uses a large international dataset to develop statistical models describing lice infestation and body condition of sea trout. This analysis accounts for considerable temporal and geographic variability, and for underlying ecological drivers of lice infestation (temperature and rainfall). Results are considered with reference to suggested sea lice risk thresholds.

MATERIALS AND METHODS

Sampling

Ireland

Sea trout were collected annually at a range of locations around the Irish coast. Sampling was primarily by gill netting in estuaries over the May to June period in 1991 to 2015. See Gargan et al. (2003) for a detailed description of the sampling strategy.

Information was available on the location of active salmon farms in Ireland from Irish Marine Institute sea lice monitoring annual reports, and linear sea distance from river mouth to the nearest active salmon farm was calculated. Where a farm was not in production in a given year, distance from the river to the next nearest active farm was applied.

Scotland

Sea trout were caught in sweep nets at sea at various locations on the west coast of Scotland primarily during the May to July period in 1997 to 2015. See Middlemas et al. (2010) for a detailed description of the sampling strategy.

Data provided by the Scottish Environmental Protection Agency was used to identify active salmon farms in Scotland, and the distance between each sampling site and the nearest salmon farm was estimated using an automated approach (Middlemas et al. 2010).

Data

Data were collated from 17 locations in Ireland (N = 7714 fish) over the period 1991 to 2015 and from 8 locations in Scotland (N = 16 768 fish) over the period 1997 to 2015. By observation *ijk*, the data consisted of (L_{ijk}, SL_{ijk}, SW_{ijk}, F_{ij}, T_{ij}, R_{ij}), where L_{ijk} is the number of lice counted on fish *k* at sampling location (coastal area) $j_{1,\ldots,26}$ in sampling year $i_{1,\ldots,25}$, SL_{ijk} is the total length (mm) of fish *k* and SW_{ijk} is the weight (g) of fish *k*. F_{ij} is distance to the nearest salmon farm (km) from location *j* in year *i*, T_{ij} is spring (February to May) mean daily maximum temperature (°C) at location *j* in year *i* (range minimum to maximum = 8.9 to 14.5 in Ireland and 8.2 to 10.9 in Scotland) and R_{ij} is total spring rainfall (mm) at location *j* in year *i* (range minimum to maximum = 44.3 to 160.2 in Ireland and 75.8 to 693.7 in Scotland). Temperature and rainfall indices were chosen to cover the most important smolt migration period and post-smolt period at sea. Environmental data for Irish and Scottish locations were downloaded from Met Éireann (www.met.ie/climate-request/) and the UK Met Office (www.metoffice.gov.uk/climate/uk/summaries/datasets), respectively. There were some missing weight values (notably for Scottish data prior to 2010). Missing weight values were estimated from empirical log-transformed length–weight relationships from the combined dataset.

Analysis

The analysis focused on sea trout post-smolts, hence any individuals larger than 250 mm length and/or 300 g weight were excluded. In the overall dataset, most sea trout post-smolts were sampled within 80 km of the nearest salmon farm. The database also included a small number of fish (N = 212) sampled from Irish east coast locations >200 km from a farm, but there were no fish sampled between 80 and 200 km. Following preliminary analysis, the samples from the Irish east coast were excluded, as these few strongly outlying data points exerted excessive leverage and caused heterogeneity in model residuals. The final dataset for analysis comprised N = 20 506 post-smolts (N = 6515 from Ireland and N = 13 991 from Scotland). Statistical models were used to explore aquaculture and environmental effects on lice infestation and weight at length (body condition) of sea trout post-smolts.

Lice infestation

The effects of temperature, rainfall and distance to the nearest salmon farm on lice infestation of sea trout were investigated using generalized linear mixed-effects models (GLMM). Farm distance was standardized by subtracting the mean and dividing by the standard deviation. Both environmental variables (temperature and rainfall) were expressed as categorical variables having 3 levels (e.g. low, medium, high), where the upper limit of each level was the 25th, 50th and 75th percentile of the variable, adjusted slightly to retain approximately equal numbers of fish in each category. Lice numbers were modelled as a count using fish length as a covariate and including random effects on the intercept of sampling location and year. Preliminary Poisson-distributed models were overdispersed, hence negative binomial models were fitted. A set of 10 candidate models (Table 1) was defined *a priori*, to test covariates and interactions anticipated from ecological knowledge of the system, e.g. a possible increased impact of sea lice in years of less rain and higher temperatures, when transitional waters are warmer and more saline, hence a more favourable environment for sea lice populations. Models were fitted using the lme4 package in R (Bates et al. 2015). Akaike's Information Criterion (AIC) was used to compare model fits. AIC was considered with reference to the number of covariates in each model, and individual non-significant covariates and interactions were considered uninformative if they did not induce a net reduction (ΔAIC > 2) in model AIC (Arnold 2010). All models within 2 AIC units of the best fitting model were considered to have similar fit to the data. Model validation used residual plots to check for het-

Table 1. The *a priori* model set tested for lice infestation and body condition (weight at length) of sea trout post-smolts. For modelling body condition, the response (body weight, *SW* and covariate body length, *SL*) were log-transformed to apply a linear relationship. SL_{ijk} is the total length (mm) of fish k at sampling location (coastal area) $j_{1,\ldots,26}$ in sampling year $i_{1,\ldots,25}$; F_{ij} is distance to the nearest salmon farm (km) from location j in year i; T_{ij} is spring (February to May) mean daily maximum temperature (°C) at location j in year i, R_{ij} is total spring rainfall (mm) at location j in year i, and α_i and α_j are the random effects of year and location, respectively

Model	
1	$\text{Response}_{ijk} = SL_{ijk} + F_{ij} + T_{ij} + R_{ij} + F_{ij} \times R_{ij} + F_{ij} \times T_{ij} + \alpha_i + \alpha_j$
2	$\text{Response}_{ijk} = SL_{ijk} + F_{ij} + T_{ij} + R_{ij} + F_{ij} \times R_{ij} + \alpha_i + \alpha_j$
3	$\text{Response}_{ijk} = SL_{ijk} + F_{ij} + T_{ij} + R_{ij} + F_{ij} \times T_{ij} + \alpha_i + \alpha_j$
4	$\text{Response}_{ijk} = SL_{ijk} + F_{ij} + T_{ij} + R_{ij} + \alpha_i + \alpha_j$
5	$\text{Response}_{ijk} = SL_{ijk} + F_{ij} \times R_{ij} + \alpha_i + \alpha_j$
6	$\text{Response}_{ijk} = SL_{ijk} + F_{ij} \times T_{ij} + \alpha_i + \alpha_j$
7	$\text{Response}_{ijk} = SL_{ijk} + T_{ij} \times R_{ij} + \alpha_i + \alpha_j$
8	$\text{Response}_{ijk} = SL_{ijk} + F_{ij} + \alpha_i + \alpha_j$
9	$\text{Response}_{ijk} = SL_{ijk} + \alpha_i + \alpha_j$
10	$\text{Response}_{ijk} = F_{ij} + \alpha_i + \alpha_j$

erogeneity of residuals. Linearity in the relationships between lice infestation and tested covariates was evaluated by plotting Pearson residuals against each covariate in the model and fitting a GAM to visualize any non-linear patterns. Likelihood ratio tests were used to evaluate whether categorical covariates had a significant overall effect. The effects on lice infestation of important covariates and interactions were visualised using the R package effects (Fox 2003). The full lice model for combined data had the form:

$$L_{ijk} \sim NB(\mu_{ijk}, k)$$
$$E(L_{ijk}) = \mu_{ijk} \text{ and } \text{var}(L_{ijk}) = \mu_{ijk} + \mu_{ijk}^2/k$$
$$\log(\mu_{ijk}) = SL_{ijk} + F_{ij} + T_{ij} + R_{ij} + F_{ij} \times R_{ij} + F_{ij} \times T_{ij} + \alpha_i + \alpha_j$$
$$\alpha_i \sim N(0, \sigma^2_{\text{year}})$$
$$\alpha_j \sim N(0, \sigma^2_{\text{location}})$$

where *NB* is a negative binomial and μ and k are the parameters of the *NB* distribution function. α_i and α_j are the random effects of year and location respectively, which have normal distribution N with mean 0 and variance σ^2.

The model fitting and validation process was applied first to the whole dataset, and then to each of Irish and Scottish data separately.

Body condition

This analysis used only fish for which weight was measured (N = 10 862 overall), rather than estimated from a log-linear length–weight relationship. Weight of sea trout smolts was modelled using Gamma GLMM including length as a covariate, where both weight and length were log-transformed to support a linear relationship. Tested covariates and interactions (Table 1) and the modelling process were the same as for the lice infestation models above. The model fitting and validation process was again applied first to the whole dataset and then to each of Irish and Scottish data separately. The full sea trout weight model for all data combined had the form:

$$SW_{ijk} \sim \text{Gamma}(\mu_{ijk}, \tau)$$
$$E(SW_{ijk}) = \mu_{ijk} \text{ and } \text{var}(SW_{ijk}) = \frac{\mu^2_{ijk}}{\tau}$$
$$\log(\mu_{ijk}) = \alpha + \log(SL_{ijk}) + F_{ij} + T_{ij} + R_{ij} + F_{ij} \times R_{ij} + F_{ij} \times T_{ij} + \alpha_i + \alpha_j$$
$$\alpha_i \sim N(0, \sigma^2_{\text{year}})$$
$$\alpha_j \sim N(0, \sigma^2_{\text{location}})$$

where μ and τ are the parameters of the Gamma distribution function.

Table 2. Parameters of selected models of sea trout post-smolt lice infestation for Scottish and Irish data combined (N = 20 506 smolts), Irish data only (N = 6515) and Scottish data only (N = 13 991)

	Estimate	SE	*z*	p
All data				
(Intercept)	1.846	0.208	8.862	<0.001
Length	0.595	0.020	30.401	<0.001
Farm distance	–0.145	0.034	–4.209	<0.001
Rain-moderate	0.130	0.086	1.508	0.132
Rain-wet	0.019	0.112	0.169	0.866
Temp-warm	0.442	0.084	5.263	<0.001
Temp-hot	0.666	0.109	6.123	<0.001
Farm:Rain-moderate	–0.338	0.046	–7.392	<0.001
Farm:Rain-wet	–0.386	0.051	–7.623	<0.001
Farm:Temp-warm	0.054	0.047	1.134	0.257
Farm:Temp-hot	–0.176	0.048	–3.676	<0.001
Ireland				
(Intercept)	2.304	0.205	11.215	<0.001
Length	0.401	0.031	12.917	<0.001
Farm distance	–0.528	0.067	–7.855	<0.001
Rain-moderate	0.221	0.121	1.819	0.069
Rain-wet	–0.227	0.215	–1.057	0.291
Temp-warm	0.017	0.111	0.155	0.877
Temp-hot	0.441	0.118	3.751	<0.001
Farm:Rain-moderate	–0.147	0.075	–1.971	0.049
Farm:Rain-wet	–0.034	0.107	–0.319	0.750
Farm:Temp-warm	–0.524	0.110	–4.744	<0.001
Farm:Temp-hot	–0.077	0.068	–1.132	0.257
Scotland				
(Intercept)	2.211	0.464	4.759	<0.001
Length	0.675	0.026	26.310	<0.001
Farm distance	0.032	0.055	0.584	0.559
Rain-moderate	–0.112	0.446	–0.252	0.801
Rain-wet	–0.325	0.385	–0.845	0.398
Temp-warm	0.284	0.281	1.015	0.310
Temp-hot	0.125	0.660	0.189	0.850
Farm:Rain-moderate	–0.527	0.074	–7.138	<0.001
Farm:Rain-wet	–0.637	0.074	–8.583	<0.001
Farm:Temp-warm	0.235	0.059	3.974	<0.001
Farm:Temp-hot	–0.111	0.115	–0.972	0.331

RESULTS

Lice infestation

Model selection using AIC and residual plots resulted in the same single best fitting lice count model for all data combined and for each of Ireland and Scotland separately (Table 2). Residual plots showed no evidence of heterogeneity or of a non-linear relationship with any tested variable. Lice models for Ireland and the combined data indicated that lice infestation was significantly greater for sea trout caught closer to salmon farms; the farm distance effect was not significant for Scotland (Table 2). The effects of temperature and rainfall varied between the datasets, but both variables interacted significantly with farm distance in all datasets. The effect of salmon farm distance on sea trout lice infestation increased with temperature, with greatest predicted impact in hot years (Fig. 1). The interaction between farm distance and rainfall was more complex, with a strong salmon farm impact in moderate and wet years, but a less clear impact in dry years, as background levels of sea lice (levels at maximum observed distance from a farm) appear to be highest in dry conditions (Fig. 2). The interactions between farm distance and each of rainfall and temperature were both significant overall (chi-square, $p < 0.001$). Random effects on the intercept of location and year are shown (Fig. 3).

Body condition

There was also a single best fitting sea trout body condition model for all data combined. This model indicated that sea trout had significantly reduced weight at length (poorer condition) closer to a salmon

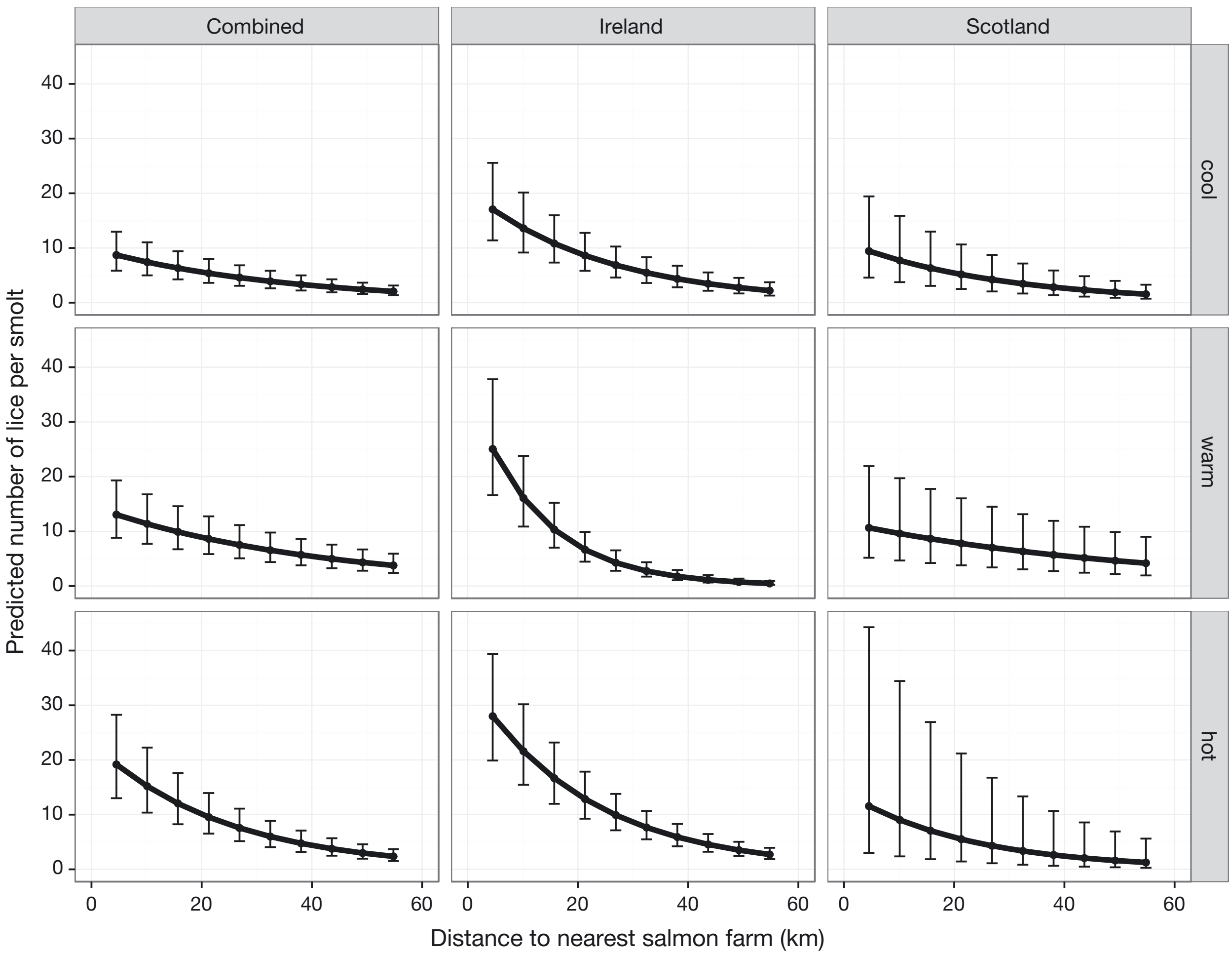

Fig. 1. Effect of proximity to a salmon farm on lice infestation of sea trout post-smolts at 3 observed levels (cool <10.3°C, warm 10.3 to 10.8°C, hot >10.8°C) of mean daily maximum temperature in spring (February to May). Ireland, Scotland and combined data are shown. Vertical bars are 95% CI

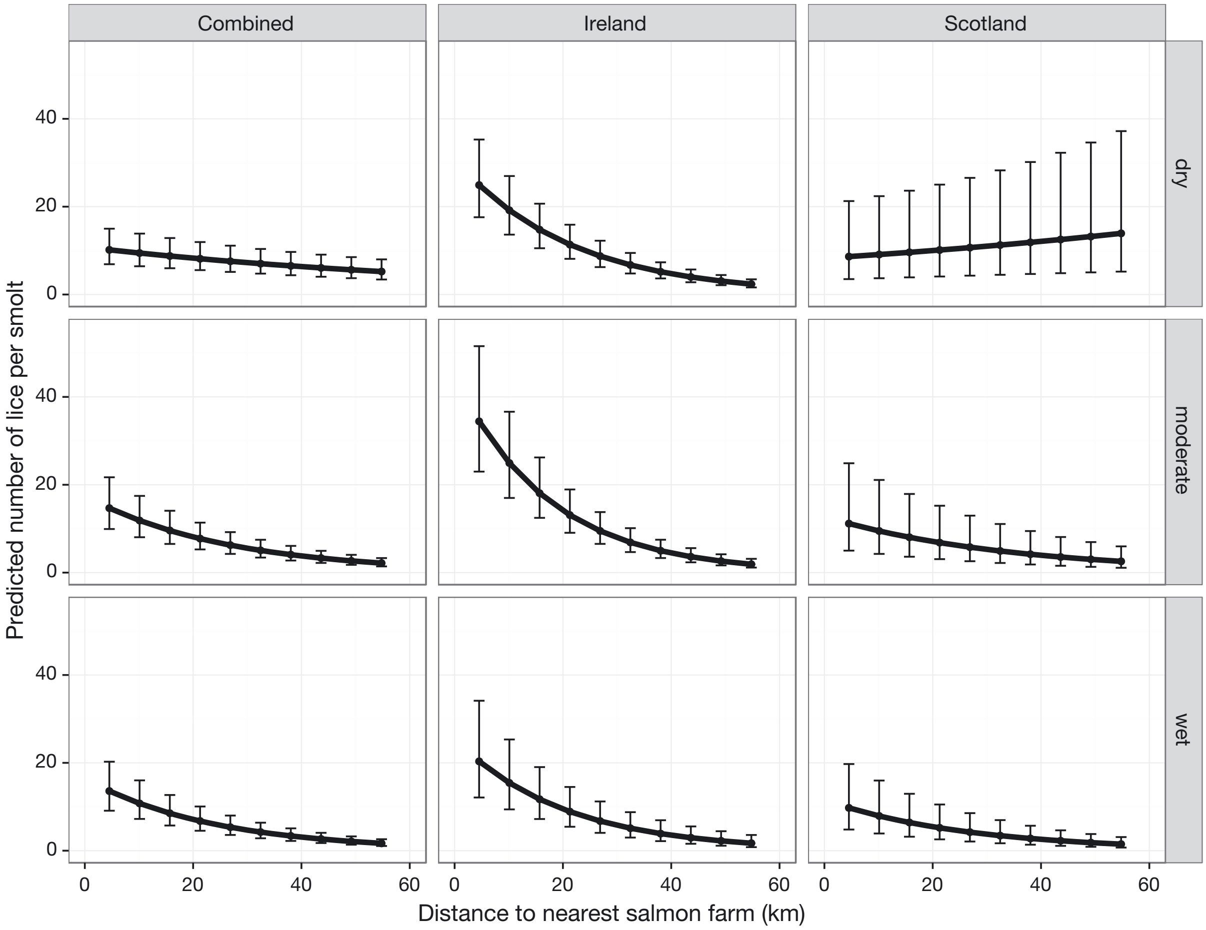

Fig. 2. Effect of proximity to a salmon farm on lice infestation of sea trout post-smolts at 3 observed levels (dry 40 to 100 mm, moderate 100 to 125 mm, wet >125 mm) of total spring (February to May) rainfall. Ireland, Scotland and combined data are shown. Vertical bars are 95% CI

farm (Table 3). This effect was most evident in dry years, when a sea trout of average length (180 mm) caught within 10 km of a farm could weigh up to 10 g less than a fish of similar length caught >40 km from a farm (Fig. 4). There was not a strong farm effect on sea trout condition in the wettest years. The interaction between farm distance and rainfall was significant overall (chi-square, $p < 0.001$). Temperature was not included in the selected model of sea trout body condition using all data combined. Random effects on the intercept of location and year are shown (Fig. 5). The selected condition models for each of Irish and Scottish data both retained only length and farm distance as important covariates. The Irish model showed a strongly significant positive effect of farm distance, i.e. sea trout captured farther from a salmon farm had significantly greater weight at length, i.e. better body condition. The farm effect for Scotland was only marginally significant ($p = 0.025$) but negative (Table 3).

DISCUSSION

We analysed a 25 yr dataset including 94 individual river and lake systems in 25 areas along the Atlantic coasts of Scotland and Ireland. Statistical models indicated significantly greater numbers of lice on sea trout captured at locations closer to a salmon farm, and showed that the salmon farm effect on lice infestation was greater in warmer years. Sea trout closer to salmon farms also had reduced weight at length, with the greatest impact in dry years. The models accounted for underlying effects of temperature and rainfall as well as variability associated with unmeasured temporal and biogeographic factors. These findings, using a much larger dataset over a longer time period than previous studies in the same areas (Gargan et al. 2003, Middlemas et al. 2013), clearly demonstrate that distance to the nearest salmon farm is an important driver of lice infestation and body condition of sea trout across ranges of geography and

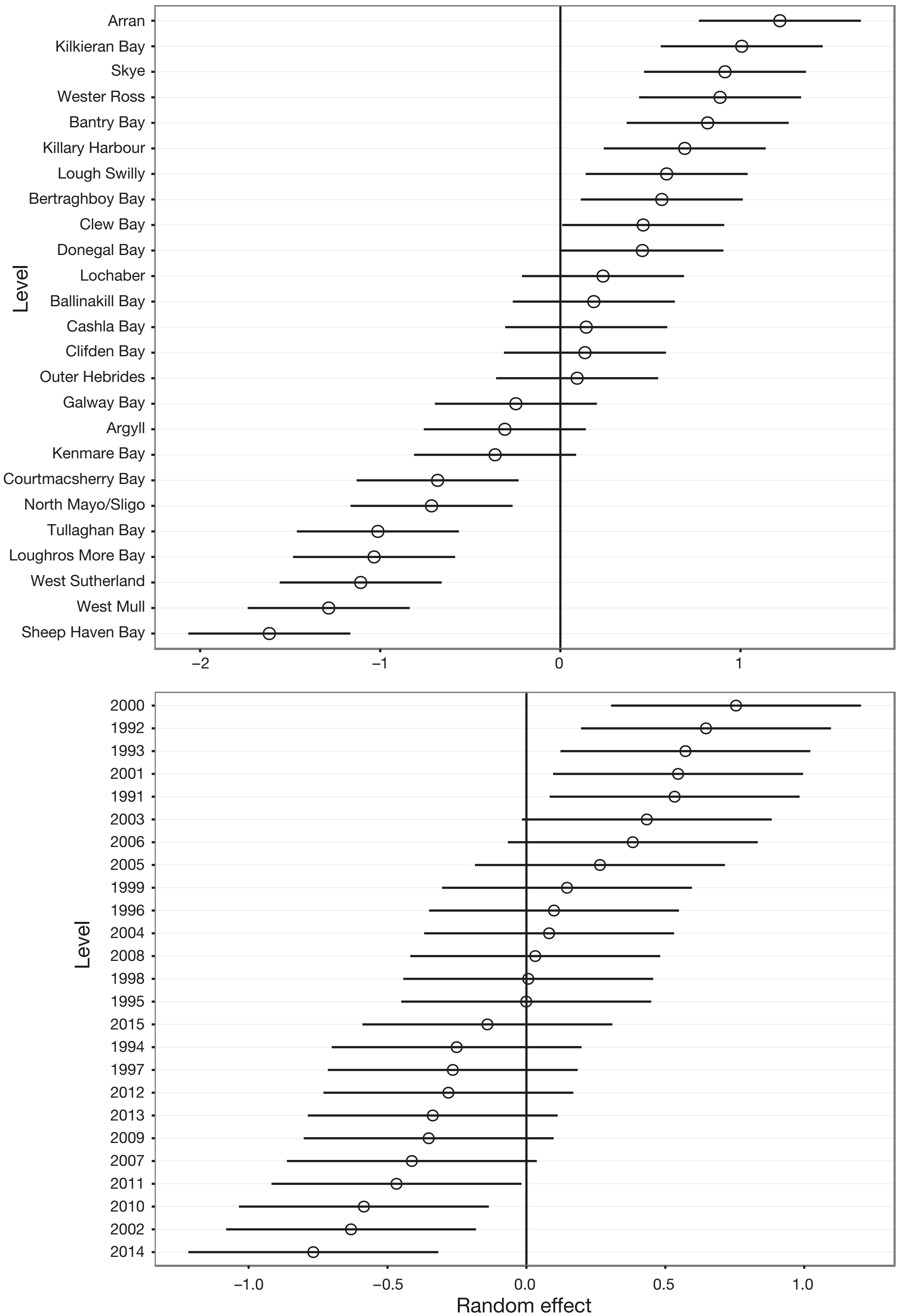

Fig. 3. Random effects (with 95% CI) on the intercept of location and year from the lice infestation model fit to combined data

Table 3. Parameters of selected models of sea trout log-weight at length for Scottish and Irish data combined (N = 10 862 smolts), Irish data only (N = 6479) and Scottish data only (N = 4383)

	Estimate	SE	*t*-value	p
All data				
(Intercept)	−2.496	0.018	139.846	<0.001
Log length	0.753	0.003	239.896	<0.001
Farm distance	0.009	0.001	11.386	<0.001
Rain-moderate	−0.001	0.003	−0.191	0.848
Rain-wet	−0.005	0.004	−1.263	0.207
Farm:Rain-moderate	−0.002	0.001	−1.195	0.232
Farm:Rain-wet	−0.012	0.001	−10.734	<0.001
Ireland				
(Intercept)	−2.240	0.018	127.650	<0.001
Log length	0.705	0.003	220.958	<0.001
Farm distance	0.008	0.001	13.801	<0.001
Scotland				
(Intercept)	−2.740	0.031	−88.252	<0.001
Log length	0.798	0.006	141.187	<0.001
Farm distance	−0.002	0.001	−2.241	0.025

environment. The temporal and spatial scale of the study extends the conclusions of previous studies that also observed increased salmon lice levels closer to salmon aquaculture sites (Tully et al. 1999, Bjørn et al. 2001, Bjørn & Finstad 2002, Gargan et al. 2003, Bjørn et al. 2011, Serra-Llinares et al. 2014) and provides a predictive framework for this effect.

Factors that increase levels of lice infestation are of considerable importance in sustainable management of sea trout populations. Previous studies found that in areas with epidemics, lice are implicated in the mortality of 32 to 47% of all migrating sea trout smolts (Bjørn et al. 2001), and 48 to 86% of wild salmon smolts (Holst & Jakobsen 1998, Vollset et al. 2015). Bjørn et al. (2001) found that one-third of the sea trout post-smolts captured at sea in northern Norway had salmon lice above a critical level found to cause mortality in laboratory trials. For sea trout that returned prematurely to freshwater, it was estimated that 47% had these critical lice levels (Bjørn et al. 2001).

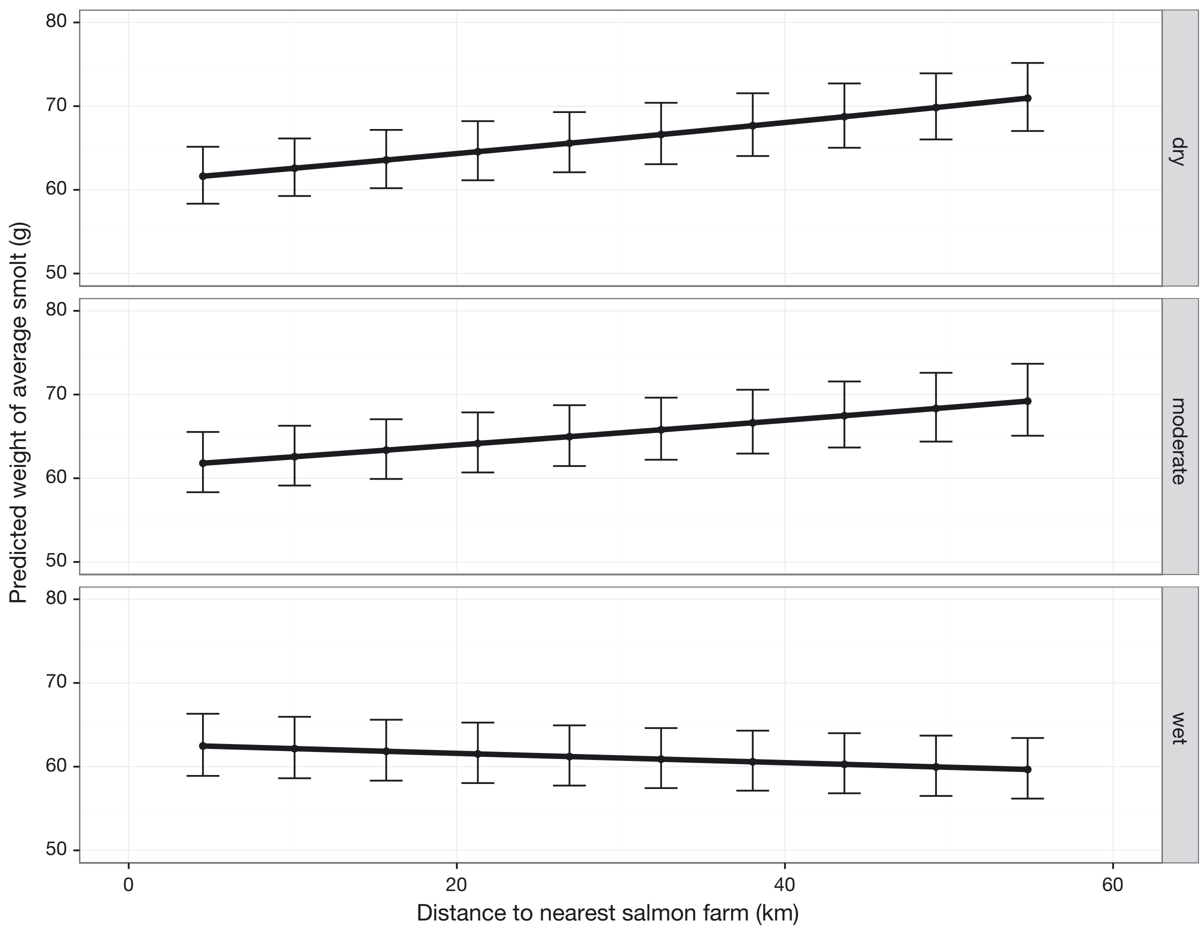

Fig. 4. Effect of proximity to a salmon farm on weight of an average length (180 mm) sea trout post-smolt at 3 observed levels (dry 40 to 100 mm, moderate 100 to 125 mm, wet >125 mm) of total spring (February to May) rainfall. The combined model is shown. Vertical bars are 95% CI

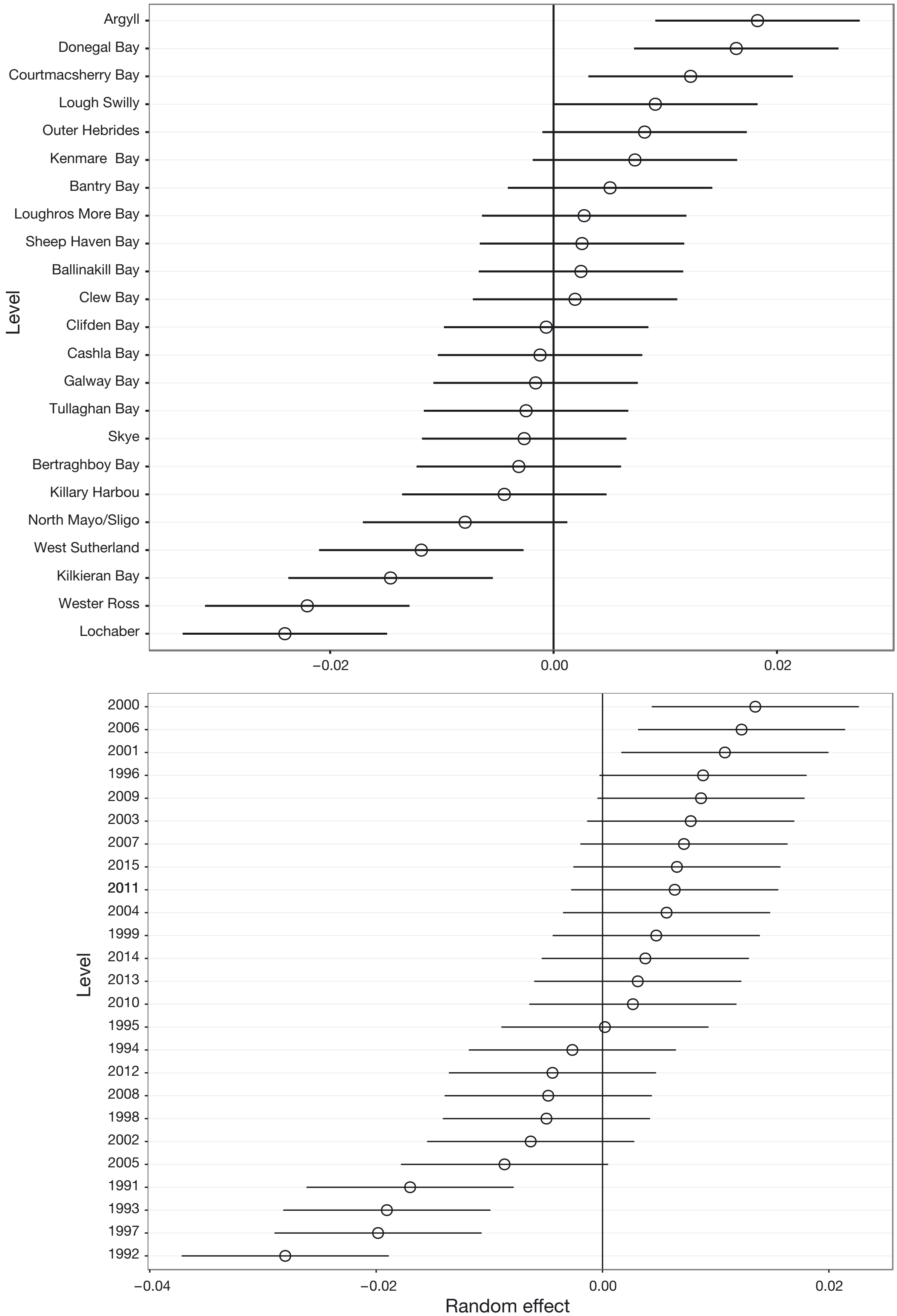

Fig. 5. Random effects (with 95% CI) on the intercept of location and year from the sea trout body condition (weight at length) model fit to combined data

Distance to a salmon farm

Wells et al. (2006) found that lice infestations of >13 lice per fish were associated with physiological stress and increased mortality risk in sea trout. Taranger et al. (2015) developed a salmon lice risk index to estimate the increased mortality due to salmon lice infections, and suggested that an infestation rate of >0.2 lice per gram (equal to approximately 15 lice on a fish of 74 g; the average observed weight in the present study) would exert a mortality rate of 50%. Our models predict levels of lice infestation in this range for sea trout caught within 15 km of a salmon farm (up to 20 km in hot years; Fig. 1). Of the 25 locations sampled for our study, 17 were ≤20 km from a salmon farm.

These results help to explain previous Irish studies that record very high marine mortality rates for sea trout in salmon aquaculture bays. In the Irish Burrishoole system, the percentage of sea trout smolts that survived to return as finnock in the same year ranged from 11 to 32% (mean 21%) prior to the onset of marine salmon aquaculture. Throughout the 1990s, finnock return rates were about 33% of this historical average after the introduction of salmon farming (Poole et al. 2006). Data from 2 other trap facilities in the west of Ireland indicate marine survival <2% in the majority of years when salmon aquaculture was in operation (Gargan et al. 2006a). The development of salmon aquaculture in western Ireland during the mid-1980s coincided with the collapse in sea trout rod catches in the Irish Connemara district (Whelan & Poole 1996, Gargan et al. 2006b). This rod catch collapse is linked to salmon lice infestation on sea trout (Tully & Whelan 1993, Tully et al. 1999, Gargan et al. 2003). For the west of Scotland, Middlemas et al. (2013) estimated that the influence of a farm becomes negligible beyond 31 km. These authors observed considerable uncertainty around the fitted probabilities of exceeding the critical threshold, likely due to the relative scarcity of sampling sites >20 to 30 km from the nearest salmon farm, a feature also present in the larger dataset used in the present analysis. Where farms are separated by <20 km, there may be additive interactions between them.

Salmon farming practices

Previous studies demonstrate that the majority of nauplii arise from ovigerous lice infesting farmed salmon in spring (Tully & Whelan 1993, Heuch & Mo 2001, Butler 2002). Studies also show that the presence of salmon farms significantly increases the level of sea lice infestation on sea trout post-smolts (Tully et al. 1999, Mackenzie et al. 1998, Grimnes et al. 2000, Butler 2002). In an examination of salmon lice infection on wild salmonids in marine protected areas in Norway, Serra-Llinares et al. (2014) found a positive correlation between the production of lice infective stages from fish farms and the mean abundance of lice on wild fish. Other studies record higher lice levels on sea trout in the second year of the farm production cycle, when larger over-wintered salmon are present (Butler 2002, Revie et al. 2002, Marshall 2003, Gillibrand et al. 2005, Hatton-Ellis et al. 2006, Middlemas et al. 2010, 2013). Gargan et al. (2003) demonstrated both high and low levels of lice infestation in estuaries close to salmon farms, and suggested that lice production and dispersal from farms may differ among sites and between regions. These authors commented that such variation may be expected given differences in topography, hydrodynamics, salinity and fish behaviour. Middlemas et al. (2013) observed that both fish movement and lice dispersal influence the distance over which any lice effect on sea trout can be detected. Results from a lice dispersal model (Gillibrand & Willis 2007) demonstrated that infective sea lice levels peak 7 to 12 km seawards of the source. Other studies show that the direction and distance of lice dispersal can be influenced by site-specific factors, such as prevailing wind and currents, and local topography (Amundrud & Murray 2009, Stucchi et al. 2011). The amount of infective larvae produced in an area will also depend on the number of wild and/or farmed fish, the number of mature female lice per fish and water temperature (Boxaspen & Næss 2000, Heuch et al. 2000, Stien et al. 2005).

The present analysis does not explicitly account for local farming practices, e.g. stage of farm production, size of farms or lice loads on farmed fish. There are national differences in the salmon farming industry; the Scottish farming industry is about 10 times larger than that in Ireland and operated on a single generation site basis for the majority of the time period covered in our analysis. However, the data presented cover a wide range of locations over an extended time period and this may capture considerable variability in farming practice and location. Inclusion of site-specific information, e.g. local topography, salinity, hydrodynamic lice dispersal models and farm production cycle, would be required to demonstrate finer-scale effects. Serra-Llinares et al. (2014) recommended that in order to establish more precise management practices, the development and validation of accurate planktonic larval distribution and abundance models is needed. Combining predictions of abundance and distribution of lice from fish farms in time and space from hydrodynamic models (Asplin et al. 2011) with critical abundance thresholds for effects on wild salmonid populations according to politically specific sustainability goals could support area management systems based on 'maximum sustainable lice loads' or 'lice quotas'.

Sampling effects

The salmon farm effect on sea trout body condition was much weaker for Scottish than Irish fish (and actually positive). This contrast may reflect differences in sampling strategy between countries: Irish sea trout were captured in inner estuaries or river mouths and had returned prematurely from the sea, whereas the majority of sea trout in the Scottish samples were captured in sweep nets at sea. Premature return of lice-infested sea trout to freshwater has been reported in Ireland since lice epizootics have been recorded (Whelan 1991, Tully & Whelan 1993) and later in Scotland (Butler & Walker 2006, Hatton-Ellis et al. 2006). Bjørn et al. (2001) found that sea trout and Arctic char that returned prematurely to freshwater had higher relative infection intensities than fish caught at sea at the same time, and commented that premature return of the most infected fish to freshwater may therefore be triggered to reduce the physiological consequences of the infection (Bjørn & Finstad 1997, Finstad et al. 2000). Bjørn et al. (2001) commented that most records of sea lice on sea trout are from fish returning prematurely to freshwater or hyposaline conditions (Tully et al. 1993, Birkeland & Jakobsen 1997, Tully et al. 1999), and that this behaviour may give a biased indication of the lice infestation in the total marine-phase population. If this is the case, sampling methods targeting fish at sea alone might reduce observations of the highest intensity infestation levels (Lester 1984). Overall, the present study showed consistent and strong impacts of salmon farming on lice infestation of sea trout.

Environmental effects

Local environmental conditions are known to affect sea lice transmission in coastal waters (e.g. Amundrud & Murray 2009). The present study found that the salmon farm effect on lice infestation of sea trout was greater in years of higher temperature, while farm impacts on body condition were more severe in drier years. There was also some evidence that background lice levels were greatest in dry years. Revie at al. (2002) did not find a temperature effect on sea louse abundance within salmon cages, suggesting that the temperature effect observed in the present study is probably associated with transmission dynamics in the surrounding wild system. Rate of development (and population structure), and reproductive rate and output of sea lice are known to be temperature-dependent, with faster generation time in warmer temperatures (Tully 1992). Rainfall is expected to affect lice infestation rates in 2 ways, either by causing floods that facilitate rapid movement of smolts through coastal areas of high lice abundance, or by reducing salinity of transitional waters and creating a less favourable environment for lice (e.g. McLean et al. 1990, Todd et al. 2000, Penston et al. 2004). Our results suggest that the potential impact of a salmon farm on sea lice infestation may be exacerbated in warmer years. This evidence of temperature and rainfall effects implies that management should incorporate environmental variability, e.g. in setting farm lice thresholds. Climate effects, associated with shifts in temperature and rainfall regime, should also be anticipated in management of sea lice on salmon farms in the future.

Sub-lethal impacts

Parasite infestation is associated with important sub-lethal impacts on fitness (e.g. Lafferty & Kuris 1999). The present study found that weight at length was significantly reduced for sea trout caught closer to salmon farms. This result is consistent with most existing evidence (although see contrasting results from small-scale studies by Sharp et al. 1994 in Scotland and Mo & Heuch 1998 in Norway). Reduced condition factor and body mass are recorded for lice-infested sea trout (Bjørn & Finstad 1997, Dawson et al. 1998) and may reflect adverse stress responses and dehydration (Pickering 1981, Bjørn & Finstad 1997, Wendelaar Bonga 1997, Wagner et al. 2008). A number of studies also record impaired swimming performance (Wagner et al. 2003) and feeding activity in lice-infested fish, typically once the salmon lice have moulted to the pre-adult and adult stages (Dawson et al. 1998, Wells et al. 2006, 2007). Fjørtoft et al. (2014) demonstrated that sea trout growth was slower during the first and second summers at sea when salmon farming was active, with the growth reduction after the first summer in the sea corresponding to a body mass reduction of 20 to 40%. This compares to a 14% reduction in the weight of a sea trout of mean length in the present study. Butler & Walker (2006) also recorded a decrease in marine growth rates for River Ewe (Scotland) sea trout close to salmon farms, and concluded that the decline in growth was at least partly caused by salmon lice epizootics emanating from the farms. Poole et al. (1996) demonstrated that a significant reduction in sea trout marine growth in the Burrishoole system in western Ireland was most likely linked to premature return to freshwater of lice-infested sea trout.

Thorstad et al. (2015) commented that sea trout may suffer a compromised immune system from mechanical damage to the skin and primary and secondary stress responses, and thus an increased risk of secondary infection; Bjørn & Finstad (1997) found a reduced lymphocyte:leukocyte ratio, indicative of reduced disease resistance. Lice-compromised sea trout may also experience an increased mortality risk from predators (Thorstad et al. 2015). The impaired body condition for sea trout recorded in the present study is important as it provides larger-scale evidence that lice infestation (probably from salmon farms) can have sub-lethal effects that could potentially drive impaired fitness, e.g. potential vulnerability to predation, compromised immune system and increased risk of disease, reduced marine growth and reduced fecundity.

CONCLUSIONS

Taranger et al. (2015) approved the philosophy of the 'strategy for an environmentally sustainable aquaculture industry' (Anon 2009, p. 16), which states that no disease, including lice, should have a regulatory effect on wild fish. Many of their recommendations referred to mathematical modelling of lice production, dispersal and infestation risk around salmon farms, but they highlighted risk assessment using large datasets as a key component of understanding and managing the impact of sea lice on wild salmonids. We collated a unique large-scale and long-term dataset that records lice infestation of sea trout in 94 systems around the Atlantic coast of the British Isles. Statistical models of these data extend previous studies that found an effect of salmon farming on lice infestation of sea trout by accounting for environmental factors and considerable biogeographic variability. Results also confirmed that sea trout close to salmon farms have significantly impaired body condition, implying a range of possible sub-lethal impacts on fitness. Our analysis highlighted unresolved issues in management of the ecological impacts of salmon farming in Britain and Ireland. This outcome has strong implications for current lice control management strategies, coastal zone planning, recovery of sea trout stocks in aquaculture areas and the scale of aquaculture-free zones.

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LITERATURE CITED

Amundrud TL, Murray AG (2009) Modelling sea lice dispersion under varying environmental forcing in a Scottish sea loch. J Fish Dis 32:27–44

Anon (1995) Report of the sea trout working group, 1994. Department of the Marine, Dublin

Anon (1997) Report of the workshop on the interactions between salmon lice and salmonids. Edinburgh, 11–15 November 1996. ICES CM 1997/M:4 Ref:F

Anon (2009) Strategy for an environmentally sustainable Norwegian aquaculture industry. Ministry of Fisheries and Coastal Affairs, Oslo

Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. J Wildl Manag 74:1175–1178

Asplin L, Boxaspen KK, Sandvik AD (2011) Modeling the distribution and abundance of planktonic larval stages of *Lepeophtheirus salmonis* in Norway. In: Jones S, Barnes R (eds) Salmon lice: an integrated approach to understanding parasite abundance and distribution. Wiley-Blackwell, Oxford, p 31–50

Bates D, Maechler M, Bolker B, Walker S (2015) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-9. https://CRAN.R-project.org/package=lme4

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 (2002) Salmon lice, *Lepeophtheirus salmonis* (Krøyer), infestation in sympatric populations of Arctic char, *Salvelinus alpinus* (L.), and sea trout, *Salmo trutta* (L.), in areas near and distant from salmon farms. ICES J Mar Sci 59:131–139

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

Bjørn PA, Sivertsgård R, Finstad B, Nilsen R, Serra-Llinares

RM, Kristoffersen R (2011) Area protection may reduce salmon louse infection risk to wild salmonids. Aquacult Environ Interact 1:233–244

Boxaspen K, Næss T (2000) Development of eggs and the planktonic stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. Contrib Zool 69:51–55

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 Publishing, 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, Edinburgh, 16–18 July 2002. Blackwell Science, Oxford, p 93–118

Costello MJ (2009) How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. Proc R Soc B 276: 3385–3394

Dawson LHJ, Pike AW, Houlihan DF, McVicar AH (1998) Effects of salmon lice *Lepeophtheirus salmonis* on sea trout *Salmo trutta* at different times after seawater transfer. Dis Aquat Org 33:179–186

Finstad B, Grimnes A, Bjørn PA, Hvidsten NA (2000) Laboratory and field investigations of salmon lice [*Lepeophtheirus salmonis* (Krøyer)] infestation on Atlantic salmon (*Salmo salar* L.) post-smolts. Aquacult Res 31:795–803

Fjørtoft HB, Borgstrøm R, Skaala Ø (2014) Differential changes in growth patterns of anadromous brown trout and Atlantic salmon from the River Etneelva over a 25-year period. Mar Biol Res 10:301–307

Fox F (2003) Effect displays in R for generalised linear models. J Stat Softw 8:1–27

Frazer LN (2009) Sea-cage aquaculture, sea lice and declines of wild fish. Conserv Biol 23:599–607

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, Edinburgh, 16–18 July 2002. Blackwell Science, Oxford, p 119–135

Gargan PG, Roche WK, Forde GP, Ferguson A (2006a) 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, Poole WR, Forde G (2006b) A review of the status of Irish sea trout stocks. In: Harris G, Milner N (eds) Sea trout: biology, conservation and management. Blackwell Publishing, Oxford, p 25–44

Gillibrand PA, Willis KJ (2007) Dispersal of sea louse larvae from salmon farms: modelling the influence of environmental conditions and larval behaviour. Aquat Biol 1: 63–75

Gillibrand P, Hay D, Penston M, Murray A (2005) Sea lice and sea trout. Are salmon farms causing increased parasitism on wild salmonids in Scotland? Ocean Challenge 14:24–30

Grimnes A, Jakobsen PJ (1996) The physiological effects of salmon lice infection on post smolt of Atlantic salmon. J Fish Biol 48:1179–1194

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

Hatton-Ellis M, Hay DW, Walker AF, Northcott SJ (2006) Sea lice *Lepeophtheirus salmonis* infestations of post-smolt sea trout in Loch Shieldaig, Wester Ross, 1999–2003. In: Harris G, Milner N (eds) Sea trout: biology, conservation and management. Blackwell Publishing, Oxford, p 372–376

Helland IP, Uglem I, Jansen PA, Diserud OH, Bjørn PA, Finstad B (2015) Statistical and ecological challenges of monitoring parasitic salmon lice infestations in wild salmonid fish stocks. Aquacult Environ Interact 7: 267–280

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, Nordhagen JR, Schram TA (2000) Egg production in the salmon louse [*Lepeophtheirus salmonis* (Krøyer)] in relation to origin and water temperature. Aquacult Res 31:805–814

Holst JC, Jakobsen PJ (1998) Dodelighet hos utvandrende postsmolt av laks somfolge av lakselusinfeksjon. Fiskets Gang 8:13–15

Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. Limnol Oceanogr 44: 925–931

Lehmann T (1993) Ectoparasites: direct impact on host fitness. Parasitol Today 9:8–13

Lester RJG (1984) A review of methods for estimating mortality due to parasites in wild fish populations. Helgol Meeresunters 37:53–64

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

Marshall S (2003) The incidence of sea lice infestations on wild sea trout compared to farmed salmon. Bull Eur Assoc Fish Pathol 23:72–79

McLean PH, Smith GW, Wilson MJ (1990) Residence time of sea louse, *Lepeophtheirus salmonis* K., on Atlantic salmon, *Salmo salar* L., after immersion in fresh water. J Fish Biol 37:311–314

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, Raffell JA, Hay DW, Hatton-Ellis M, Armstrong JD (2010) Temporal and spatial patterns of sea lice levels on sea trout in western Scotland in relation to fish farm production cycles. Biol Lett 6:548–551

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

Mo TA, Heuch PA (1998) Occurrence of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on sea trout (*Salmo trutta*) in the inner Oslo Fjord, south-eastern Norway. ICES J Mar Sci 55:176–180

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

Penston MJ, McKibben MA, Hay DW, Gillibrand PA (2004) Observations on open water densities of sea lice larvae in Loch Shieldaig, western Scotland. Aquacult Res 35: 793–805

Pickering AD (1981) Stress and fish. Academic Press, London

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

Revie CW, Gettingby G, Treasurer JW, Rae GH, Clark N (2002) Temporal, environmental and management factors influencing the epidemiological patterns of sea lice (*Lepeophtheirus salmonis*) infestations on farmed Atlantic salmon (*Salmo trutta*) in Scotland. Pest Manag Sci 58:576–584

Revie C, Dill L, Finstad B, Todd CD (2009) Sea lice working group report. NINA Special Report 39. Norwegian Institute for Nature Research, Trondheim

Rousset F, Thomas F, De Meeûs T, Renaud F (1996) Inference of parasite-induced host mortality from distributions of parasite loads. Ecology 77:2203–2211

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

Sharp L, Pike AW, McVicar AH (1994) Parameters of infection and morphometric analysis of sea lice from sea trout (*Salmo trutta*, L.) in Scottish waters. In: Pike AW, Lewis JW (eds) Parasitic diseases of fish. Samara Publishing, Treasaith, p 151–170

Stien A, Bjørn PA, Heuch PA, Elston DA (2005) Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. Mar Ecol Prog Ser 290: 263–275

Stucchi DJ, Guo M, Foreman MGG, Czajko P and others (2011) Modelling sea lice production and concentrations in the Broughton Archipelago, British Columbia. In: Jones SRM, Beamish RJ (eds) Salmon lice: an integrated approach to understanding parasite abundance and distribution. Wiley-Blackwell, Chichester, p 117–152

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

Todd CD, Walker AM, Hoyle JE, Northcott SJ, Walker AF, Ritchie MG (2000) Infestations of wild adult Atlantic salmon (*Salmo salar* L.) by the ectoparasitic copepod sea louse *Lepeophtheirus salmonis* Krøyer: prevalence, intensity and the spatial distribution of males and females on the host fish. Hydrobiologia 429:181–196

Tully O (1992) Predicting infestation parameters and impacts of caligid copepods in wild and cultured fish populations. Invertebr Reprod Dev 22:91–102

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* (Kroyer) (Copepoda: Caligidae) parasitic on sea trout, *Salmo trutta* L., off the west coast of Ireland during 1990 and 1991. Aquacult Res 24: 545–555

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

Vollset KW, Krontveit RI, Jansen PA, Finstad B and others (2015) Impacts of parasites on marine survival of Atlantic salmon: a meta analysis. Fish Fish 17:714–730

Wagner GN, McKinley RS (2004) Anaemia and salmonid swimming performance: the potential effects of sublethal sea lice infection. J Fish Biol 64:1027–1038

Wagner GN, McKinley RS, Bjørn PA, Finstad B (2003) Physiological impact of sea lice on swimming performance of Atlantic salmon. J Fish Biol 62:1000–1009

Wagner GN, Fast MD, Johnson SC (2008) Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. Trends Parasitol 24:176–183

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

Wendelaar Bonga SE (1997) The stress response in fish. Physiol Rev 77:591–625

Whelan K (1991) Disappearing sea trout: decline or collapse. The Salmon Net 23:24–31

Whelan KF, Poole WR (1996) The sea trout stock collapse, 1989–1992. In: Reynolds J (ed) The conservation of aquatic systems. Proc Seminar 18–19 February 1993. Royal Irish Academy, Dublin, p 101–110

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