



Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population

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ABSTRACT: Atlantic salmon *Salmo salar* has shown declines in abundance associated with reduced survival during marine life stages. Key impacts on survival may include a changing ocean environment and salmon louse *Lepeophtheirus salmonis* infestation from aquaculture. A 26 yr record from the Erriff River (Western Ireland) was used to evaluate the contribution of sea lice from salmon aquaculture to declining returns of wild 1 sea-winter (1SW) salmon. Statistical models suggested that returns were >50% lower in years following high lice levels on nearby salmon farms during the smolt out-migration. The long-term impact of salmon lice was explored by applying predicted annual loss rates as a multiplier to observed 1SW salmon returns. This produced a 'lice-corrected' return time series, i.e. an estimate of how returns might have looked in the absence of a serious aquaculture lice impact. The corrected time series was adjusted to account for some reduction in recruitment due to lost spawners. Comparing observed and lice-corrected time series suggested that salmon lice have strongly reduced annual returns of 1SW Erriff salmon, but that the salmon lice impact does not explain a declining trend in this population.

KEY WORDS: *Lepeophtheirus salmonis* · *Salmo salar* · Salmon smolts · Salmon farming · Ricker stock recruitment

INTRODUCTION

Atlantic salmon *Salmo salar* is an iconic anadromous fish species that has shown marked declines in abundance in recent decades (Limburg & Waldman 2009). Decreased survival rate in the marine environment, rather than in natal rivers, seems to explain the current poor state of many salmon populations (ICES 2016). Marine survival can be partitioned into coastal (transitional and inshore waters) and oceanic (offshore and open ocean) components. The coastal component operates during the first migration of juvenile salmon (smolts) out of their natal river. Events during such early life stages can have an impact on subsequent marine survival of salmon (Holsman et al. 2012). The oceanic component refers to fish in summer nursery areas offshore and in winter feeding areas. In addition to natural mortality, each compo-

ment of marine survival is influenced by anthropogenic pressures.

Coastal pressures frequently interact (Parrish et al. 1998) and include local pollution (Larsson et al. 1996, McCormick et al. 1998, Johnson et al. 2007) and increased rates of sea lice *Lepeophtheirus salmonis* infestation associated with salmon aquaculture (e.g. Krkošek et al. 2007, Costello 2009). Sea cage aquaculture causes sea lice on sympatric wild fish to increase (Frazer 2009). Marine survival of wild pink salmon has been related negatively to lice density on farmed salmon (Marty et al. 2010, Krkošek et al. 2011) and to observed lice infestation on out-migrating juvenile wild fish (Peacock et al. 2013). The negative impact of sea lice on salmonid survival appears to be exacerbated by warmer environmental conditions (Bateman et al. 2016, Shephard et al. 2016). In the ocean, salmon respond to large-scale climate

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forcing (ICES 2016) by the North Atlantic Oscillation (NAO) and the Atlantic Multi-decadal Oscillation (AMO) that drive sea surface temperature (SST) and thus salmon thermal habitat (Friedland et al. 1993, 2003, Jonsson & Jonsson 2004, Mills et al. 2013) and associated prey dynamics (Beaugrand & Reid 2012, Defriez et al. 2016). Recent studies suggest that ocean warming has had a negative impact on oceanic growth and survival (McCarthy et al. 2008, Todd et al. 2008, Friedland et al. 2009) and genetic diversity (Horreo et al. 2011) of Atlantic salmon.

Strong environmental impacts on marine life stages of salmon have made it difficult to use observational data to separate the effects of sea lice from other effects on survival, and so much relevant work applies field trials using cultivated salmon smolts treated with anti-parasitic agents (Gargan et al. 2012, Krkošek et al. 2012). Some trials indicate that baseline survival of smolts has an important influence on the success of lice treatment, with poorer environmental conditions increasing vulnerability to sea lice impacts. Hence, population-level effects of sea lice on wild salmon cannot be estimated independently of the other factors that affect marine survival (Vollset et al. 2016). The contribution of sea lice to overall marine survival of wild Atlantic salmon remains an important knowledge gap, particularly in the context of changing oceanographic conditions and the long-term decline of many populations. Parsing out coastal sea lice effects might contribute to understanding of changing high-seas marine survival, and possibly guide management of lice on salmon farms to reduce impacts on wild populations (Peacock et al. 2013).

The Erriff River system in the west of Ireland is designated as a Special Area of Conservation for Atlantic salmon under the European Union Habitats Directive (92/43/EEC). This system has supported salmon angling since the late 19th century, with annual returns of fish to the river being recorded for several decades. Salmon aquaculture commenced in the Erriff estuary (Killary Harbour) in the mid-1980s, and licensed annual production increased from 450 t in 1986 to 2200 t by 2006. Levels of sea lice infestation on the Killary salmon farm have been recorded since 1991. The position of this salmon farm at the entrance to a narrow fjord (Fig. 1) makes the Erriff system an excellent ‘natural experiment’ on the pos-

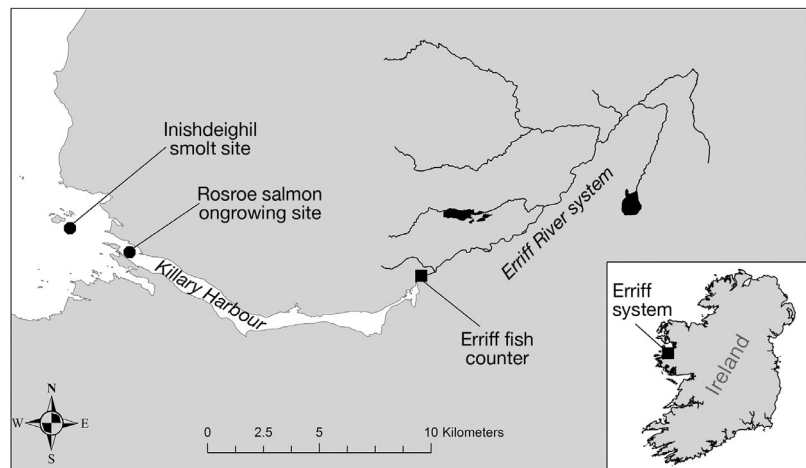


Fig. 1. Erriff River system and Killary Harbour, Ireland, showing the location of the salmon aquaculture sites and the fish counter

sible effects of sea lice from aquaculture on marine survival of a wild Atlantic salmon population. We used a 26 yr record from the Erriff to investigate relationships between sea lice (salmon lice *Lepeophtheirus salmonis*; hereafter simply sea lice) infestation on the Killary salmon farm and annual returns of wild 1 sea-winter (1SW) Erriff salmon, while accounting for unexplained inter-annual variability in marine survival of this population.

MATERIALS AND METHODS

Study system

The Erriff River has a catchment area of 166 km² and discharges into Killary Harbour, a 15 km long fjord in the west of Ireland (Fig. 1). Data series used in the current study comprised:

(1) Annual wild Atlantic salmon *Salmo salar* returns: (a) count of 1SW Erriff fish returning to the river, and (b) estimated return (accounting for annual commercial fishing mortality at sea, F ; see below) of Erriff salmon to the Irish coast (1987–2016).

(2) Annual aquaculture lice count estimate: average number of mobile (pre-adult and adult) sea lice (*Lepeophtheirus salmonis*) fish⁻¹ on the Killary salmon farm (Fig. 2) in April (www.marine.ie/Home/site-area/areas-activity/aquaculture/sea-lice), multiplied by an estimate of the total number of fish on the farm (taken as 0 in 1986 prior to farming and recorded for 1991–2016). For years when the smolt on-growing site (Fig. 1) was active, estimated total lice from this site were added to the total for the salmon farm. The current analysis related the number of returning 1SW

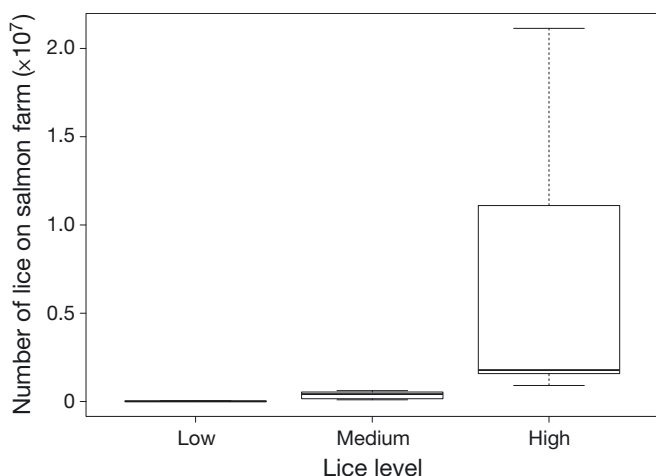


Fig. 2. Numbers of sea lice in each level of the categorical lice variable $Lcat2_i$. Summary statistics are the median of the data, the lower and upper quartiles (25% and 75%) and the minimum and maximum values. There are 8 data points (years) for the Low lice level, and 9 data points in each of Medium and High lice levels

salmon to the number of sea lice on aquaculture sites in the previous year, i.e. when those 1SW fish outmigrated as smolts. Aquaculture lice counts for April were used as an index of lice infestation pressure on wild migrating salmon smolts because records from 2002–2016 ($N = 15\,684$ smolts, Inland Fisheries Ireland unpublished data) indicated that 88% of the wild salmon smolt run in the Erriff catchment occurs between 1 April and 10 May.

Estimation of annual wild salmon returns

Two salmon return series were used. Salmon entering the Erriff are recorded by a fish counter approximately 200 m upstream of the river mouth. The annual count of 1SW salmon S returning to the Erriff River in year i (S_{iRiver}) was calculated as the sum of 1SW salmon rod caught (killed) below the fish counter and the number recorded by the counter. S_{iRiver} represents exact known counts of fish entering the river, but does not account for variable levels of F prior to return. Estimated return to the Irish coast (S_{iCoast}) was estimated by using F time series to expand S_{iRiver} . Commercial drift and draft net fisheries for wild salmon both operated off the Irish coast during the early study period, viz. 1987–2006, but fishing was restricted to inshore draft netting from 2007–2016. F was calculated slightly differently for these 2 time periods:

(1) Combined (drift and draft net) mean annual exploitation rate F for 1SW salmon has been calcu-

lated for 2 west of Ireland salmon stocks: Corrib and Burrishoole (Ó Maoiléidigh et al. 2015). These averaged F estimates (Fig. 3) were used to raise S_{iRiver} to an estimate of S_{iCoast} for 1987–2006, where $S_{iCoast} = S_{iRiver} / (1 - F)$. These estimated S_{iCoast} values suggest that Erriff fish contributed about 1.3% to the total annual catch of salmon in the Irish drift net fishery. This value is somewhat uncertain, as F was derived from a subsample of the overall commercial catch (Ó Maoiléidigh et al. 2015). However, it is similar to independent estimates of the contribution of Erriff salmon to the drift net catch based on assigning captured fish to their natal river using a genetic signature. Genetic assignment suggested that the total drift net catch comprised 1.7% Erriff fish in 2005 and 2.5% Erriff fish in 2006 (Anon 2008).

(2) Total annual catch in the Killary draft net fishery S_{id} is recorded and can be allocated to 3 local rivers including the Erriff. These 3 rivers have salmon conservation limits (CLs) of 1383 (Erriff), 136 (Culfin) and 165 (Delphi), where CL is defined as the spawning stock level that produces long term average maximum sustainable yield as derived from the adult to adult stock and recruitment relationship, and is quantitatively derived for each river by the Irish Standing Scientific Committee for Salmon. The Erriff CL represents 82% of the summed CL for the 3 rivers in Killary; F for 2007–2016 was thus calculated as $0.82 \times S_{id} / (0.82 \times S_{id}) + S_{iRiver}$ and $S_{iCoast} = S_{iRiver} / (1 - F)$ as above.

Statistical analysis: estimating the lice effect on salmon returns

By observation i , the data consisted of (S_i, Y_i, L_i) , where S_i is the number of Erriff salmon returning (to either the river or the coast) in sampling year $Y_{i1, \dots, 30}$ (1987–2016) and L_i is the estimated total number of sea lice on the Killary salmon farm (on-growing and smolt sites) in the previous year Y_{i-1} (no data for 1987–1990). Sea lice number was also interpreted as a categorical variable with 3 intensity levels (Low, Medium, High) in order to facilitate interpretation of lice impacts across (continuous) Y_i . Two approaches to categorizing L_i were tested: (1) $Lcat_i$ according to 0–25th, 25th–75th and 75th–100th percentiles of L_i , and (2) $Lcat2_i$ using natural divisions in L_i , which had groups of data points at 3 distinct levels (Fig. 2).

We developed statistical models to quantify possible effects of sea lice on each of S_{iRiver} and S_{iCoast} (1987 and 1992–2016), while accounting for an observed declining trend in salmon returns, and also for other

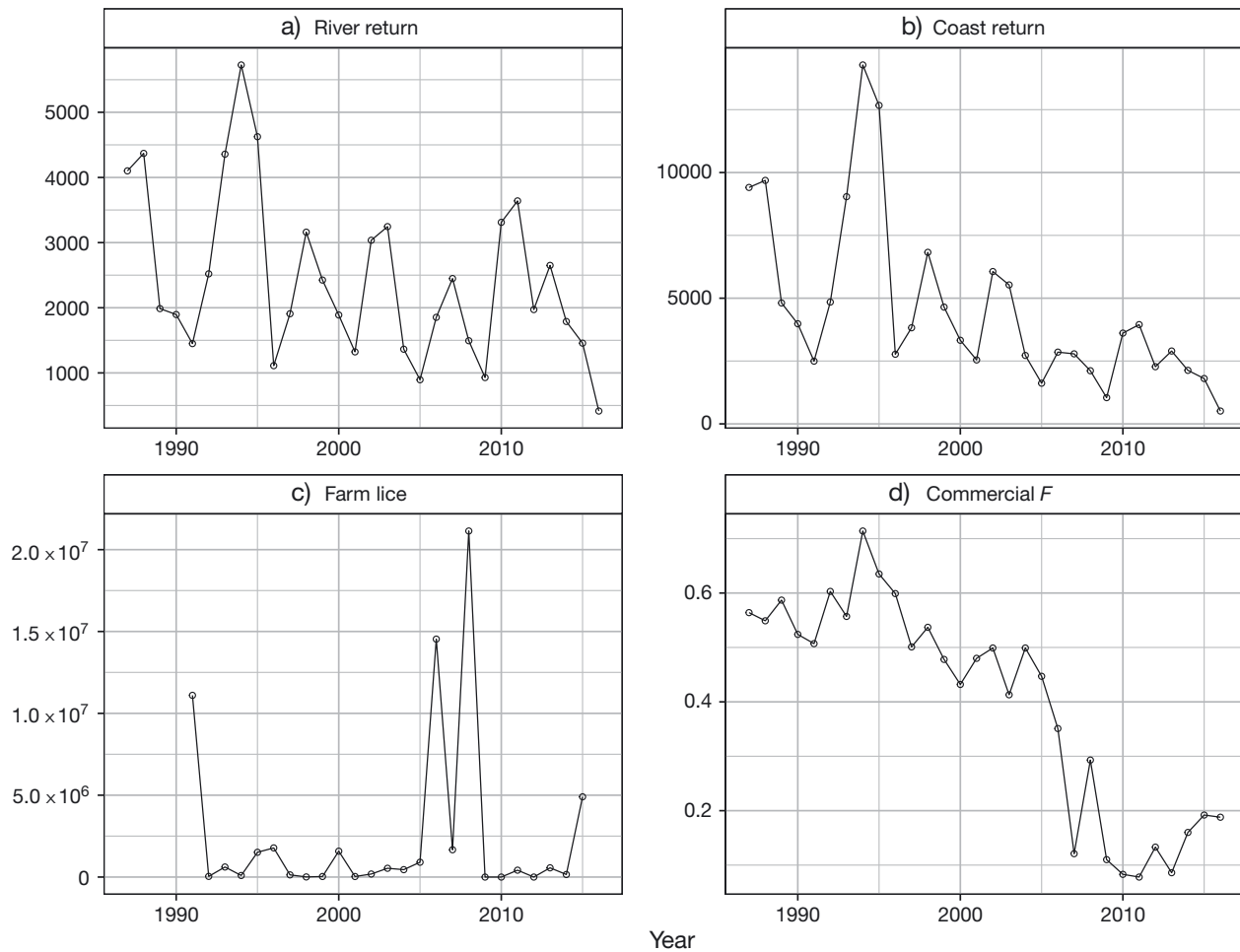


Fig. 3. Time series of returns of 1 sea-winter (1SW) Erriff River Atlantic salmon (a) to the river (S_{iRiver}) and (b) to the Irish coast (S_{iCoast}); (c) estimated number of sea lice in the Killary salmon farm; and (d) estimated commercial fishing mortality (F) for Erriff salmon

unexplained annually varying environmental drivers of marine mortality. The negative trend in Erriff salmon returns was incorporated by using standardised (subtracting the mean and dividing by the standard deviation) Y_i as a continuous fixed variable. Unexplained annual effects on salmon returns were incorporated by specifying year as a categorical variable $Ycat_i$, and including this variable as a random effect α_i on the intercept. $Ycat_i$ thus captures inter-annual effects on returns that cannot be accounted for by the lice and Y_i covariates (see Elston et al. 2001) and which are expected to largely comprise environmental variability. As an observation level random effect (OLRE), $Ycat_i$ also acts as a simple and robust means to account for overdispersion in count data (Harrison 2014). The 5 variables specified above (S_i , Y_i , L_i , $Lcat1_i$, $Lcat2_i$) were used to specify a comprehensive set of 7 candidate models, all including $Ycat_i$ as a random effect α_i (Table 1).

The same modelling process was applied to each of S_{iRiver} and S_{iCoast} separately. In each case, the model set (Table 1) was fit using a Poisson GLMM (lme4 package in R, Bates et al. 2015). The full model had the form:

Table 1. Set of 7 candidate models of the number of 1 sea-winter (1SW) Erriff River Atlantic salmon returning to the river and to the Irish coast (1987 and 1992–2016). Model parameters are defined in ‘Materials and methods’

No.	Model
1	$\log(\mu_i) = Y_i + \alpha_i$
2	$\log(\mu_i) = \ln(L_i) + \alpha_i$
3	$\log(\mu_i) = \ln(L_i) + Y_i + \alpha_i$
4	$\log(\mu_i) = Lcat1_i + \alpha_i$
5	$\log(\mu_i) = Lcat1_i + Y_i + \alpha_i$
6	$\log(\mu_i) = Lcat2_i + \alpha_i$
7	$\log(\mu_i) = Lcat2_i + Y_i + \alpha_i$

$$S_i \sim \text{Poisson}(\mu_i) \quad (1)$$

$$E(S_i) = \text{var}(S_i) = \mu_i \quad (2)$$

$$\log(\mu_i) = L_i + Y_i + \alpha_i \quad (3)$$

$$\alpha_i \sim \mathcal{N}(0, \sigma^2_{Ycat}) \quad (4)$$

Akaike's Information Criterion (AIC) was used to compare model fits, where any models within 2 AIC units of the best-fitting model would be considered to have similar fit to the data. Various diagnostics were used to explore model fit and statistical assumptions: (1) plots of standardised (Pearson) residuals were checked for homogeneity, (2) linearity in the relationships between salmon return and tested (continuous) covariates was evaluated by plotting Pearson residuals against each covariate in the model and fitting a GAM to visualize any non-linear patterns, and (3) temporal autocorrelation in model residuals was evaluated using the acf function in R.

Selected (lowest AIC) final models for both S_{iRiver} and S_{iCoast} included sea lice characterised as $Lcat2_i$. The effect on return of 1SW Erriff salmon of sea lice level ($Lcat2_i$: Low, Medium, High) in each of these selected models was visualized using the R package 'Effects', where other variables were held at average values (Fox 2003). The random effect of year $Ycat_i$ was plotted with 95% confidence intervals. Salmon returns at each lice level were also predicted (predict function in R) and plotted for each level of $Ycat_i$ (26 levels, i.e. years), considering 3 periods of the time series Y_i (Early, Mid, Recent) to show how the predicted (within year) lice effect on salmon returns compared to the (across year) random year effect (assumed to express annually-varying environmental effects on returns).

Predicting long-term salmon returns without sea lice

The models above predicted that the average return of 1SW Erriff salmon to the river is reduced by 18.6% following a year of Medium lice levels and 52.2% following a year of High lice levels; returns to the coast were predicted to be reduced by 2.3 and 49.6%, respectively. We used these lice impact levels and a fitted stock-recruitment relationship to estimate how annual salmon returns might have looked over the last 25 yr in the absence of a serious impact of sea lice from aquaculture:

(1) Observed annual salmon returns (each of S_{iRiver} and S_{iCoast}) were first 'lice-corrected' (multiplied up) according to the annual loss rates predicted from modelling; loss rates were expressed as the percentage difference between predicted salmon returns at

each of Medium and High lice levels and the predicted return at Low lice levels in an average year. For example, the observed return to the river in 1992 was 2520 salmon, but because the lice level was 'High' during the smolt run in 1991, it is predicted that this run represents a 52.2% reduction compared to the run that would have happened in Low lice conditions (given average environmental conditions as expressed by $Ycat_i$). The lice-corrected return Se_i was thus calculated as $Se_{1992} = 2520 / (100 - 52.2) \times 100 = 5272$ salmon.

(2) To realistically estimate the cumulative impact of sea lice on long-term returns of Erriff salmon, it was then necessary to account for likely diminished recruitment associated with loss of potential spawners (hereafter 'missing spawners') that never returned to the river/coast because they suffered lice-related mortality as smolts. 85% of Erriff salmon migrate as 2 yr smolts, resulting in a 4 yr generation time (White et al. 2016). Adult-to-adult Ricker stock recruitment (SR) relationships were produced for each of river and coast returns (see Fig. 6), where S is the observed return S_i and R is the lice-corrected return 4 yr later, Se_{i+4} . These SR curves were used to estimate peak (asymptotic) recruitment Rp , and the peak stock Sp at Rp , for each of S_{iRiver} and S_{iCoast} . The number of 'missing spawners' Sm_i in each year was then estimated as $Sm_i = Se_i - S_i$, with Se_i being capped at Sp on the assumption that once Sp is exceeded, there is no further positive effect on subsequent recruitment.

(3) A lice-corrected adult-to-adult return rate, RR , was then estimated for each year Y_i in each of S_{iRiver} and S_{iCoast} , assuming that each S_i comprised 85% 4 yr and 15% 5 yr fish (White et al. 2016), such that RR_i is the weighted mean of (Se_i / S_{i-4}) and (Se_i / S_{i-5}) with weightings being 85 and 15, respectively. These RR_i are an estimate of the number of returning fish expected (given Low lice levels) from each parent fish. 85% of missing fish Sm_i were then allowed to contribute recruits Sr_i to the return 4 yr later according to the estimated return rate RR_i , where this contribution $Sr_{i+4} = (0.85 \times Sm_i) \times RR_{i+4}$. The remaining 15% of missing fish contributed to recruitment 5 yr later as $Sr_{i+5} = (0.15 \times Sm_i) \times RR_{i+5}$. To restrict un-quantified uncertainty in this process, missing fish were only considered to contribute recruits to a single generation.

(4) Finally, a total expanded return $Stot_i$, including the annual lice-correction and the associated (1 generation) effect on recruitment, was calculated as $Stot_i = Se_i + Sr_i$. Time series of S_i and $Stot_i$ were plotted together for visual comparison, with the first 4 yr of $Stot_i$ obviously not including any Sr_i as there were no lice data for their respective parent generations.

RESULTS

Estimating the lice effect

Model 7 (see Table 1) was the best fitting model for both S_{iRiver} ($\Delta AIC = 3.8$) and S_{iCoast} ($\Delta AIC = 4.0$). The model including only year as a continuous variable (Model 1, Table 1), had $\Delta AIC > 8.0$ compared to Model 7 fitted to S_{iRiver} , and $\Delta AIC > 11.0$ compared to Model 7 fitted to S_{iCoast} indicating that $Lcat2_i$ strongly improved model fit. Diagnostic plots did not show important heterogeneity or non-linearity in residuals, and there was no significant temporal autocorrelation. There were significant negative effects of the continuous year variable Y_i on each of S_{iRiver} and S_{iCoast} i.e. long-term declines in 1SW salmon returns (Table 2). There were also significant negative effects of High sea lice levels $Lcat2_i$ during the smolt out-migration on each of S_{iRiver} and S_{iCoast} in the following year (Table 2). Predicted returns were reduced at Medium and strongly reduced at High lice levels. For an average random year $Ycat_i$ and continuous year Y_i ; the predicted S_{iRiver} (1394 fish) at High lice levels was 52.2% less than the predicted return (2919 fish) at Low lice levels (Fig. 4a); predicted S_{iCoast} (2226 fish) at High lice levels was 49.6% less than the predicted return (4419 fish) at Low lice levels (Fig. 4b).

The OLRE $Ycat_i$ captures any important patterns in the response variable that cannot be modelled by other terms in the model (Zuur et al. 2015). Strong variation in salmon returns across levels of $Ycat_i$ indicated considerable inter-annual variation in salmon returns to the river and coast (Fig. 5), probably reflecting environmental effects. However, the predicted 52.2% reduction in S_{iRiver} following 'High' lice levels is greater than the average year-to-year ($Ycat_i$ to $Ycat_{i+1}$) change in predicted returns (mean =

Table 2. Results from selected models (Model 7, see Table 1) of annual returns of 1 sea-winter (1SW) Erriff River Atlantic salmon returning to the river (S_{iRiver}) and to the Irish coast (S_{iCoast})

River returns	Estimate	SE	z-value	p
(Intercept)	7.979	0.143	55.917	<0.001
Year	-0.277	0.081	-3.412	<0.001
Lice level Medium	-0.206	0.197	-1.045	0.296
Lice level High	-0.739	0.196	-3.772	<0.001
Coast returns				
(Intercept)	8.394	0.129	65.064	<0.001
Year	-0.551	0.073	-7.512	<0.001
Lice level Medium	-0.023	0.178	-0.128	0.898
Lice level High	-0.686	0.177	-3.871	<0.001

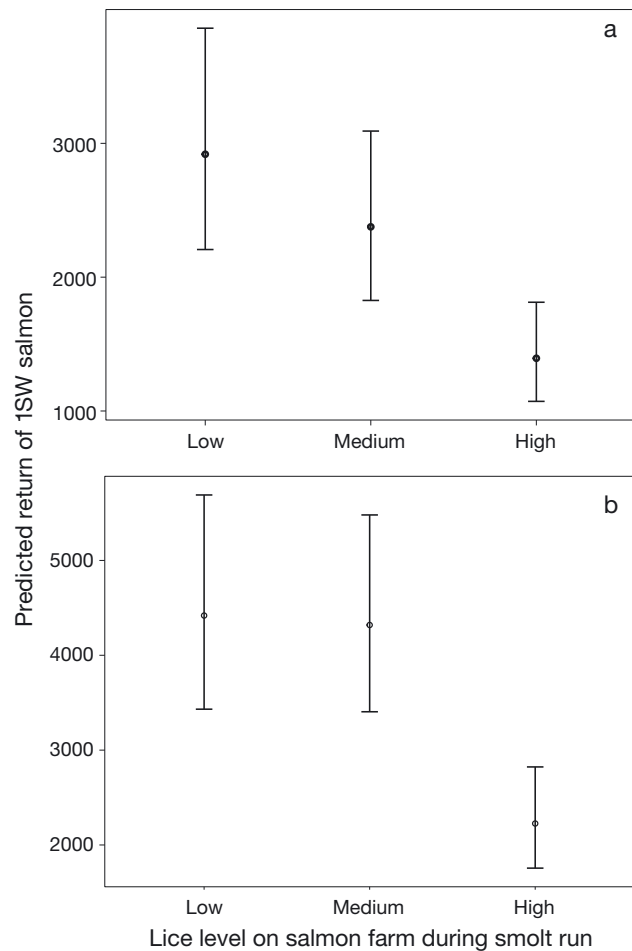


Fig. 4. Predicted return of 1 sea-winter (1SW) Erriff River Atlantic salmon to (a) the river (S_{iRiver}) and (b) the Irish coast (S_{iCoast}) at 3 levels of sea lice density at the Killary salmon farm during the smolt run. Error bars are 95% confidence intervals

44.6%, range = 0.6% to 262.7%) for the Early value of Y_i , suggesting that the lice impact is meaningful in the context of background environmental forcing. This comparison showed similar results for S_{iCoast} .

Predicting the contribution of sea lice impacts to long-term returns of Erriff salmon

Adult-to-adult Ricker SR curves, assuming a 4 yr generation time, showed a (visually) reasonable fit for both river and coast returns, suggesting that estimates of Rp and Sp were acceptable (Fig. 6). Comparing observed salmon returns S_i with lice-corrected returns $Stot_i$ for S_{iRiver} and S_{iCoast} (Fig. 7) showed that while the sea lice effect can strongly reduce annual returns S_i , 'correcting' for this effect

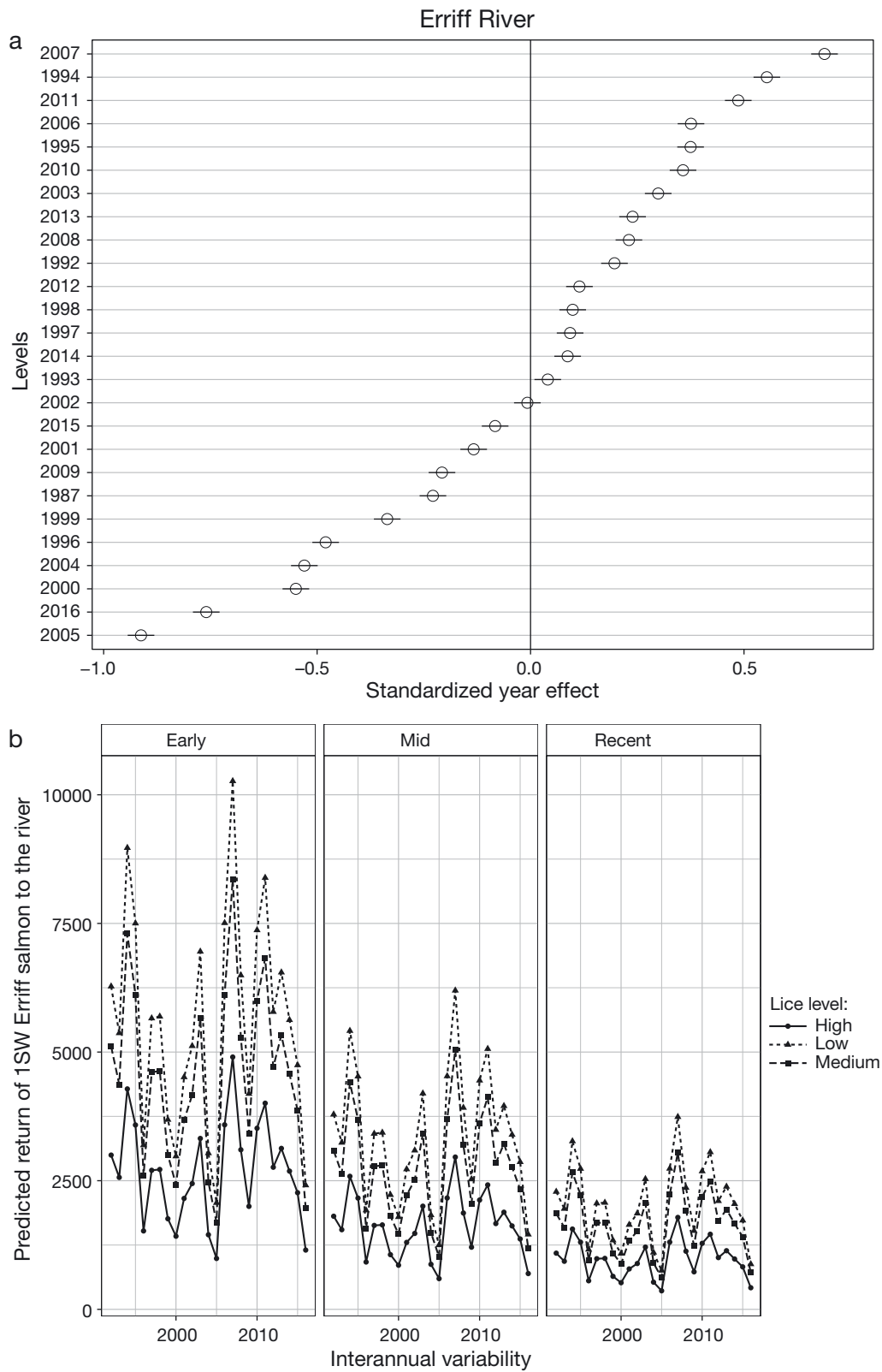


Fig. 5. (a,c) Random effects (with 95 % CI) on the intercept of year ($Ycat_i$) from the selected model (Model 7, Table 1) of returns of 1 sea-winter (1SW) Erriff River Atlantic salmon to (a) the river (S_{iRiver}) and (c) the Irish coast (S_{iCoast}). (b,d) Random year effect (assumed to express unexplained inter-annual variability) on predicted returns of these salmon to (b) the river and (d) the Irish coast in 3 different periods of the return time series (Early, Mid, Recent) and at 3 levels of estimated salmon lice infestation ($Lcat2_i$) on the Killary salmon farm

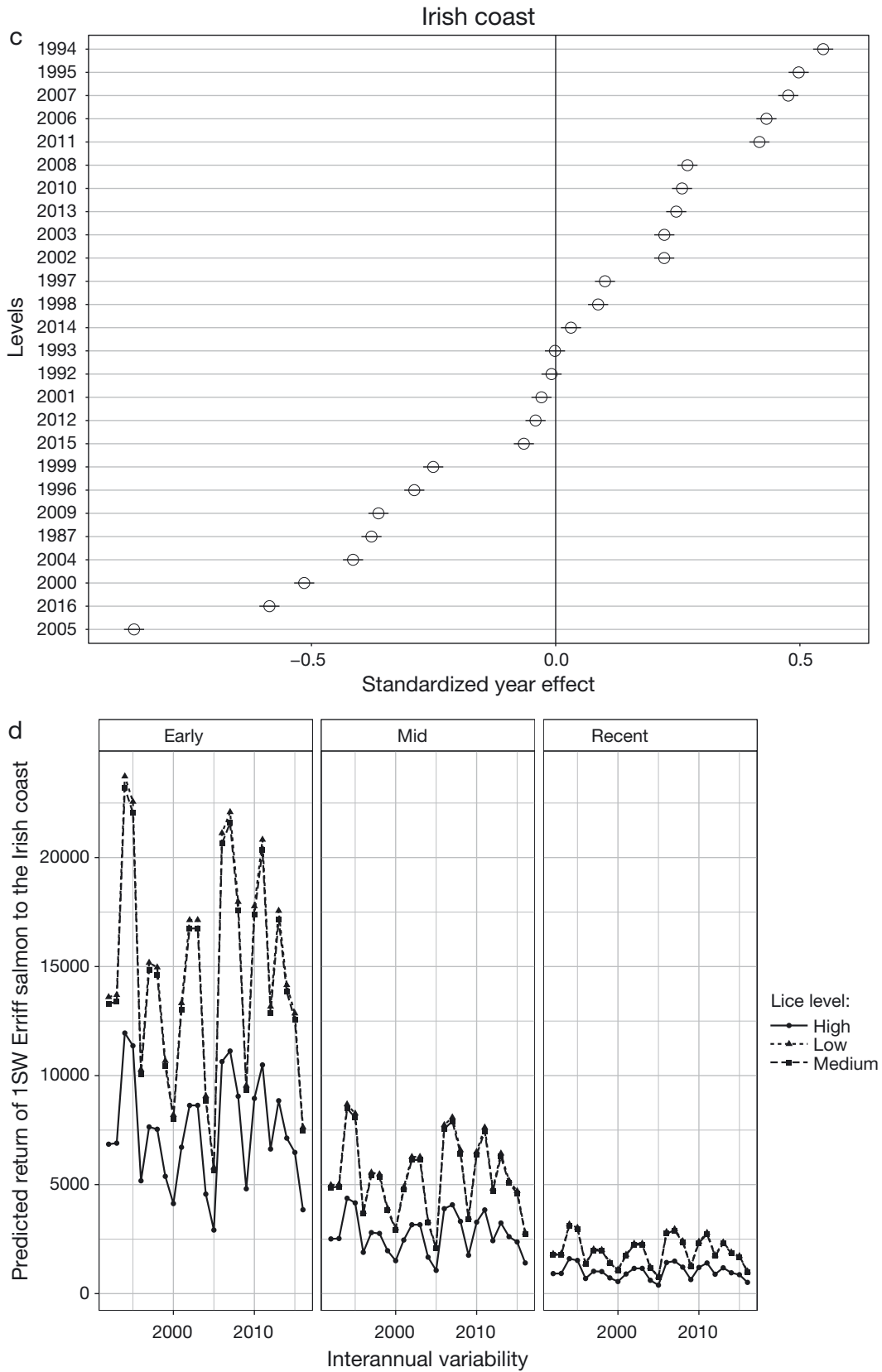


Fig. 5 (continued)

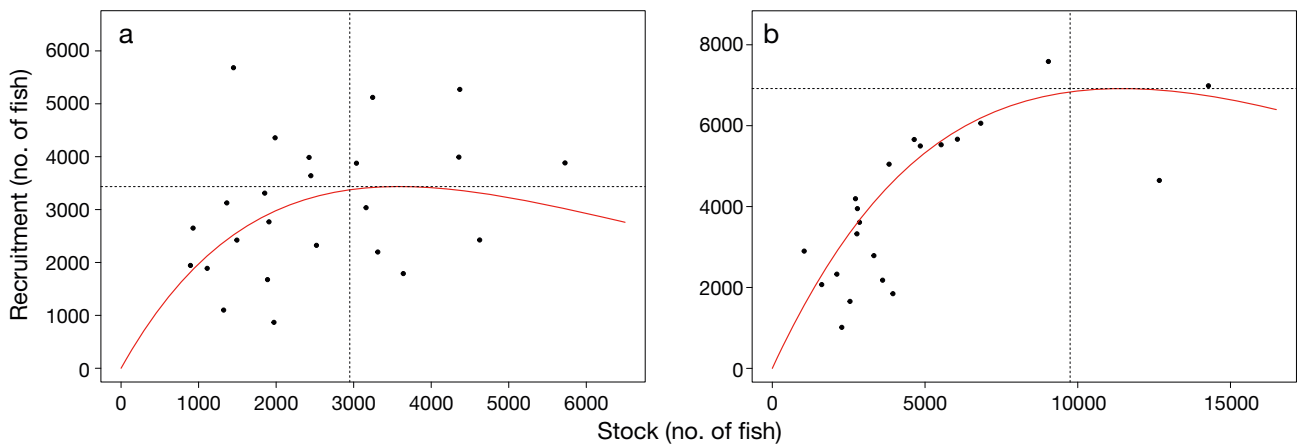


Fig. 6. Ricker stock recruitment curves fit to adult-to-adult stock-recruitment data for 1 sea-winter (1SW) Erriff River Atlantic salmon returns to (a) the river (S_{iRiver}) and (b) the Irish coast (S_{iCoast}). Stock values are observed returns; recruitment values are 'corrected' according to the annual lice effect estimated from statistical models. A 4 yr generation time (adult return to adult return) is assumed. The horizontal dashed lines are peak recruitment (R_p) and the vertical lines are peak stock (S_p)

does not remove the declining trend. The marked decline in the last 3 yr of both time series reflects relatively low estimated salmon return rates RR_i for these years (Table 3).

DISCUSSION

We analysed a 30 yr time series of returns of 1SW Erriff salmon, with 26 yr of corresponding estimated lice counts from the Killary salmon farm. Wild salmon returns were strongly reduced (>50%) following years when there had been high lice levels on the salmon farm during the smolt out-migration. This result accounts for the effect of unexplained among-year variation in returns, which probably reflects how marine survival varies naturally independent of

lice-induced mortality (Vollset et al. 2016). 'Correcting' for the estimated lice effect predicted that Erriff salmon returns might now be twice as large without observed anthropogenic sea lice impacts, but would probably show a similar long-term decline.

Infectious disease is a contributing factor in 8% of cases where a species is listed by the IUCN as Critically Endangered (Smith et al. 2006). Peacock et al. (2013) estimated that the percentage mortality of pink salmon in the Broughton Archipelago of British Columbia, Canada, due to sea lice infestations ranged from 3.8% for returns in 2010 to 90.1% for returns in 2002; Bateman et al. (2016) estimated that lice-induced mortality in the same region was 9 to 39% in 2015. Our results demonstrate that sea lice infestation from coastal salmon aquaculture is likely to be an important contributor to observed decline in

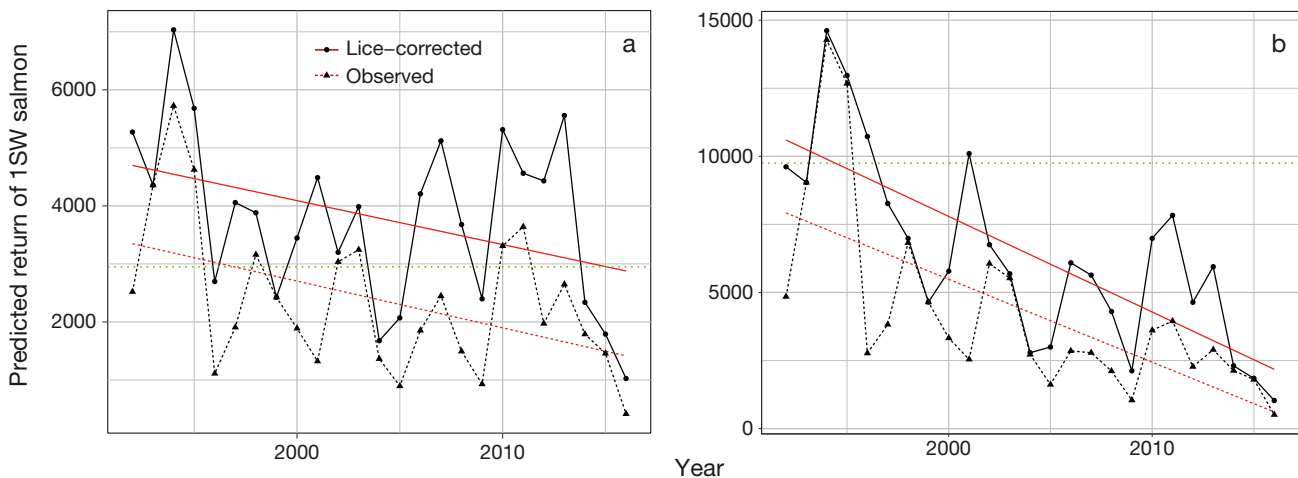


Fig. 7. Observed (S_i) and 'lice-corrected' (Se_i) returns of 1 sea-winter (1SW) Erriff River Atlantic salmon to (a) the river and (b) the Irish coast. The green line is peak recruitment (R_p) estimated from the Ricker curve (see Fig. 6)

Table 3. Estimated annual adult-to-adult return rates (RR_i) for 1 sea-winter (1SW) Erriff River Atlantic salmon to the river or the Irish coast

Year	River RR_i	Coast RR_i
1992	1.21	0.99
1993	2.01	1.74
1994	3.68	3.58
1995	3.78	4.91
1996	1.02	1.29
1997	1.02	0.95
1998	0.71	0.53
1999	0.51	0.36
2000	1.51	1.06
2001	1.61	1.40
2002	1.05	0.99
2003	1.58	1.16
2004	0.86	0.80
2005	0.79	0.63
2006	1.53	1.13
2007	1.60	0.99
2008	2.09	1.42
2009	2.06	1.20
2010	2.08	1.41
2011	1.56	1.41
2012	1.53	1.06
2013	2.69	2.57
2014	0.92	0.82
2015	0.50	0.48
2016	0.41	0.42

returns of wild Atlantic salmon to the Erriff River system. This finding upholds a substantial literature on the impacts of sea lice on salmonids, and successive experiments using anti-parasite lice treatments. A meta-analysis of differential survival between control and parasiticide-treatment groups of cultured Atlantic salmon showed that returns of treated fish were 39% greater (Krkošek et al. 2012). Our results for the Erriff predict that the return of 1SW salmon migrating in a high lice year may be reduced by more than 50% compared to the return from wild smolts that were not exposed to high levels of sea lice from salmon aquaculture during early out-migration.

Sea lice present during the spring smolt out-migration through Killary Harbour could have salmon farm and/or wild salmon sources. Gargan et al. (2012) found that the number of wild salmonids was very low during this period, and that sea lice abundance on local farmed salmon was 3 to 4 orders of magnitude greater than the estimate for wild salmonids. A study on the production of sea lice larvae from farmed and wild salmon and its relation to the infestation of wild sea trout found that farmed salmon contributed 95% of the total production of *L. salmonis* nauplii in the mid-west Irish coast region (Tully & Whelan 1993). These observations suggest that sea

lice infestation pressure on wild Erriff smolts originates overwhelmingly from aquaculture.

Lice-induced mortality may have 2 components. Short-term mortality probably occurs when attached lice reach the pre-adult and adult life stages, causing severe osmoregulatory problems indicated by highly elevated plasma chloride levels and increased plasma osmolality (Bjørn & Finstad 1997, Dawson et al. 1998, Wells et al. 2006). A longer-term reduction in survival may be associated with impacts that impair on-going fitness during migration. The impact of sea lice seems to vary with baseline survival of salmon; a meta-analysis of studies using anti-parasite treatments on salmon smolts found that in groups with low recapture in the control group (low baseline survival), the effect of treatment was high, while in groups with high recapture in the control group (high baseline survival), there was no effect of treatment (Vollset et al. 2016). This result implies that the detrimental effect of lice is exacerbated in situations when the salmon smolts also have to cope with increased pressure from other causes of mortality, e.g. unfavourable environmental conditions. A post hoc plot of standardised salmon returns to the Erriff S_{iRiver} shows that observed returns approximately track the random year effect $Ycat_i$ (expressing environmental variability). However, the 4 lowest returns on record occurred when a high lice year coincided with poor baseline survival, while the only 2 occasions when a high lice year produced a greater than average run (1992 and 2007) were during high baseline survival (Fig. 8).

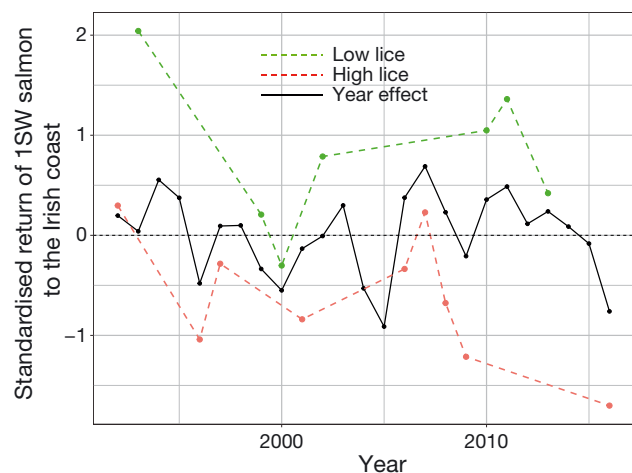


Fig. 8. Observed Erriff River Atlantic salmon returns to the river (S_{iRiver}), standardised to 0 for years estimated to have 'High' and 'Low' levels of sea lice (years of Medium lice level are excluded for clarity). Year effect is the random effect of year ($Ycat_i$), assumed to express environmental effects on salmon returns

Our results show very low return rates of Erriff salmon in the most recent years, corresponding to apparent declines in marine survival of Atlantic salmon (ICES 2016). Oceanic life stages of salmon are susceptible to climate forcing by the NAO and the AMO that drive SST and thus thermal habitat (Friedland et al. 1993, 2003, Jonsson & Jonsson 2004, Mills et al. 2013) and associated prey dynamics (Beaugrand & Reid 2012, Defriez et al. 2016). Recent studies suggest that warming SST has had a negative impact on oceanic growth and survival (McCarthy et al. 2008, Todd et al. 2008, Friedland et al. 2009) of Atlantic salmon, possibly mediated through productivity and trophic interactions (Beaugrand & Reid 2003, Mills et al. 2013). Hence, aquaculture sea lice impacts on wild Atlantic salmon are imposed upon possibly declining baseline survival.

The negative effect of sea lice from aquaculture may be unusually strong for the Erriff wild salmon population because the Killary salmon farm is located in the mouth of a long and narrow fjord. It is also the case that the 26 yr time series of salmon runs and lice counts, while valuable, still refer to only a single system. A preliminary analysis using these records attempted to identify specific environmental components of marine mortality in addition to sea lice. There were insufficient data for this exercise and so the simpler and more robust random year approach presented here was followed. Despite this limitation, it seems reasonable to expect important lice impacts in other systems where salmon farm(s) with high spring lice levels occur in bays and estuaries with rivers having wild salmon populations. A study of chemically treated and untreated salmon smolt releases in 3 west of Ireland bays (including Killary) found that lice-induced mortality of adult salmon can be significant, and that an increase in mortality of salmon smolts can be expected where farm lice levels are not maintained at sufficiently low levels in spring (Gargan et al. 2012). This observation is consistent with research on pink salmon (e.g. Bateman et al. 2016). A potential 50% lice-induced reduction in annual return of wild Atlantic salmon is likely to have serious general implications for long-term viability of populations in aquaculture areas. Natal homing in salmon results in a high level of genetic structuring, and smaller salmon rivers typically have a relatively low effective population size (Nikolic et al. 2009). As such populations decline, they are likely to become vulnerable to inbreeding and related demographic problems (e.g. Lande et al. 2003) that can erode future evolutionary potential of salmon populations (McGinnity et al. 2003) and lead to an

extinction vortex (Fagan & Holmes 2006). Many Atlantic salmon populations are already under pressure from (possibly climate-mediated) reductions in marine survival. The addition of significant lice-related mortality during the coastal stage of smolt out-migration could be critical.

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