Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate

P.G. Gargan, G. Forde, N. Hazon, D.J.F. Russell, and C.D. Todd

Abstract: Sea trout (*Salmo trutta*) stock collapses in coastal areas of western Ireland subject to salmon aquaculture were contemporaneous with high abundances of larval sea lice (*Lepeophtheirus salmonis*) on juvenile sea trout. Whereas sea trout remain in near-shore waters throughout their marine migration, Atlantic salmon (*Salmo salar*) smolts typically move quickly offshore into oceanic waters. It might therefore be predicted that salmon smolts would be less vulnerable to coastal stressors and less likely to be negatively affected by infestations of sea lice early in their marine phase. Groups of microtagged, hatchery-reared Atlantic salmon smolts were fed either untreated pellets or pellets incorporating the in-feed sea louse treatment SLICE (emamectin benzoate) prior to eight experimental releases in three marine locations over a 3-year period. In total, 74 324 smolts were released and analysis of tag recaptures from returning adult salmon showed that emamectin-treated smolts experienced increased survivorship and were 1.8 times more likely to return compared with control fish. These results suggest that sea lice-induced mortality on adult Atlantic salmon returns in Ireland can be significant, and that sea lice larvae emanating from farmed salmon may influence individual survivorship and population conservation status of wild salmon in these river systems.

Résumé : Les effondrements des stocks de truites de mer (*Salmo trutta*) dans les régions côtières de l'ouest de l'Irlande affectées par l'aquaculture de saumons coïncident dans le temps avec les fortes abondances de larves de poux de mer (*Lepeophtheirus salmonis*) sur les jeunes truites de mer. Alors que les truites de mer demeurent dans les eaux près des côtes tout au cours de leur migration en mer, les saumoneaux des saumons atlantiques (*Salmo salar*) typiquement s'éloignent rapidement des côtes vers les eaux océaniques. On pourrait alors prédire que les saumoneaux du saumon sont moins vulnérables aux facteurs de stress sur les côtes et moins susceptibles d'être affectés négativement par les infestations de poux de mer tôt durant leur phase en mer. Nous avons nourris des groupes de saumoneaux du saumon atlantique élevés en pisciculture et porteurs de micro-étiquettes ou bien de granules non traitées ou alors de granules contenant le traitement SLICE (benzoate d'émamectine) par l'alimentation contre les poux de mer avant huit libérations expérimentales dans trois sites marins sur une période de 3 ans. Un total de 74 324 saumoneaux ont été relâchés; l'analyse des retours d'étiquettes chez les saumons adultes qui reviennent montre que les saumons traités à l'emamectine connaissent une survie plus élevée et sont 1,8 fois plus susceptibles de revenir que les poissons témoins. Nos résultats laissent croire que les effets de la mortalité causée par les poux de mer sur les retours des saumons atlantiques en Irlande peuvent être significatifs et que les larves de poux de mer provenant des élevages de saumons peuvent influencer la survie individuelle et le statut de conservation des populations de saumons sauvages dans ces systèmes hydrographiques.

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Introduction

The rapid development of marine salmon aquaculture since the late 1980s and early 1990s in Europe, and on the Atlantic and Pacific coasts of North America, has raised concerns regarding the ecological impacts of farmed salmon, including the effects of sea lice (*Lepeophtheirus salmonis*), on wild salmonid stocks. However, McVicar (2004) commented that risk analysis had rarely been used in researching the possible links between salmon lice abundances in fish farms and the performance of wild salmonid populations. In particular, McVicar (2004) argued that no cause–effect relationship between sea lice on farms and the current low level of salmonid stocks in Europe and eastern Canada had been established, and that the potential impact of sea lice from salmon farms was then, and indeed still remains, a controversial issue.

In eastern Canada, wild Atlantic salmon populations are depressed and salmon farming has been suggested to be a

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P.G. Gargan and G. Forde. Inland Fisheries Ireland, Swords Business Campus, Swords, Co. Dublin, Ireland.
N. Hazon, D.J.F. Russell, and C.D. Todd. Scottish Oceans Institute, University of St Andrews, Scotland KY16 8LB, UK.

Corresponding author: Patrick G. Gargan (e-mail: paddy.gargan@fisheriesireland.ie).

possible contributor to observed recent declines (Cairns 2001). On the Canadian west coast, declines in returns of wild pink (*Oncorhynchus gorbuscha*) and coho (*Oncorhynchus kisutch*) salmon to the Broughton Archipelago region of British Columbia have been linked to the presence of caligid sea lice from Atlantic salmon (*Salmo salar*) farms in this region (Krkošek et al. 2007; Connors et al. 2010). For example, Krkošek et al. (2005) concluded that sea lice infestation pressure imposed by a single salmon farm was four orders of magnitude greater than natural levels, resulting in a maximum infection pressure near the farm that was 73 times greater than ambient levels along 30 km of two wild Pacific salmon migration corridors. More recently, however, Marty et al. (2010) reported no negative impact of farm sea lice numbers, or tonnage of farm production, on productivity of wild pink salmon stocks in the same region. Despite the continuing controversy concerning the impacts of farm-derived sea lice on wild salmonid stocks, mortality of salmonids attributable to sea lice infestation has been widely documented (see review by Costello 2009), and the observed population declines have often been associated with infestations of sea lice (Frazer 2008). In reviewing the available literature, Revie et al. (2009) commented that the weight of evidence is that sea lice of farm origin can present, in some locations and for some host species populations, a significant threat to wild salmonid stocks. In western Ireland the development of the Atlantic salmon farming industry commenced during the mid 1980s, with many production sites located in estuaries close to river mouths. Numerous wild sea trout (*Salmo trutta*) fisheries experienced a striking and contemporaneous decline in sea trout catches during the late 1980s (Whelan and Poole 1996; Gargan et al. 2006), and this was linked to sea lice infestation (Tully et al. 1999; Gargan et al. 2003).

In contrast to sea trout, few data are available on the impact of sea lice on outward-migrating Atlantic salmon smolts. Studies in Ireland (Tully and Whelan 1993), Scotland (Butler 2002), and Norway (Heuch and Mo 2001) have indicated that in salmon aquaculture bays in springtime the majority of caligid copepod nauplii arise from ovigerous sea lice infesting farmed salmon. Finstad et al. (1994, 2000) showed that fjord-migrating Atlantic salmon postsmolts descending the long and intensively farmed fjords of western and central Norway can become infected soon after their first entry to seawater. Similarly, on the eastern North Pacific coasts of Canada, higher infestation rates of sea lice were found on juvenile pink and chum salmon adjacent to Atlantic salmon farms compared with areas not exposed to fish farming (Morton et al. 2004). The potential therefore clearly exists for Pacific and Atlantic salmon postsmolts migrating through estuaries to become infested with sea lice both from wild and farmed salmon.

The prophylactic in-feed sea lice treatment, emamectin benzoate (SLICE; hereafter emamectin), has been used extensively in recent years by the salmon farming industry, and it has been shown to prevent, or markedly reduce, levels of infestation following transfer of hatchery smolts to seawater (Stone et al. 2002). To determine if sea lice infestation of early postsmolt Atlantic salmon might be a significant source of mortality in large Norwegian fjords, Skilbrei and Wennevik (2006) compared the survivorship of emamectin-treated and control (untreated) juveniles released on three occasions in springtime of the one year and found protected fish in their third release showed significantly higher return rates; but experimental evidence for multiple years would be necessary to more confidently affirm a causal connection between sea lice infestations and host mortality. The salmon rivers in western Ireland typically discharge into relatively small embayments compared with the elongate and extensive western Norwegian fjords. Irish smolts might therefore move offshore more quickly and encounter perhaps lesser early infestation pressures than in Norway. Moreover, localized infestation pressures are likely to vary from year to year. We therefore chose to undertake multiple releases of treated and control smolts, and did so over 3 consecutive years in three areas, with the objective of assessing the potential for increased early marine mortality of salmon postsmolts attributable to sea lice.

Materials and methods

Study area

The study was undertaken in three river systems in western Ireland entering bays with salmon farming activity: the River Erriff enters Killary Harbour, the Owengowla River flows into Bertraghboy Bay, and the Invermore River discharges into Kilkieran Bay (Fig. 1). Two other large salmon rivers—Delphi (Killary Harbour) and Ballynahinch (Bertraghboy Bay)—also discharge to bays in the study area. The direct transit distance for out-migrating Atlantic salmon smolts from river mouth to the open sea is short in all three estuaries (16 km, Killary Harbour; 14 km, Bertraghboy Bay and Kilkieran Bay). Upstream traps to monitor returning adult salmonids were placed on all three rivers.

Salmon smolt releases

Salmon smolts cultured from the western Ireland Lough Corrib (Cong) hatchery strain were used in all eight experimental releases. Whilst cultured smolts are known to display typically lower marine survivorship than naturally migrating wild smolts (e.g., Kallio-Nyberg et al. 2004), experimental use of hatchery fish (as opposed to naturally migrating wild smolts) allowed standardization and synchronization of treatment and control groups, the administration of emamectin at the prescribed dosage and duration, and release of smolts on a given date. Both the emamectin-treated and control groups of smolts were microtagged using coded wire tags (Northwest Marine Technology) to permit allocation of recaptured return adults to their experimental treatment and release river. All smolts were adipose fin-clipped to indicate visually the presence of an internal microtag. Each treatment and control group initially comprised ~5000 smolts (Table 1). Totals of 37 135 treated and 37 189 control fish were ultimately released in the three river systems during the spring smolt migration (April) over the 3 consecutive years (2003–2005; Table 1).

Within each year, both the treatment and control groups of smolts were transferred on the same day to lake cages on the Invermore and Owengowla fisheries for imprinting. For the River Erriff, smolts were transferred to, and maintained in, two large fibreglass tanks on the riverbank with gravity water feed from the river. Smolts were held for periods of 5–8 weeks during imprinting and experimental treatment prior

Fig. 1. Location of Erriff, Owengowla, and Invermore rivers in western Ireland, with location of upstream traps. The location of marine salmon farms in Killary Harbour, Bertraghboy Bay, and Kilkieran Bay are also shown.

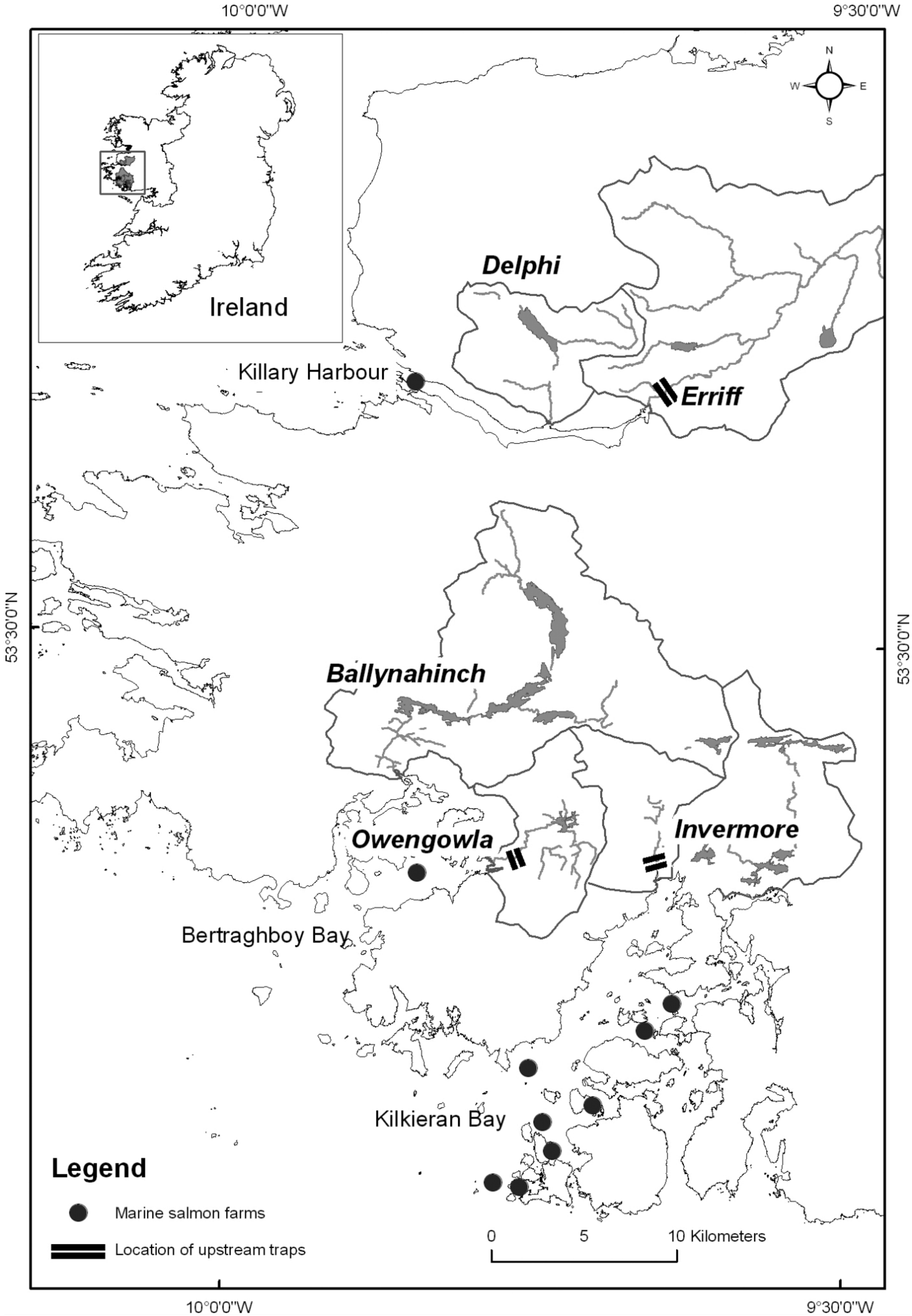


Table 1. Summary data for all treatment and control groups of Atlantic salmon smolts released in 2003–2005.

Location	Group	Transfer date	No. stocked	Release date	Mean fork length (cm) on release	Estimated no. migrating
Owengowla	Treated	27 Feb. 2003	5178	28 Apr. 2003	18.8	4955
Owengowla	Control	27 Feb. 2003	5163	28 Apr. 2003	18.5	4822
Owengowla	Treated	24 Feb. 2004	5043	7 Apr. 2004	17.7	4655
Owengowla	Control	24 Feb. 2004	5088	7 Apr. 2004	17.9	4699
Owengowla	Treated	24 Feb. 2005	5070	7 Apr. 2005	19.2	4583
Owengowla	Control	24 Feb. 2005	5116	7 Apr. 2005	18.5	4735
Invermore	Treated	26 Feb. 2003	5215	29 Apr. 2003	17.4	4589
Invermore	Control	26 Feb. 2003	5197	29 Apr. 2003	17.2	4594
Invermore	Treated	24 Feb. 2004	5050	8 Apr. 2004	17.5	4653
Invermore	Control	24 Feb. 2004	5058	8 Apr. 2004	17.5	4671
Invermore	Treated	23 Feb. 2005	5100	8 Apr. 2005	18.8	4716
Invermore	Control	23 Feb. 2005	5132	8 Apr. 2005	18.0	4750
Erriff	Treated	9 Mar. 2004	4641	12 Apr. 2004	18.4	4325
Erriff	Control	9 Mar. 2004	4500	12 Apr. 2004	18.8	4229
Erriff	Treated	28 Feb. 2005	5100	4 Apr. 2005	18.2	4659
Erriff	Control	28 Feb. 2005	5100	4 Apr. 2005	18.6	4689

to their release on the completion of smoltification. Fish were maintained on emamectin-free food pellets (Skretting Emerald Transfer 2.3 mm pellets) during imprinting and emamectin-impregnated pellets were used for the treatment group diet for the 7 days prior to release. Emamectin was administered at the recommended dose of 0.5% biomass·day^{-1} for 7 days (Slice Data Sheet, Schering-Plough Animal Health, UK). To ensure that treatment was adequate to afford protection against sea lice infection, and not excessive to the extent of perhaps impairing subsequent survival, 29 smolts from five of the eight treatment groups (Owengowla 2004, 2005; Invermore 2004, 2005; Erriff 2005) were taken on the day of release and assayed for concentrations of emamectin benzoate in skin and muscle tissue. Both control and treated fish at any one location were released on the same day. All groups were released ~150–200 m upstream of the estuary at each of the three locations during April to maximize adult return rates (Ó Maoiléidigh et al. 1994). A sample of at least 50 fish was taken from each group to quantify tag loss and to provide data on mean length at release.

Estimated numbers of released smolts migrating

Ideally, one would assess the smoltification status of experimental fish by controlled seawater challenge, but this was not feasible or practicable at the field locations. However, for the purposes of the present experiments, we made the assumption that the smoltification status of both treated and control groups for each release within a river were directly comparable. The numbers of smolts successfully migrating from each release were estimated by accounting for mortality and tag loss prior to their release (Table 1). These numbers were further adjusted downwards by a per capita mortality rate of 0.16%·day^{-1} to account for mortality of smolts after their release (A. Cullen, Furnace Research Station, Marine Institute, Newport, Co. Mayo, Ireland, unpublished data).

Estimating total tagged returning adults

Adult salmon were recaptured in the offshore drift net fishery (operating up to 6 nautical miles (n.mi.) from the coast), the inshore draft net fishery, rod angling fisheries, and upstream traps. The commercial and recreational fisheries operated generally between May and July inclusive and the numbers of tagged salmon were recorded by fishery inspectors. Because not all of the adult salmon catches are inspected for adipose fin-clipped salmon, an annual "raising factor" is routinely applied to adjust the catch sample to the total catch. Accordingly, to estimate percent marine survivorship, the total number of tagged salmon actually taken in these fisheries was estimated by multiplying the number of tagged salmon in the samples from each fishery area by the ratio of the total declared salmon catch in these areas to the sample size examined. It is necessary to apply a different raising factor for each of the six sampling areas (North, Northwest, West, Kerry, Cork, South coast) because the proportion of the catch examined varies by area. An estimate of the noncatch fishing mortality (NCFM)—due to losses from nets attributable to seals and operator handling of nets, and nonreporting of catches—also was applied, depending on the fishery area. The experimental upstream traps on the Owengowla, Invermore, and Erriff rivers allowed all remaining microtagged salmon escaping the coastal fisheries and successfully entering the rivers to be examined for microtags.

Presence of farmed salmon during the springtime smolt migration

Since the mid-1990s the Irish Marine Institute has monitored sea lice (*L. salmonis* and *Caligus elongatus*) levels on all Irish salmon farms (Jackson et al. 1997). Those data provide an indication of sea lice abundances on farms in these three bays prior to the experimental releases (O'Donohoe et al. 2004, 2005, 2006). Under average western Ireland seawater temperature conditions (~10 °C) sea lice nauplii and copepodids are expected to survive 3 and 8 days, respectively (Johnson and Albright 1991). Therefore, sea lice levels are presented here for the inspections undertaken for a period of 15 days prior to the experimental releases, to account for ovigerous farm sea lice which could potentially contribute to local larval production (Table 2). An estimate of the total number of farmed salmon present in each bay at the time of smolt release, based on best estimates from Fishery Inspector

Table 2. Salmon farm data.

Date	River	Estuary	No. of sites operating	Avg. ovigerous lice (range)	Avg. mobile lice (range)	Estimated no. of over-wintered farmed fish
2003	Owengowla	Bertraghboy	1	0	0.35	466 000
2004	Owengowla	Bertraghboy	1	1.92 (1.90–1.93)	13.3 (7.94–18.63)	289 000
2005	Owengowla	Bertraghboy	0	—	—	—
2003	Invermore	Kilkieran	8	0.1 (0–0.27)	4.16 (0.2–21.1)	1 585 000
2004	Invermore	Kilkieran	3	0.30 (0–0.91)	1.25 (0.84–1.76)	1 200 000
2005	Invermore	Kilkieran	5	0.96 (0–2.22)	8.29 (0.02–28.97)	1 270 000
2004	Erriff	Killary harbour	1	1.84	6.1	229 500
2005	Erriff	Killary harbour	1	0.71	1.94	255 600

Note: Sea lice data include the average (avg.) numbers of ovigerous, adult female and the avg. "mobile" (i.e., postchalimus) lice abundances. The estimated numbers of farmed salmon present are for the spring period prior to experimental smolt releases. The farm at Betraghboy Bay was fallow in spring 2005.

reports (G. Forde, unpublished data), is also presented. Farmed salmon were present in the bays for all release groups in every year, with the exception of Bertraghboy Bay in 2005; in the latter case, the farm remained "fallow" and out of production in springtime.

Estimate of wild salmonid hosts present in bays in springtime

The main run of wild adult salmon and sea trout occurs in these rivers during the summer months. Therefore, the only wild salmonids within these bays during the infective period of the smolt run would be low numbers of early-returning multi-sea-winter (MSW) salmon. Upstream salmon trap counts and angling rod catch data were used to estimate the number of wild salmon and sea trout returning to rivers prior to the time of salmon smolt releases. These data provide the best indication of the potential contribution of wild fish to sea lice production in bays during smolt migration. A rod exploitation rate of 25% (Solomon and Potter 1992) was assumed for MSW salmon in springtime to allow estimation of the total early-running spring salmon stock.

Statistical analyses

Calculation of condition factor

Condition factor of individual fish can be calculated in numerous ways. The metric of choice is the relative mass index (W_r) (Blackwell et al. 2000), but calculation of the standard equation requires data for multiple year classes. In the absence of length and mass data for multiple year classes of ranched adults of the Corrib strain, we chose here to use Fulton's K (whereby $K = [W/L^3] \times 100\,000$; W is mass in grams and L the length in millimetres) in the knowledge that this index provides for the present purposes a simple and reliable comparator of condition amongst experimental and control groups, albeit only within that one strain.

Chi-squared contingency table tests (including Yates' correction for continuity) were applied to the tag recaptures. Whilst Williams' correction generally is the preferred methodology for χ^2 contingency tests (Sokal and Rohlf 1995), we opted for Yates' correction because it provides a more stringent and conservative test of significance. We used here only the raw data, not the raised estimates. On the basis that the only difference between the treated and control groups was the presence of emamectin in the feed pellets, the null hypothesis in this analysis was that emamectin had no influence on smolt survivorship. The alternative hypothesis is that emamectin provided protection from sea lice infestation for the early postsmolt stage of the marine migration. To provide an overall conclusion to the eight independent experimental releases, a meta-analytical approach (Sokal and Rohlf 1995) was adopted for the χ^2 analyses by combining probabilities.

For released smolts the analysis focused on whether there were significant differences in length between treated and control fish. The data included all rivers and years, but were unbalanced because there was no release for the River Erriff in 2003 and sample sizes varied. The response term, smolt length, was transformed to the natural logarithm to correct for a violation in normality. A linear model was fitted including treatment, river, and year and up to a three-way interaction. Factors were removed by backwards selection if they were not significant at the 5% level. Because the interest here lay in the effect of treatment within the sampled rivers and years themselves, all factors were included as fixed effects. The assumptions of normality and constant variance were assessed using Shapiro–Wilk and Levene's tests.

To determine the effect of treatment within rivers within years, we used multiple pairwise t tests with log length as the response term. This approach is preferable to post hoc analyses, such as Tukey's honestly significant difference (HSD), which provide differences between all possible combinations, and with appropriate adjustment of the p values: because our interest was only in specific planned comparisons, such an adjustment of p values would not be appropriate. If variances between the groups were uneven then a Welch modified t test was undertaken. If data were non-normal, Mann–Whitney tests were conducted. There is debate as to whether the results from such planned comparisons should be adjusted for multiple testing. Advice against adjusting p values is strongest when the data are balanced. Given the present unbalanced data we show both the uncorrected p values and those adjusted for false discovery rate (fdr). The fdr adjustment is considered preferable to Bonferroni correction, and similar adjustments, because the latter are more likely to incur type II error than to appropriately minimize the type I error rate (Nakagawa 2004).

For return adults we used the same analytical framework as for smolts in assessing the effect of treatment, year, and river on length, mass, and condition factor. We excluded data from any river in a particular year if there were <5 values for either emamectin-treated or control fish. For analyses of length, this allowed all rivers to be considered in 2004, but only Invermore in 2003, and Owengowla and Invermore in 2005. Lengths of all fish were included, irrespective of date of capture. Because fish will lose mass and condition after river entry, analyses for these response variables were restricted to fish captured before 31 August in any year. This resulted in further exclusion of the Invermore River in 2003 and 2005. Owing to the resulting combinations of factors for mass and condition factor, it was not possible to investigate the three way interaction, or year × river interaction. As for smolts, the effect of treatment within rivers and years was analysed by pairwise *t* tests and Mann–Whitney tests, as appropriate. All analyses were carried out in R software (R Development Core Team 2010).

Results

Experimental smolt analyses and farm salmon abundances

There was no significant three way interaction ($F_{[3,689]}$ = 0.63, p = 0.595) or year × treatment interaction ($F_{[2,692]}$ = 2.21, p = 0.11) for log length. Both treatment × river ($F_{[2,694]}$ = 3.89, p = 0.021) and year × river ($F_{[2,694]}$ = 8.41, p < 0.0001) were, however, significant; these indicate an effect of treatment which varied with river, but which may not indicate an effect within a given river. The multiple *t* tests indicated a significant effect of treatment for two rivers in 2005 (Table 3): Owengowla River treated smolts were significantly longer (19.4 cm ± 0.3 SE) than control fish (18.6 cm ± 0.2) and for the Invermore River the difference also was 0.8 cm (control: 18.0 cm ± 0.2; treated: 18.8 cm ± 0.3). However, in neither case did this remain significant following adjustment for fdr (Table 3).

From analysis of the concentrations of emamectin, the levels for all smolts were below the maximum residual limit (MRL) of 100 μg·kg^{-1}, and within the range 31.4–78.6 μg·kg^{-1} (44.6% of samples). All five tested groups included individual fish below the limit of detection (LOD, 9 μg·kg^{-1}; 35% of samples), whilst four groups (20.4% of samples) included fish below the limit of quantification (LOQ, 29 μg·kg^{-1}). It is therefore probable that not all salmon in the experimental groups would have had adequate levels of emamectin benzoate to be fully protected from sea lice infestation.

Estimates of the number of farmed and wild salmon present in springtime, prior to experimental salmon smolt release and wild smolt out-migration, indicated that the number of wild salmonids in these bays was very low (average 38, maximum 264 salmonids) in all years. Local farmed salmon abundances were three to four orders of magnitude higher than the estimate for wild salmonids (Table 2), indicating that a significantly greater sea lice infestation pressure for wild smolts was likely to originate from farmed sources.

Recaptures of treated and control groups of adult salmon

In total, 472 1SW tagged adult salmon were recaptured. The majority of recaptures were from the offshore commercial salmon drift net fishery, during June and July (Table 4). Salmon also were captured in inshore draft net fisheries, rod fisheries, and terminal traps. Higher returns were recorded for all eight groups of treated fish, although some returns were only marginally higher than controls (Table 4). The χ^2 contingency table tests showed the observed ratio of returns differed significantly from expected for three releases (Owengowla 2004, 2005, and Erriff 2006; Table 4). Moreover, the meta-analysis provided a highly significant overall outcome (Fisher's combined probability test, χ^2 = 91.16, df 16, p << 0.001) for the combined probabilities from all eight releases. As expected, the combined probability also was significant when analyzing only the seven releases undertaken when farms were in production (χ^2 = 90.87, df 14, p << 0.001).

Whilst the meta-analysis results from the numbers of tags retrieved show a clear and highly significant overall effect of emamectin treatment on subsequent survivorship of post-smolts, the unraised tag returns cannot be utilized in estimating percent marine mortality. From the raised returns of tags, the percentage of returning adult fish from emamectin-treated groups ranged from 1.9% (Invermore 2004) to 6.7% (Owengowla 2006), with a mean of 3.7% (Fig. 2); the comparable percentages for control fish were lower—ranging from 0.2% (Erriff 2006) to 6.7% (Owengowla 2006), with a mean of 2.1%. The highest marine survival over the study period (6.7%) was seen for both treated and control groups released from the Owengowla River in 2005 when the salmon farm was fallow.

Twenty one adult salmon were recaptured as 2SW fish, 2 years after their release. Most of those recaptures occurred during the commercial salmon fishery close season and therefore no raising factor was applied to these particular data. No clear trend in returns from the treatment and control group pairings was evident, and this perhaps reflects the small numbers of 2SW adults. However, overall, more (14) 2SW salmon adults returned from treated than control (7) groups, and no 2SW salmon returned from control groups for the River Erriff.

Length, mass, and condition factor of adult salmon

Length and mass data were available for only one third of the recaptured salmon examined for microtags. For the analyses of length of returning adults there were no significant interactions (treatment × year × river [$F_{[1,202]}$ = 0.001, p = 0.971]; year × river [$F_{[1,203]}$ = 0.53, p = 0.466]; treatment × year [$F_{[2,204]}$ = 1.68, p = 0.189]; treatment × river [$F_{[2,206]}$ = 2.71, p = 0.069]). There was neither a significant effect of river ($F_{[2,208]}$ = 1.67, p = 0.191) nor treatment ($F_{[1,210]}$ = 3.19, p = 0.076) on length. There was, however, a significant effect of year ($F_{[2,211]}$ = 4.07, p = 0.019). Multiple comparisons did, however, show a significant difference between treated and control fish returning to the River Erriff in 2004 (t_{53} = –2.90, p = 0.005, adjusted p = 0.032), with treated fish (65.8 cm ± 0.7) being longer than control fish (62.3 cm ± 1.0).

Masses of return adults showed significant river × treatment ($F_{[2,99]}$ = 8.50, $p \leq$ 0.001) and year × treatment ($F_{[1,99]}$ = 9.58, p = 0.003) interactions. The multiple *t* tests showed a significant effect of treatment on mass in 2004 for the rivers Erriff (t_{46} = –3.33, p = 0.002, adj. p = 0.007) and Owengowla (t_{16} = 3.12, p = 0.008, adj. p = 0.016), but these effects differed in direction for the two rivers. The higher mass occurred in the treated group for the River Erriff (control: 2.34 kg ± 0.15; treated: 2.94 kg ± 0. 11) and the control

Table 3. Summary test statistics for multiple *t* tests of lengths of treated and control smolts released in each river and year.

Year	River	Method	Test statistic	df	*p*	Adjusted *p*
2003	Owengowla	*t* test (Welch)	–1.46	92.89	0.1473	0.295
2003	Invermore	*t* test	–0.72	79	0.4736	0.541
2004	Erriff	*t* test (Welch)	1.47	67.39	0.1466	0.295
2004	Owengowla	*t* test	0.44	88	0.6607	0.661
2004	Invermore	*t* test	–1.03	88	0.3067	0.491
2005	Erriff	Mann–Whitney	1218.00	—	0.3866	0.515
2005	Owengowla	*t* test	–2.35	93	0.02111	0.084
2005	Invermore	*t* test	–2.59	86	0.01131	0.084

Note: Degrees of freedom (df) are not applicable to the nonparametric Mann–Whitney test. Adjusted *p* values refer to those corrected for false discovery rate.

Table 4. Number of recaptures of tagged adult salmon (unraised data) and χ^2 tests (including Yates' correction for continuity).

Release location	Group	Fishery year	Unraised return*	χ^2	*p*
Owengowla	Treated	2004	35	24.55	*<<0.0001*
Owengowla	Control	2004	3		
Owengowla	Treated	2005	51	11.09	*<0.001*
Owengowla	Control	2005	22		
Owengowla	Treated	2006	54	0.03	0.8652
Owengowla	Control	2006	53		
Invermore	Treated	2004	17	1.9	0.1683
Invermore	Control	2004	9		
Invermore	Treated	2005	37	1.64	0.2007
Invermore	Control	2005	26		
Invermore	Treated	2006	31	3.63	0.0566
Invermore	Control	2006	17		
Erriff	Treated	2005	44	0.85	0.3554
Erriff	Control	2005	34		
Erriff	Treated	2006	37	29.99	*<<0.0001*
Erriff	Control	2006	2		

Note: Italicized *p* values indicate significant departures from expected returns at the Bonferroni corrected critical value of $p < 0.006$ (1 df in all cases).

*The number of nonreturning fish can be calculated by subtracting the returns from the number released in Table 1.

group in the Owengowla River (control: 3.14 kg ±0.28; treated: 2.34 kg ± 0.12).

For condition factor there was no significant river × treatment ($F_{[2,99]} = 2.51$, $p = 0.087$) or year × treatment ($F_{[1,101]} = 0.27$, $p = 0.604$) interaction. Neither were there any significant main effects (river [$F_{[2,102]} = 0.12$, $p = 0.886$]; year [$F_{[1,104]} = 0.66$, $p = 0.417$]; treatment [$F_{1,105} = 0.83$, $p = 0.365$]), and this was confirmed by similarly nonsignificant multiple comparisons. In summary, for return adults there was no systematic variation in length, mass, or condition factor and emamectin treatment had no consistent effect on these variables.

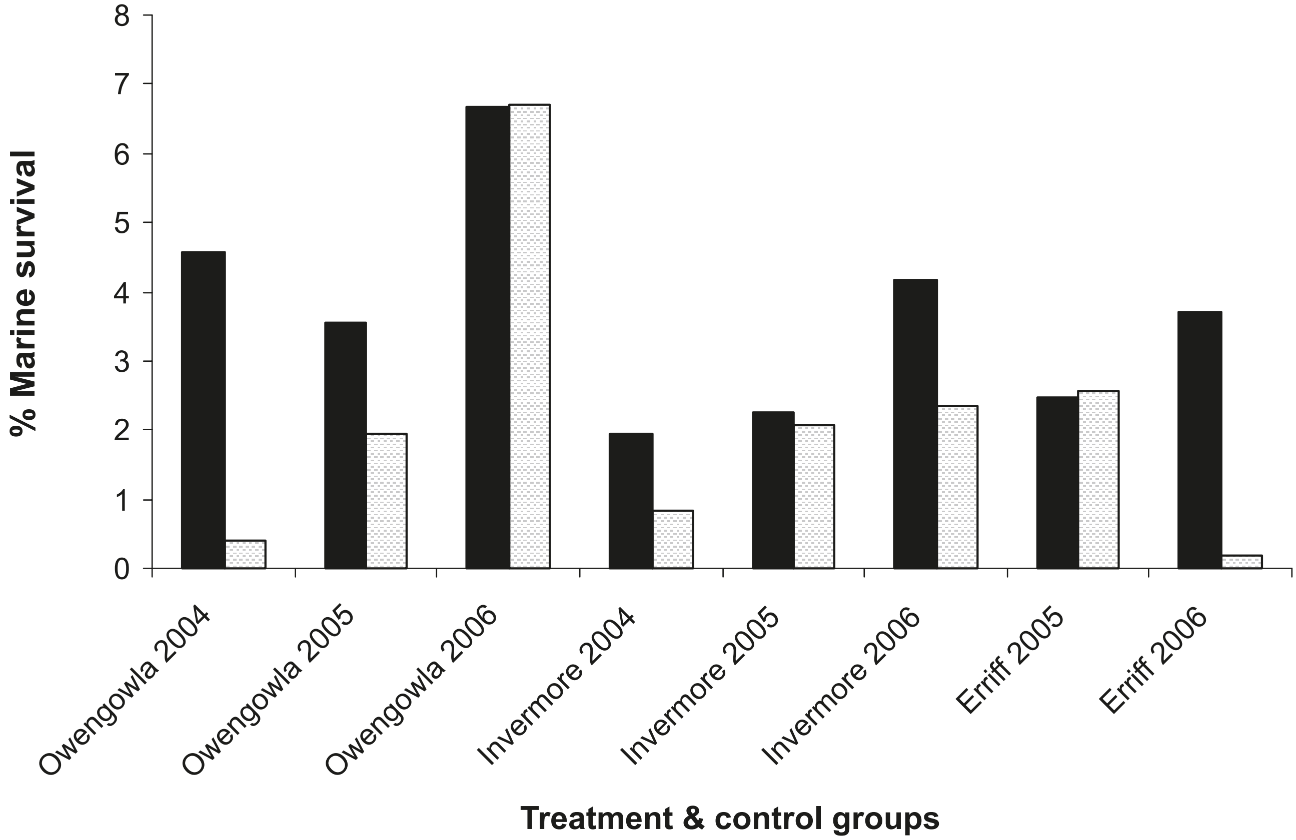
Discussion

The early stages of the marine migration of Atlantic salmon bring postsmolts into contact with infective sea lice copepodids originating both from salmon aquaculture facilities and from wild salmonids in the same vicinity. In fjordic systems in northwestern Europe, the infective copepodids appear to concentrate at salinity discontinuities near river outfalls (McKibben and Hay 2004; Penston et al. 2004) and Tully et al. (1993) reported a predominance of larval chalimus sea lice stages on wild sea trout juveniles in areas adjacent to salmon farms: this implies that salmonids are rapidly infested, perhaps by pulses of copepodids soon after entering seawater. The physiological and behavioural effects of sea lice were greater in fish infected 2 weeks after seawater transfer than in fish infected 6 weeks after seawater transfer (Dawson et al. 1998). Sea lice infestation may, therefore, have a disproportionately detrimental impact on the survival of wild smolts soon after seawater entry.

Mortality of salmonids attributable to sea lice infestation has been well documented (see, for example, Costello 2009 and Revie et al. 2009 for reviews), and the feeding activity of sea lice can cause mechanical damage, including skin and fin erosion (Bjørn and Finstad., 1997; Dawson et al. 1998), and can lead to osmotic stress and death (Grimnes and Jakobsen 1996; Nolan et al. 1999; Finstad et al. 2000). Physiological studies indicate that as few as 11 sea lice on Atlantic salmon smolts can cause mortality (Finstad et al. 2000). Stone et al. (2002) have demonstrated that prior treatment of smolts in freshwater with emamectin will result in an extended period of protection in those critical first weeks at sea, when fish are actively adapting to saline conditions and perhaps most vulnerable to infestation by sea lice.

There now is clear evidence that marked and predictable interannual variation in larval infestation pressure can occur

Fig. 2. Percent marine survival estimate (from raised data) of salmon smolts returning as one sea-winter adults for each experimental release. Treated and control groups are shown in black and grey, respectively. The ratio of return rates of treated:control fish ranged from 1:1 (Owengowla 2006) to 21.6:1 (Erriff 2006), with a median ratio of 1.8:1.



within defined sea lochs or fjords according to the 2-year production cycle typically applied by the Scottish salmon aquaculture industry (McKibben and Hay 2004). Sea lice copepodids have been found in plankton samples only when gravid female sea lice were present on local fish farms, and there was a virtual absence of larvae during the first year of the commercial production cycle (McKibben and Hay 2004; Penston et al. 2004). In a more recent continuation of those studies in a fjordic sea loch in northwestern Scotland, Middlemas et al. (2010) have shown that the percentage of wild sea trout with sea lice above a critical level typically is higher during the second year of farm production, and that a link is likely between farm larval sea lice production and infestations of local wild sea trout.

On the basis of a review of the empirical data and the analytical outcomes for the breadth of studies undertaken in Canada, Norway, Scotland, and Ireland on salmonid – sea lice interactions, Revie et al. (2009) concluded that although the evidence was largely indirect or circumstantial that sea lice emanating from salmon farms exert detrimental effects on wild salmonids, the weight of available evidence was that sea lice of farm origin can present a significant threat. Previously, Brooks and Jones (2008) had acknowledged that salmon farms may contribute sea lice to the wider marine environment; but they argued that research to date had not determined the relative contributions from wild and farmed sources of lice. The challenge therefore remains to confirm the interaction strengths between wild fish and salmon farms as sources of infestation, and of sea lice as a population regulating factor in local declines of wild salmonids (Revie et al. 2009; Marty et al. 2010).

Whilst acknowledging the importance and utility of modeling studies of farm–wild interactions (e.g., Krkošek et al. 2007; Amundrud and Murray 2009; Connors et al. 2010), this requires advancement in observational and experimental approaches to affirm direct links (or lack thereof) between larval sea lice production from farms, infestation of wild fish, and wild fish population declines. The present study progresses our understanding of this interaction and shows a significantly higher return of adult salmon from emamectin-treated groups over control groups for all three aquaculture bays. It is important to emphasize that the meta-analysis for the tags actually retrieved (i.e., unraised) and including the Owengowla 2005 release (when the farm was fallow in Betraghboy Bay) provides a highly significant overall outcome for these trials, despite the returns from Owengowla 2005 showing no significant difference. But these data also illustrate the need for large trials involving multiple river systems —with high numbers of tagged smolts at each release—and repeated releases in multiple years, in order that observers can take account of the inherent experimental and ecological variability. Other studies of Atlantic salmon in rivers in central Norway (Hvidsten et al. 2007) and southwest Norway (Finstad and Jonsson 2001) have demonstrated that in years of high sea lice infection pressure, the returns of chemically protected fish tended to be higher than unprotected control groups. In a recent long term study, Jackson et al. (2011) released emamectin-treated and control groups of ranched salmon in 10 experimental releases over 9 years, but in only one location with salmon aquaculture in western Ireland. Whilst the return rate of treated fish was higher in 9 of their 10 releases, they concluded that sea lice infestation was only a minor component of overall marine mortality for the particular stock studied. This conclusion arose from their observations of marked overall declines in percent marine survivorship over the 9 years of their releases, irrespective of emamectin treatment. But that does not preclude the importance of a clear overall pattern of higher survivorship to adulthood of released smolts treated with emamectin.

Given that emamectin protects postsmolt Atlantic salmon from sea lice infestation for only a few weeks (Stone et al. 2002), it is apparent that our prophylactic treatment would have been effective only for the earliest stages of the marine migration. The implications of the overall highly significant result of the present trials are that sea lice-induced compromise of control fish soon after seawater entry was operative. Stone et al. (2002) reported that emamectin benzoate administered at a dose of 50 $\mu g \cdot kg^{-1}$ fish$\cdot$day^{-1} for 7 consecutive days is highly effective against both the immature chalimus stages and the motile preadult and adult stages of sea lice. They further noted that where in-feed treatments are used, variation in individual feeding responses and behaviour may result in a small proportion of fish receiving a lower dose, making 100% efficacy difficult to achieve. The high numbers of salmon smolts in the present treated groups for which emamectin was below the LOD (9 $\mu g \cdot kg^{-1}$) and LOQ (29 $\mu g \cdot kg^{-1}$) might therefore indicate that the impact of sea lice infestation shown here could be even greater than presently reported if such low emamectin levels did not afford sufficient protection to smolts. Efficacy of emamectin may also be reduced because of lice resistance (Anonymous 2008).

Parasite-induced mortality estimates ranging from 0 to >95% of fish in the wild salmon smolt run have been reported in Norway (Holst et al. 2003; Heuch et al. 2005; Bjørn et al. 2008), and Johansen et al. (2011) concluded that there is a risk of high abundances of sea lice on farmed salmon in Norway comprising a hazard to local wild salmonid populations. Our results suggest that sea lice-induced mortality on adult salmon returns can be significant and the median ratio of return rates of treated:control fish was almost double at 1.8:1. Taken together, the above data do indicate that sea lice outbreaks have the potential to be an important factor regulating wild Atlantic salmon stock sizes. The high marine survival both of the treated and control groups for Owengowla 2005 (during an absence of salmon farm production) do suggest that fallowing of salmon aquaculture sites could result in a significant improvement in subsequent marine survival of wild postsmolts, but this result is unreplicated. Fallowing of salmon farms along a migration route for one year (2003) in British Columbia reduced sea lice abundances (Morton et al. 2005) and those salmon cohorts experienced high marine survival (Beamish et al. 2006), though Marty et al. (2010) found no evidence of a negative effect of farm lice abundances on pink salmon production.

Results from the present study indicate that marine salmon farms may comprise a significant source of sea lice infestation for Atlantic salmon smolts migrating through coastal waters. An increase in the mortality of salmon smolts can be therefore expected in locations where farm sea lice levels are not maintained at sufficiently low levels in spring. The challenge to wild fishery managers and the aquaculture industry alike is to objectively identify that level, and to ensure that its achievement is both practicable and economically feasible and sustainable. A recent report on sea lice control on salmon farms in Ireland (Anonymous 2008) has documented the difficulties in maintaining adequate control of sea lice infestations. In view of the numbers of cultured salmon typically held at modern salmon farm sites, and even in cases of low infestation levels per farmed fish, the conservation status of wild Atlantic salmon in specific localities could be compromised in some years unless sea lice levels are effectively controlled at near-zero levels on over-wintered farmed salmon. In this context, the long term status of Atlantic salmon in two rivers (Ballynahinch and Erriff) entering bays in the present study remains a concern, particularly as both have been designated as Special Areas of Conservation (SAC) for salmon under the European Union Habitats Directive (Council Directive 92/43/EEC). But attaining near-zero levels of sea lice on farmed salmon has cost implications, and treatment over-use might lead to the development of resistance to the active compound (e.g., Lees et al. 2008).

A number of initiatives that need to be addressed to ensure effective sea lice management have been identified for Irish salmon farms (Anonymous 2008). Amongst these are changes to production strategy (e.g., single generation sites, “all-in all-out” bay by bay salmon production) and a new approach to the use of licensed sites. In the long term, given the range of difficulties likely to militate against continuous effective sea lice control on salmon farms, it may be necessary to introduce whole-bay spring fallowing of farms. Alternatively, farms in close proximity to important salmon rivers may need to be relocated to achieve sufficient spatial separation and to minimize tidal connectance to ameliorate the potential impact of sea lice infestation on wild salmon stocks.

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