Estimating the temporal overlap between post-smolt migration of Atlantic salmon and salmon lice infestation pressure from fish farms

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ABSTRACT: To be able to design effective management to alleviate wild fish from parasite infestation pressure from fish farms, it is pivotal to understand when post-smolts migrate past areas of potential exposure to salmon lice *Lepeophtheirus salmonis*. Here, data from release groups of coded-wire-tagged Atlantic salmon *Salmo salar* smolts and their subsequent recaptures in a trap net in the outer fjord 12 to 97 km from the various release sites were used to estimate the smolts' progression rate and their arrival time in an outer fjord in Norway. The arrival time estimates to the outer fjord are compared with modelled infestation pressure from local fish farms. The overall progression rate varied from 0.8 to 31.2 km d^{-1} (0.05 to 2.20 body lengths s^{-1}), with mean and median values of 8.8 and 7.8 km d^{-1}, respectively (0.60 and 0.54 body lengths s^{-1}). The progression rate varied with water discharge from the rivers into the fjords, fish length, condition factor and smolt origin. Simulated arrival time and capture of wild smolts suggest that smolts from the different rivers arrive in the outer fjord system with a difference of up to 4 wk. The arrival time for the rivers with the longest migration was estimated to be from mid-May throughout June. Infestation pressure from fish farms increased from the beginning of June in 2 of 3 study years, suggesting that an increase in lice exposure from fish farms will overlap with smolts from late-migrating populations in some but not all years.

KEY WORDS: Fish farm · *Lepeophtheirus salmonis* · Management · Progression rate · *Salmo salar* · Sea lice

INTRODUCTION

The initial post-smolt migration of salmon from the river to the ocean is generally a period of high mortality (Lacroix et al. 2005, Thorstad et al. 2007, 2011a,b, 2012b, Lacroix 2008, Dempson et al. 2011). This mortality partially results from a combination of the vulnerability of salmon smolts during the physiologically challenging transition from freshwater to saltwater habitat (Strand & Finstad 2007, Strand et al. 2011) and the aggregation of predators in near-shore habitats (Hvidsten & Lund 1988, Handeland et al. 1996). Consequently, the migration speed through this transition zone can be understood as an optimal strategy to reduce predator encounters by moving quickly while at the same time adjusting to the physiological stress associated with the transition from freshwater to saltwater (Thorstad et al. 2012b).

In addition to natural challenges, cumulative anthropogenic factors that affect rivers and near-shore habitats have increased, including factors such as pollution, bycatch in fisheries, river regulation and climate change (Thorstad et al. 2011b). The most pressing anthropogenic factor affecting Atlantic salmon post-smolts is thought to be aquaculture (Costello 2006). Farmed fish in net pens can function as source populations for diseases and parasites such as sea lice that can then be transferred to wild fish

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(Tully & Nolan 2002, Vollset et al. 2015). Therefore, to minimize the potential impacts of sea lice, it is thought that coordinated winter and early spring delousing in farms can minimize the production of infectious free-living stages of lice during the migration of wild salmon smolts (Heuch et al. 2005, Serra-Llinares et al. 2014). For instance, Peacock et al. (2013) documented how coordinated and correct use of winter delousing in nearby farms had a positive effect on the recruitment of wild pink salmon *Onco-rhynchus gorbuscha*. Thus, understanding the timing and duration of smolt migrations through areas of high concentrations of fish farms is essential to be able to optimize and evaluate the effect of such mitigation efforts.

One commonly used method to study the behaviour of salmon smolts through near-shore environments is the use of acoustic tags (Lacroix et al. 2005, Thorstad et al. 2007, Lacroix 2008, Skilbrei 2010, Dempson et al. 2011, Thorstad et al. 2011a,b, 2012b). However, the main disadvantages of using acoustic tags are potential tag effects, handling of the fish and difficulty in distinguishing live individuals from predated individuals (Thorstad et al. 2012a, Gibson et al. 2015). An alternate method is to employ a mark–recapture study design with the use of less invasive group tagging techniques such as coded wire tags (CWTs, Vollset et al. 2016). Although resolution is lost compared to acoustic tags, the uncertainties associated with predation and tagging effects are reduced. The method does not give detailed information on migration speeds of individual fish, but can be used to calculate progression rates during outward migration of salmon smolts.

Using cultivated Atlantic salmon *Salmo salar* smolts from 3 cultivation sites from 2 stocking programmes, we used a mark–recapture study design to assess and predict the progression rate of salmon post-smolts through the estuary and early marine migration. First, we modelled how river discharge, fish size, condition factor and fish origin influenced the progression rate. Second, we compared the catches of wild post-smolts in a trap net with the simulated progression rates and times of fjord entry from the different rivers in the system. Finally, we estimated the modelled salmon lice *Lepeophtheirus salmonis* infestation pressure from surrounding fish farms and compared it with the modelled time of arrival for the largest river in the region, the Vosso River. Understanding and predicting the migration timing of post-smolts will enable managers to provide guidelines for effective lice treatment in aquaculture to minimize impacts on wild fish.

MATERIALS AND METHODS

Study area

The study area is located on the west coast of Norway (Fig. 1; Vosso: 60° 64′ N, 5° 95′ E, Dale: 60° 58′ N, 5° 78′ E). The key geographical feature of the area is a deep and narrow fjord that surrounds the large island of Osterøy. The fjord opens up into an archipelago in the outer fjord system, and this geography offers various potential migration routes for post-smolts. The main water discharge follows the deepest channel down Byfjorden and up Hjeltefjorden. However, surface water also flows through Radfjorden and Herdlefjorden depending on freshwater discharge, wind and tidal cycles. The surface water (0–5 m) inside the Osterfjord (indicated in the map by the presence of a pontoon bridge; Fig. 1) is primarily fresh or brackish (<10 ppt) during the post-smolt migration and only seldom registers salinity values >20 ppt (Skilbrei 2012). Unpublished data from acoustic tagged smolt (B.T. Barlaup unpubl.) suggest that the majority of individuals follow the main flow of the system and migrate to the south of Osterøy (southern route, Fig. 1). No data exist to show what channels are preferred in the outer region of the fjord. There are close to 40 approved fish farm locations in the region which can be defined as the migration route of the salmon smolt from the inner fjord. The production in these farms is dependent on local fallowing regimes. All farms in the inner fjord produce rainbow trout *Oncorhynchus mykiss*, while most farms in the outer region produce Atlantic salmon *Salmo salar*.

Cultivated smolt production and mark–recapture methods

During the study period, the production of cultivated smolts occurred in the Evanger net-pen facility, Voss hatchery and Dale hatchery (Table 1). Both the Evanger and Voss hatchery smolts are hatched from eggs from the living gene bank of the Vosso population in Eidfjord. Voss hatchery smolts were reared until the smolt stage (1 yr old) in standard hatchery tanks, while Evanger smolts were reared in a net-pen facility in Lake Evanger, within the Vosso watershed. For the Dale River system, wild brood fish were collected in the Dale River, and 1 yr old smolts were produced in the hatchery by the river. In the following text, the 3 groups will be treated as separate groups in the analysis and are
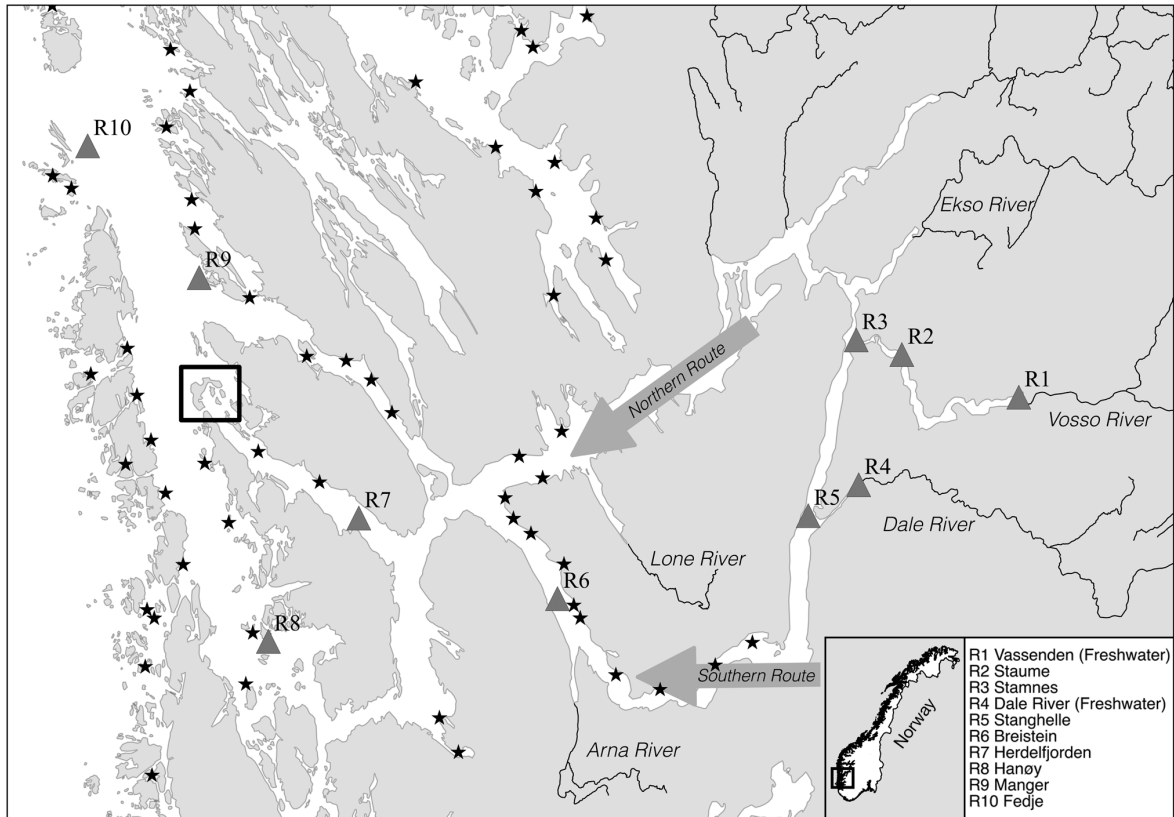
Fig. 1. Study area at the SW Norwegian coast (inset). Triangles indicate release site locations of cultivated Atlantic salmon *Salmo salar* smolts. Rectangle indicates location of the trap net at Herdla. Arrows indicate northern and southern route of migration past Osterøy Island. Locations of the most important anadromous rivers in the system are indicated by river names (Ekso, Vosso, Dale, Arna and Lone). Stars show fish farm locations

Table 1. Number of Atlantic salmon *Salmo salar* released according to year, location and origin. Location labels correspond to those shown in Fig. 1. Empty cells: no data

| Year | Location | Dale hatchery | | Lake Evanger net-pen | | Voss hatchery | |
		Released	Recaptured	Released	Recaptured	Released	Recaptured
2012	R1 Vassenden			10000	3		
	R2 Straume			5000	1		
	R3 Stamnes			5000	3		
	R5 Stanghelle	14032	42				
	R6 Breistein	4619	25	10000	9	12000	38
	R9 Manger			10000	0	12000	0
2013	R1 Vassenden			15000	0		
	R2 Straume			5000	1		
	R3 Stamnes			5000	1		
	R5 Stanghelle	12885	31				
	R6 Breistein	10628	40	10000	25		
	R9 Manger			10000	0		
2014	R4 Daleelva	3019	3				
	R5 Stanghelle	11467	32				
	R7 Herdlafjord	11399	59				
	R6 Breistein					9600	39
	R8 Hanøy					9600	0
	R9 Manger					10800	0
	R10 Fedje					9600	0

named Evanger, Voss hatchery and Dale hatchery. These groups will be termed 'origin'. At least 10 d prior to being released, all fish were sedated with MS222 and tagged with CWTs.

The tagging activity was conducted as part of a separate experiment assessing the effects of prophylactic treatment against salmon lice on post-smolt survival (see Vollset et al. 2014). The treatment occurred from 10 to 14 d prior to release. The smolts from the Vosso River were sorted and separated into groups that either received normal fish feed or pellets with emamectin benzoate. The treatment groups received a dosage of emamectin benzoate of 50 µg kg^{-1} body mass d^{-1} for 8 d. The Dale River smolts released in 2012 and the first group released in 2013 received an intra-peritoneal injection of emamectin benzoate (Glover et al. 2010). The controls were given a placebo injection. All other smolts released in 2013 and 2014 were treated by bathing the smolts in a solution of Substans EX (its use was demonstrated by Skilbrei et al. 2015). Although we did not expect the treatments to have any effect on the progression rate of the post-smolts during the early near-shore migration, we did include treatment in the model as a co-variable to correct for potential effects. In the initial analysis, the effect of treatment was non-significant and had little impact on the progression rate, and we have chosen to exclude it from the analysis and results sections for clarity.

Fish were released at various locations (Table 1). They were either released in the river or transported in specially constructed tanks (Voss hatchery and Evanger) or towing net pens (Dale hatchery) to various locations in the estuary and fjord (Fig. 1). To re-capture post-smolts at Herdla, we used 3 modified trap nets as outlined by Barlaup et al. (2013). All 3 traps were deployed from 4 May to 2 July 2012, 6 May to 5 July 2013 and 5 May to 8 July 2014 at various locations close to Herdla (Fig. 1). This location is approximately 65 and 90 km from the Dale River and the Vosso River, respectively, and is at the end of Herdlefjorden which is 1 out of 3 possible channels through which the post-smolts can migrate in the outer fjord. The distance from the various release locations and the trap net location varied from 12 to 97 km. Recaptured post-smolts with CWTs were then analysed in the laboratory to determine tagging location. All post-smolts caught in the trap net were visually inspected for salmon lice, and lice were identified to life history stage in the laboratory using a stereo-microscope (Hamre et al. 2013).

Wild post-smolt migration

In addition to assessing the recaptures of cultivated and CWT post-smolts, the trap nets at Herdla caught wild salmon post-smolts (i.e. post-smolts caught at Herdla and with the adipose fin intact) most likely originating from rivers within Osterfjorden.

Data analysis

Progression rate and explanatory variables

Progression rate (km d^{-1}) was calculated as the distance from release site to re-capture site, measured through the thalweg of the fjord, divided by the time (days) between the release and re-capture time. We used the southern migration route to calculate the distance for all release groups. The trap nets were checked once a day, and migration time is therefore only estimated in units of whole days. Multiple factors are thought to influence the progression rate of smolts. We included several variables in the analysis: length (total length at capture), condition (Fulton's condition factor, K), origin (Evanger, Voss hatchery and Dale hatchery), and river discharge (Table 2). To calculate discharge, we used a stream flow gauge in the Vosso River. While other rivers contribute to the overall hydraulics of the system, the Vosso River is the dominant driver of discharge in the inner fjord system. The stream flow gauge is located above the power station at Evanger in the Vosso River system. Thus, variation in flow mostly reflects variation in water from the catchment area and is, thus, strongly correlated with rainfall and snow melting in the

Table 2. Summary of variables selected to determine migration speed of Atlantic salmon *Salmo salar* smolts. Release locations are shown in Fig. 1

Variable	Range/factors	Random/Fixed
Year	2012–2014	Random
Release location	Recaptures from 5 release locations (Vosso [R1–3], Dale [R4], Stanghelle [R5], Breistein [R6], Herdlafjorden [R7])	Random
Length (cm)	11–22.3	Fixed
Condition factor K	0.65–1.27	Fixed
Discharge (m^3 s^{-1})	31–303	Fixed
Origin	Voss hatchery, Lake Evanger net-pen, Dale hatchery	Fixed

region. We used a 5 d average of discharge from day of release to present discharge based on literature estimates of the time that fish spend in the fjord system (Thorstad et al. 2012b).

Modelling progression rates of cultivated post-smolts

Our main goal was to explore how the 4 different selected variables explained the progression rate. Progression rate was log-transformed to fit a normal distribution. The data were first assessed for non-linearity by using a simple generalized additive model (GAM) model (Wood 2011). In this model, all variables were defined as fixed effects. The relationship between progression rate and length and between progression rate and condition seemed to be curvilinear (the plot of the GAM is presented in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/q008p511_supp.pdf). Accordingly, we included a quadratic term to explain these patterns. Second, a generalized linear mixed model was used. In this model, year and release location were defined as random effects; length, condition, discharge and origin, including the quadratic terms mentioned above, were defined as fixed effects (Table 2). No interaction terms were included.

To select the variables that best explained the progression rate, we used Akaike's information criterion corrected for small sample size (AIC$_c$; Burnham & Anderson 2002). All variable combinations were explored. The ΔAIC$_c$ (the difference in AIC$_c$ values from the model with the smallest AIC value) and AIC$_c$ weights (the amount of support for a candidate model) were calculated for each model (48 in total). We only considered models that had a ΔAIC$_c$ < 4 as an adequate model to explain the migratory speed of post-smolts (Burnham & Anderson 2002). All statistical analysis was performed with the statistical program R (v. 3.0.2).

Rivers (Fig. 1). Data on the time of river descent were collected either with smolt screws, trap nets in the estuary, video cameras or a combination of the above. The weighted mean date and standard deviation (SD) were calculated for each of the rivers (Table 3). The data seemed to be reasonably described by a normal distribution (see cumulative frequency plots in Fig. S2 in the Supplement). In addition to these rivers, smaller rivers and creeks may produce salmon smolts. However, the main smolt output is thought to come from these 5 rivers. Moreover, the larger Modalen River also produces salmon smolts but only in low numbers due to acidification. For Vosso, Arna, Lone and Dale, the smolt run data are based on information from 2012, but data only exist from 2008 for Ekso (Table 3).

A random sample of 10 000 fish per river was simulated from the river-specific normal distribution of the observed river descents described above. Fish lengths were then assigned based on the estimated normal distribution of the length of wild post-smolts caught in the trap net at Herdla. The effect of condition factor was held constant at an average, based on the argument that the effect of condition factor can be an artefact of cultivation. Therefore, no size and condition difference between rivers was included in the migration estimates. The estimates were also based on the average progression rate among the 3 origins (Dale, Vosso, Evanger). The progression rate from river to trap net was estimated according to the model output based on water discharge 5 d after river exit. To add stochasticity to the estimates in progression rate, the residual deviance was sampled randomly and added to each individual estimate of progression rate. The simulated arrival times of fish from the different rivers at the trap net location at Herdla were visualized by plotting the density distribution for each river on top of the catches of wild post-smolts.

Predicting wild post-smolt migration

To visualize the migration of fish in different rivers in the fjord system, a data simulation approach was used. Based on the model parameters from the top model (see Table 5), we simulated the time of capture at the trap net location from each of the rivers in the region based on the timing of wild smolt river descent from the Vosso, Dale, Lone, Arna and Ekso

Table 3. Weighted mean date and weighted standard deviation (days) for 5 rivers in Osterfjorden based on various methods

River	Weighted mean date (dd/mm)	Weighted SD date	N	Method	Year
Arna	01/05	4.28	6924	Video	2012
Lone	10/05	6.79	768	Video	2012
Dale	02/06	16.5	1449	Wolf trap	2012
Vosso	24/05	10.5	209	Smolt screw	2012
Ekso	27/05	9.6	186	Trap net and smolt screw	2008

Annual variation in smolt runs

Data did not exist for smolt migrations across years for all rivers in the region. To illustrate the extent of variation in the timing of the smolt run among years, we present data from smolt runs from the wolf trap in Dale, where we have data from 2004 to 2014.

Modelled infestation pressure from fish farms

To illustrate how lice infestation pressure changes with season during the migration in the outer region, we modelled the infestation pressure from surrounding fish farms at the trap net location at Herdla using the method described by Aldrin et al. (2013). The method does not necessarily correctly depict the infestation pressure on migrating salmon smolt. However, we do not have data on where the salmon migrate. Consequently, the point estimate of infestation pressure is used as an illustration of the temporal trend in the infestation pressure for the different years. The infestation pressure from each year was plotted on top of the modelled arrival time at the trap net location of smolt from Vosso and the wild fish caught each year at the trap net.

RESULTS

During the years 2012 to 2014, a total of 148 600 and 68 049 fish were tagged (CWT) and released from the Vosso and Dale stocking experiments, respectively. From the Vosso experiment, 52 400 fish were released beyond the trap nets at Manger or Fedje (release sites R9 and R10, Fig. 1). A total of 352 cultivated and 142 wild post-smolts were caught at the trap net location (Herdla) between 2012 and 2014. Using an ANOVA and a Tukey's honestly significant difference test, we found that length (n = 494, $z = 21.7$, p < 0.001; n = 494, $z = 6.6$, p < 0.001) and mass (n = 494, $z = 23.8$, p < 0.001; n = 494, $z = 9.4$, p < 0.001) differed significantly between wild smolts and cultivated smolts from the Dale and Vosso hatcheries, respectively, but not for smolts from Evanger (Fig. 2; length, n = 494, $z = 0.3$, p = 0.99; mass, n = 494, $z = 1.3$, p = 0.547). Furthermore, condition was significantly higher in cultivated smolts than in wild smolts, regardless of origin (Fig. 2; Dale, n = 494, $z = 19.8$, p < 0.001; Vosso, n = 494, $z = 16.1$, p < 0.001; Evanger, n = 494, $z = 9.3$, p < 0.001).

Recapture rates increased with decreasing distance between release location and the trap-net location (Fig. 3). No fish released at Manger or Fedje (release sites R9 and R10, Fig. 1) were caught at Herdla, indicating a northerly and oceanward migration trajectory. Additionally, there were no recaptures of fish from the 2 groups released at Hanøy in 2014 (release site R8, Fig. 1).

Sea louse infestation parameters on salmon post-smolts caught in the trap net were generally low for both cultivated and wild fish for all years. Further-
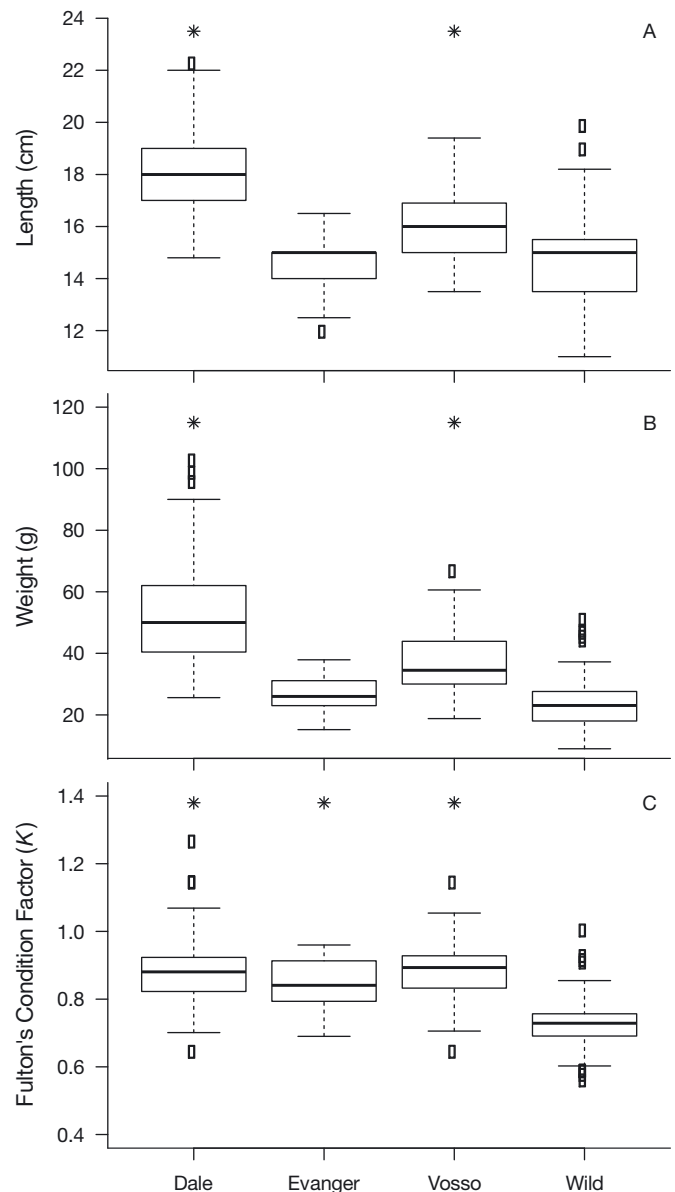

Fig. 2. Comparisons for (A) length, (B) mass and (C) condition for the different groups of cultivated Atlantic salmon *Salmo salar* smolts. Asterisks indicate which cultivated groups (Dale, Evanger, Vosso) are significantly larger than their wild conspecifics. Solid lines indicate the median, boxes are the 50% interquartile range, whiskers are 1.5 times the interquartile range, and small open rectangles are outliers
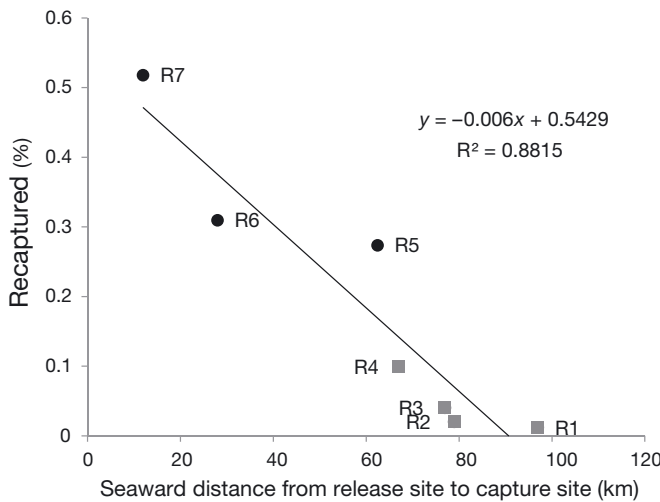
Fig. 3. Percent recapture of Atlantic salmon *Salmo salar* smolts vs. distance between release site and capture site at Herdla. Location codes (R1–R7) correspond to the triangles indicated in Fig. 1. The trend line (with R^2 and function) is drawn for illustrative purposes. Release groups from Hanøy, Manger and Fedje (beyond the trap net) had 0 recaptures and were not included. ●: releases in marine waters, ■: releases in rivers or estuaries

more, adult stages of lice were observed on post-smolts that had been released 1 to 14 d prior to recapture. Because this stage of salmon lice would not have sufficient time to develop (~40 d) before recapture and due to the simultaneous capture of sea trout *Salmo trutta* in the trap net, sea lice most likely jumped from sea trout hosts when both species were confined inside the trap net chamber prior to processing. Moreover, the low levels and strongly 0-inflated data precluded any significance test of differences in abundance of lice between years, sizes or groups (wild/cultivated). However, there seemed to be more lice on the post-smolts in 2012 than in the other 2 years, viz. 2013 and 2014 (Table 4). Additionally, wild, treated and untreated post-smolts had similar amounts of lice within years.

Migratory speed

The overall progression rate estimated from recaptured cultivated post-smolts varied from 0.8 to 31.2 km d^{-1}, with mean and median values of 8.8 and 7.8 km d^{-1}, respectively. This rate corresponds to 0.05 to 2.20 body lengths (BL) s^{-1}, with mean and median values of 0.60 and 0.54 BL s^{-1}, respectively.

The best model selected, with 94% AIC$_c$ weight, included all variables except the quadratic term of length (Tables 5 & 6). The model met the assumptions of normality, homogeneity and independence. With the other variables held constant at averaged values, progression rate increased from 4.7 km d^{-1} for a 12 cm post-smolt to 10.6 km d^{-1} for a 22 cm post-smolt (Fig. 4). Progression rate increased from 2.7 km d^{-1} for a post-smolt with a condition factor of 0.7, to approximately 9 km d^{-1} at a condition factor of 1 and then subsequently decreased (Fig. 4). Progression rate increased linearly from 4.3 km d^{-1} during days with a 5 d average discharge of 50 m^3 s^{-1} to 10.9 km d^{-1} during days with a discharge of 300 m^3 s^{-1} (Fig. 4). The average estimated progression of fish from the net pen in Evanger was clearly much higher (21.4 km d^{-1}) than in the fish from the hatcheries at Dale (6.6 km d^{-1}) and Voss (4.4 km d^{-1}; Fig. 4).

Table 4. Salmon lice *Lepeophtheirus salmonis* counted on Atlantic salmon *Salmo salar* smolts caught in a trap net at Herdla for the years 2012 to 2014. Abundance (average number of lice on all samples), intensity (average number of lice on fish with lice) and prevalence (percentage of the sample with lice) are calculated both for attached stages (copepodites, chalimus I and chalimus II) and for all stages because mobile stages may have jumped from other fish in the trap net chamber. The sample is divided into cultivated and tagged fish not treated with anti-parasitic agent (Not treated), treated with an anti-parasitic agent (Treated) and untagged wild fish (Wild)

Type	Year	N	Attached stages			All stages		
			Abundance	Intensity	Prevalence (%)	Abundance	Intensity	Prevalence (%)
Not	2012	48	0.17	1.14	15	0.54	1.53	35
treated	2013	49	0.02	1.00	2	0.02	1.00	2
	2014	69	0.00	0.00	0	0.01	0.00	1
Treated	2012	75	0.19	1.08	17	0.52	1.50	35
	2013	49	0.00	0.00	0	0.00	0.00	0
	2014	57	0.00	0.00	0	0.07	0.00	7
Wild	2012	30	0.27	2.67	10	0.63	2.71	23
	2013	71	0.03	2.00	1	0.03	2.00	1
	2014	47	0.13	2.00	6	0.34	0.00	17

Table 5. Model selection criteria for models describing the progression rate (km d^{-1}) of Atlantic salmon *Salmo salar* post-smolts. LogLik: log likelihood, AIC$_c$: Akaike's information criterion corrected for small sample sizes, ΔAIC$_c$: difference between the smallest and the respective AIC$_c$ value, weight: amount of support relative to poorer model fits. Only the top 5 models are displayed. All models include release location and year as random effects. '+' indicates that the factor (origin) is included in the model. Condition^2, Length^2: the relationship between progression rate and length and between progression rate and condition appeared curvilinear so we included a quadratic term to explain these patterns

Intercept	Condition	Condition^2	Discharge	Length	Length^2	Origin	df	logLik	AIC$_c$	ΔAIC$_c$	Weight
−8.11	15.94	−7.69	0.0034	0.080		+	10	−248.868	518.4	0	0.939
−12.53	16.89	−8.22	0.0035	0.530	−0.013	+	11	−251.022	524.8	6.44	0.038
−6.72	16.18	−7.84	0.0031			+	9	−254.457	527.4	9.06	0.01
−2.04	2.198		0.0033	0.08056		+	9	−257.374	533.3	14.89	0.001
−0.99		1.16	0.0033	0.08063		+	9	−260.191	538.9	20.53	0

Comparisons of estimated time of migration and capture of wild post-smolts

Wild Atlantic salmon post-smolts were caught between 14 May and 27 June at Herdla, with median dates of 30 May in 2012, 28 May in 2013 and 8 June in 2014. We modelled the density distribution of arrival time at the trap net location from the various rivers in 2012 and overlaid a histogram of wild fish caught at Herdla for all 3 years (Fig. 5). Plots using discharge data from 2013 and 2014 gave similar results and are presented in Figs. S3 & S4 in the Supplement. In all 3 years, the post-smolts originating from the rivers in the inner fjord (Vosso, Ekso, Dale) were estimated to migrate faster than the post-smolts from the rivers in the outer fjord (Arna,

Lone) because they entered the fjord during times of higher discharge. The estimated time between river descent and arrival time at Herdla was 3.0 d for the shortest distance (Lone River, 38 km, range: 2.1–3.3 d) and 6.5 d for the longest distance (Vosso River, 93 km, range: 5.1–8.2 d). Simulated arrival times suggest that smolts from the different rivers arrive at the outer fjord system with a difference of up to 4 wk (Fig. 5).

Annual variation in smolt run

The median dates of the smolt run from the wolf trap in Dale are presented in Fig. S7 in the Supplement. The median date of the smolt run varied 25 d among years. To exemplify how differences in marine entry time would affect our model results, we plotted the model using the mean date ±10 d. The plots are given in Figs. S5 & S6 in the Supplement and demonstrate that the modelled arrival time in the outer fjord is highly sensitive to the date when the fish leave the river.

Modelled arrival time and infestation pressure from surrounding fish farms

Infestation pressure from fish farms increased at the beginning of June in 2012 and 2014, but not in 2013. Consequently, the tail end of the migrating smolts originating from the inner fjords (illustrated by the Vosso River) would experience the highest infestation pressure in these years (Fig. 6).

Table 6. Modelled coefficients from a linear mixed-effect model of progression rate (km d^{-1}) of Atlantic salmon *Salmo salar* post-smolts. Year and release location are defined as random variables. The response variable (Speed) is log-transformed. Note that for the factor 'Origin', 'Dale' is baseline (or equal to the intercept given that the other variables are held at 0). Consequently, there are only 2 coefficients for Origin (Evanger and Vosso)

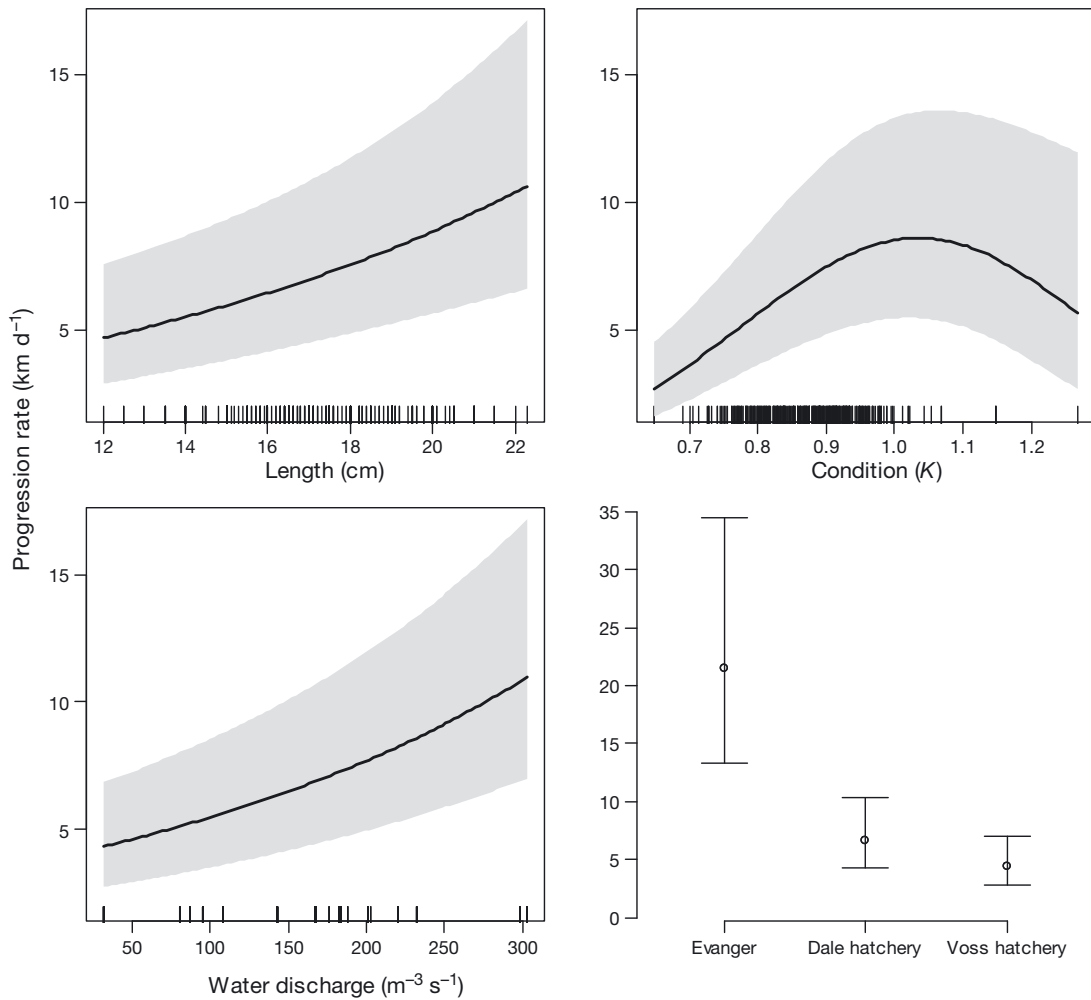| Variable		Estimate	SD	t	p
Fixed effect					
Intercept		−8.12	1.71	−4.76	<0.01
Length (numeric)		0.08	0.02	4.23	<0.01
Condition (numeric)		15.94	3.69	4.32	<0.01
Condition2 (numeric)		−7.70	2.06	−3.74	<0.01
Origin (factor)	Baseline (Dale)				
	Evanger	1.17	0.12	9.73	<0.01
	Vosso	−0.41	0.09	−4.45	<0.01
Discharge (numeric)		0.0034	0.0004	8.34	<0.01
Random effects	Level	Variance			SD
	Release location	0.05			0.23
	Year	0.11			0.33
	Residual	0.22			0.47

Fig. 4. Effect plots of fixed effects with 95% confidence intervals (shaded polygons for numeric predictor variables and whiskers for factorial predictor variables) of final model of progression rate of cultivated Atlantic salmon *Salmo salar* post-smolts. Bars indicate observations. The plots show predicted values according to length, condition, water discharge and origin when other predictors are held at average values

DISCUSSION

Correct progression rate estimates of wild salmon post-smolts through the estuary and fjord are pivotal when attempting to understand the early marine survival of salmon post-smolts and to design appropriate mitigation efforts for anthropogenic effects such as the spill-over effects of parasites from fish farms (Krkošek et al. 2013, Vollset et al. 2015) or bycatch in fisheries (Lacroix 2008). We found that the progression rate of cultivated Atlantic salmon post-smolts, calculated by the mark–recapture method using CWT tags and trap nets, is a function of fish length, condition factor, river discharge and fish origin. This result supports the theory that post-smolts use a combination of both active and passive migration during near-shore migration (Thorstad et al. 2004).

Progression rate increased as condition increased up to a condition factor of approximately 1 and then subsequently decreased. The mechanism behind this relationship could be that condition reflects an intrinsic state of the fish, either directly through the energetic state of the individual or indirectly in the form of between-individual variation in some other trait that has been further intensified in the culture tanks (due to, for example, density-dependent competition for food). For example, Brockmark & Johnsson (2010) demonstrated that the ability of trout to survive in the wild is linked to the rearing density before release. Alternatively, condition may affect progression rate by affecting the morphology of the fish, and thus the hydrodynamics of fish moving through the water (Sfakiotakis et al. 1999). In this case, however, we would expect more slender fish (lower-condition fish) to swim faster, but this pat-
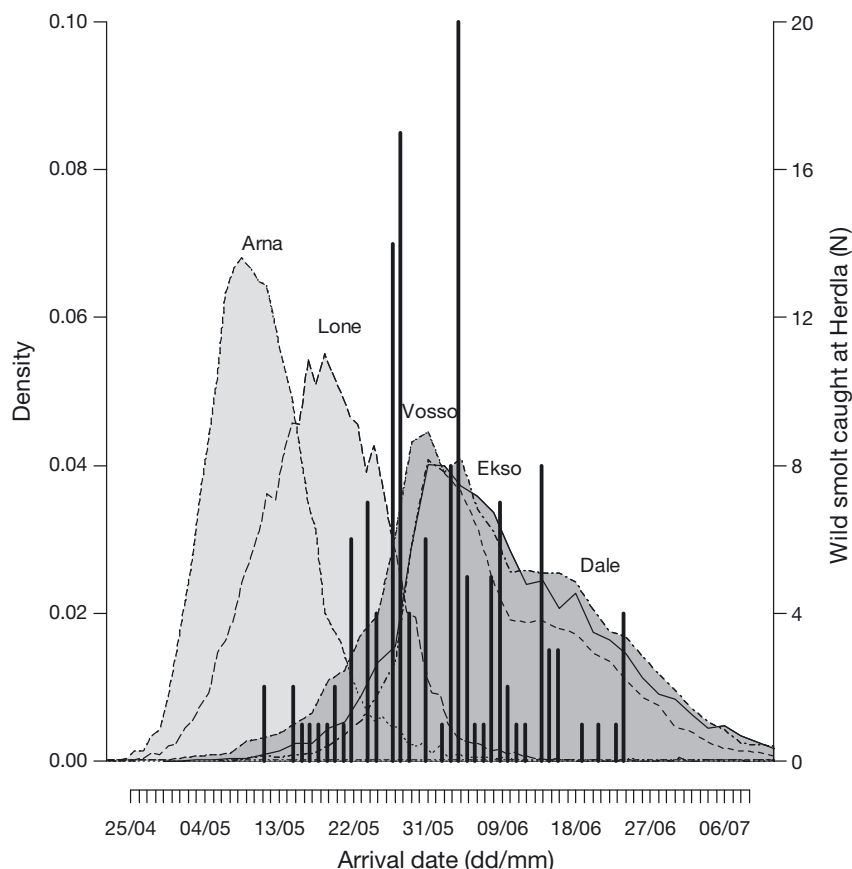
Fig. 5. Modelled density distributions of arrival time of Atlantic salmon *Salmo salar* post-smolts from different rivers at the trap net location (Herdla) in 2012. The integrated value of each river plot adds up to 1. The light grey shaded polygons are the modelled arrival times for smolts from the rivers Arna and Lone, while the dark grey shaded polygons represent the arrival times for smolts from the rivers Vosso, Ekso and Dale. Black bars are numbers of wild post-smolts caught in the trap net from 2012 to 2014

Thorstad et al. 2012b). However, results from the GAM suggested a non-linear relationship with length, and we thus decided to include length as a variable with a quadratic term. In the final model, the quadratic term was not significant, so in theory BL s^{-1} can be calculated and compared directly to other studies.

Water discharge, as measured from the Vosso River, had a significant positive effect, indicating that passive transport may be important in this system. Earlier studies have shown how the migration of post-smolts is a function of both water current and active swimming (Hedger et al. 2008, Martin et al. 2009). Early migration is thought to be more passive, with a small component of active swimming, while migration after exiting the estuary is thought to be more directional and active (Hedger et al. 2008, Martin et al. 2009). Consequently, the role of discharge in the estimation of progression rate in this study is 3-fold: (1) water currents can directly affect progression throughout the fjord system by transporting the post-smolts, (2) a high water discharge can decrease residence time in the estuary leading to a more rapid initiation of more directional and faster migration in the outer fjord, and (3) river discharge may work as an important cue for the initiation of migration. The exact mechanisms governing the response of the post-smolts are not known, but discharge directly (Urke et al. 2013) or other factors that correlate with discharge (such as increasing temperature, Jonsson & Ruud-Hansen 1985) have been suggested. In our study, we were unable to tease apart the role of passive transport and active behaviour, and a comparison between our statistical model and a more mechanistic model of migration, such as an individual-based model (Moriarty et al. 2016), is warranted.

The highest catches of wild salmon in the trap net in the outer region of the fjord were at the end of May and beginning of June. A simulation using estimated progression rate and the time of sea entry from the rivers in the region predicted that the fish that were caught in the trap were mainly fish originating from the rivers in the inner fjord (Vosso, Dale, Ekso). Con-

tern is not supported by our data. Another observation that supports the idea that condition may reflect a tank effect is the finding that origin was a statistically significant predictor of progression rate. The group with the fastest progression rate were the fish kept in large net pens in Evanger. These fish, reared in a more semi-natural environment, were more similar in body shape to wild fish and had less fin erosion (unpublished data). The decrease in progression rate for individuals above a condition factor of ~1 is statistically very uncertain as it heavily relies on a few observations. However, the results may reflect the results of Lans et al. (2011), who demonstrated that salmon given high feed rations and have a high condition (>1) migrate more slowly during riverine migration compared to fish given a low feed ration.

Not surprisingly, progression rate increased with the length of the post-smolts. In other studies, progression rate is often reported in terms of BL s^{-1} (e.g.
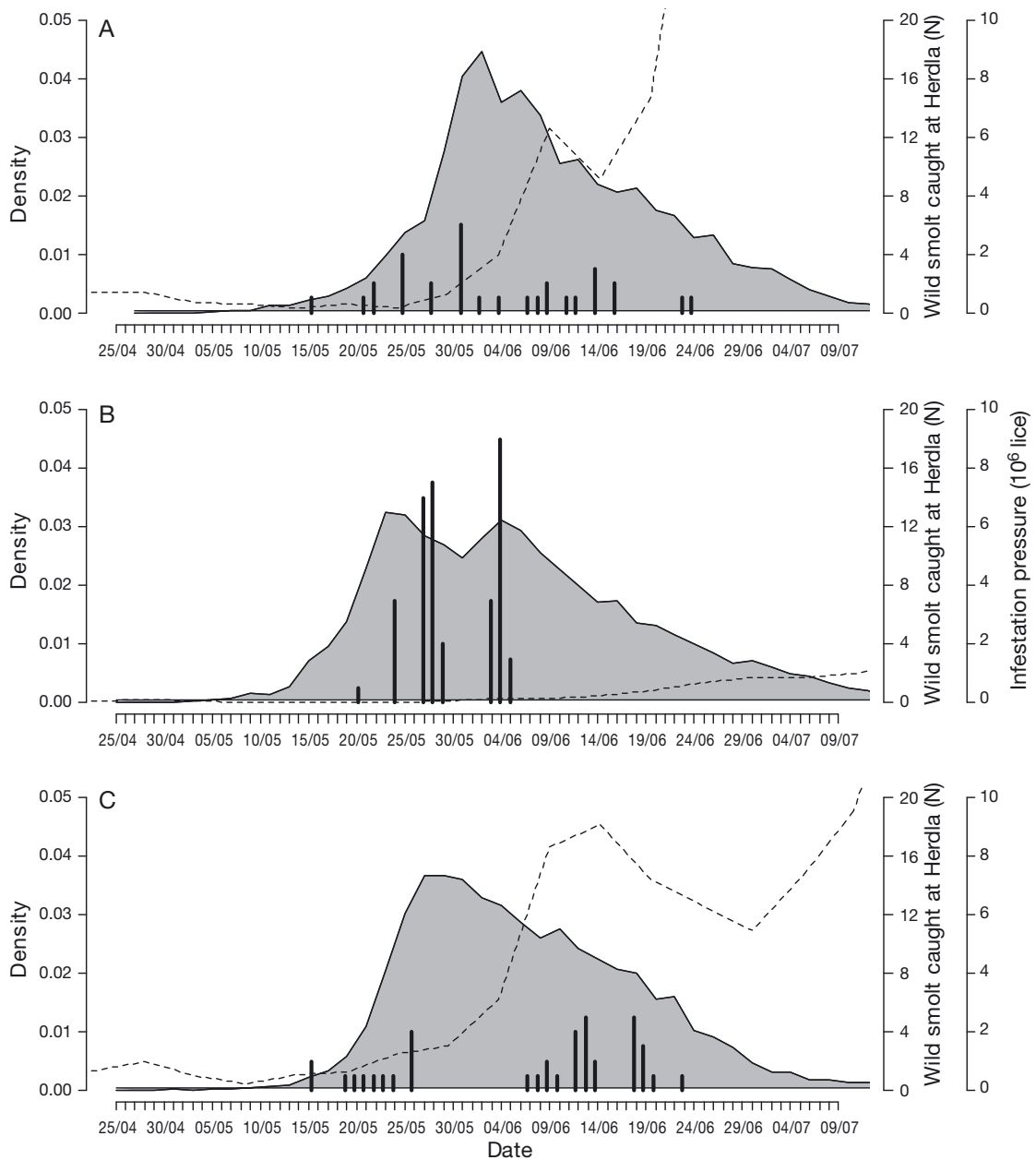
Fig. 6. Modelled density distribution of arrival time of Atlantic salmon *Salmo salar* post-smolts from the Vosso River at the trap net location (Herdla) in (A) 2012, (B) 2013 and (C) 2014. Black bars are the number of wild smolts caught in the respective years. Dashed line is the estimated sea louse *Lepeophtheirus salmonis* infection pressure based on the distance to fish farms as explained by Aldrin et al. (2013). The infestation pressure is calculated for a single point at the location of the trap net. The infestation pressure scale is shown on the right

versely, we did not observe large catches of post-smolts at Herdla in the periods during which we predicted the post-smolts from the Lone and Arna to arrive. This result can partially be explained by that the smolt output from these rivers was smaller and that the deployment of the trap net began in early May and may have missed some of the fish from these rivers. If our estimates are correct, the salmon post-smolts from the rivers with the shortest migra-

tion distance and the earliest migration (Lone and Arna) will arrive 3 to 4 wk earlier in the outer region than the salmon post-smolts from rivers in the inner region and will most likely experience a very different near-shore environment as the season progresses. Because of the vast difference between migration timing between the populations originating in the inner fjord and the outer fjord, post-smolts can be differentially affected by the coordinated

spring delousing in the region. Federal regulations in Norway state that all salmon farmers must conduct early spring delousing between 5 March and 10 April on the west coast of Norway to avoid harmful levels of salmon lice during the smolt run of wild Atlantic salmon (http://lovdata.no/dokument/SF/forskrift/2012-12-05-1140) (Heuch et al. 2005, Serra-Llinares et al. 2014). Within each region, the fish farmers can decide at what time during this period and what type of treatment should be applied during this delousing. Clearly, detailed information about when post-smolts from different rivers arrive in different regions of the fjord is very relevant to optimize this activity.

The sea lice infestation pressure increased in 2012 and 2014 at the start of June. This overlapped with the tail end of the migration of salmon from the rivers from the inner region (illustrated by the Vosso River). These 2 years correspond to when the largest fallowing zones in the outer region are in their second year of production. A pattern of high infestation pressure in areas with high biomass in surrounding fish farms has been recorded in various studies (Penston & Davies 2009, Jansen et al. 2012, Serra-Llinares et al. 2014, 2016) and has also been observed along the west coast of Norway during June according to the national sea lice surveillance programme (Taranger et al. 2015). Based on the current results, lice infestation pressure must be kept low from the end of April to the end of June to encompass all populations in the region when attempting to minimize the risk of spillover effects from fish farms to migrating wild salmon smolts.

The estimated time spent migrating from the river to reach the outer fjord system (Herdla) ranged from 2.1 to 3.3 d for smolts from the Lone River and 5.1 to 8.2 d for the Vosso River. In comparison, the annual variation in the smolt run from the Dale River varied by 25 d. It seems that the time of exit from the rivers and the migration distance are the most important predictors of the time that the fish arrive in the outer fjord in our model. Consequently, among-year and among-river variation in the smolt run is, together with the modelled infestation pressure, the key information for assessing the effect of management actions in fish farms, such as spring delousing, on populations of wild salmon. Hvidsten et al. (1998) found that the seawater entrance of smolts was negatively correlated with latitude in 5 rivers and suggested that population-specific behaviour will result in smolts that, on average, enter the sea when the sea surface temperature exceeds 8°C. Similarly, Otero et al. (2014) looked at data from 67 rivers in the North Atlantic over 5 decades and found that some of the

variation in run timing could be explained by sea surface temperature, freshwater temperature, discharge patterns, a spatial pattern extending across the North Atlantic and a temporal decadal trend. However, a large part of the variation remained unexplained, as the model was allowed to vary according to a random intercept and a random slope for the various sites. This statistical method makes sense when trying to tease out global patterns of climate change and changes in phenology but also makes it difficult to predict local patterns. Given that among-river, regional and annual variation in the marine entrance of smolts is large, any local mitigation plan to alleviate the effects of fish farming on migrating post-smolts should include data from that region's largest rivers.

An important source of error in our speed estimates is that progression rate is mainly based on cultivated smolts that had been released in marine waters (release groups at Stanghelle, Breistein and Herdlefjord, R5–R7). Studies on acoustically tagged fish have demonstrated that fish can move slowly during the estuarine transition and increase their speed when individuals reach areas of higher salinity (Martin et al. 2009). Therefore, overall swim speeds could be overestimated with exclusion of the more passive riverine migration and potential transitional phase once the fish reach areas of increased salinity. Furthermore, simultaneous releases of several thousand smolts, as conducted in the present study, may stimulate school formation and migratory behaviour (Skilbrei et al. 1994) and may be advantageous for survival and increase progression rate. For example, cultivated smolts fitted with acoustic tags released together with several thousand smolts from net pens during spring and summer migrated very rapidly out of a 22 km long fjord (~1.3 BL s^{-1}), with no loss of tagged fish (Skilbrei 2010). However, Thorstad et al. (2012b) reviewed several studies using acoustic transmitters and showed that progression rates during the early marine migration varied between 0.4 and 3.0 BL s^{-1}, on average, across studies, demonstrating that our estimates (mean = 0.6 BL s^{-1}) are most likely not overestimates.

The infestation levels of salmon lice on post-smolts were low on the fish caught in the trap net for both wild and cultivated fish. This finding is most likely because the post-smolts migrated through surface freshwater in the inner fjord and were not exposed to lice before they entered the outer fjord system, where the salinity in the surface water increased. Salmon lice are known to avoid salinity values below 20 ppm (Heuch 1995). Thus, it seems evident that the focus of spring delousing should be on keeping lice

levels low in the outer region of the fjord during the post-smolt migration from May through June. Interestingly, treatment did not seem to have any effect on the prevalence of the chalimus stages of sea lice on post-smolts even though emamectin benzoate has been documented to remove all stages of lice (Stone et al. 2002). However, the treatment may not have been effective for a sufficiently long period at this stage because the lice must start eating, die and fall off (Gjelland et al. 2014).

The trap net was located in 1 out of 3 potential channels where the fish can migrate to reach the open ocean. The location of the trap is such that it is unlikely that fish that migrated other routes would have been caught, and this is further corroborated by the fact that we did not catch any fish from the release in Hjeltefjorden (R8). However, for the estimation of the arrival time at the outer fjord, we used the location at Herdla as the arrival point. This can be problematic when trying to assess the impacts of lice on wild salmon, as we do not know what proportion of the post-smolts migrate the other possible migration channels. The shortest migration path (37 km) compared to the longest migration path (75 km) in the outer fjord system (from the pontoon bridge to the same location outside the archipelago) would lead to a ca. 4 to 5 d difference in exposure to salmon lice in the outer region. This uncertainty must be taken into consideration when adapting a management strategy. However, it must also be pointed out that this variation is dwarfed by the potential variation in the time of the smolt run between years that were observed in Dale.

The recapture rate of fish released in the river or estuary was low compared with fish released in the inner fjord closer to the recapture site. A similar pattern has been observed in the same region in larger datasets (Skilbrei et al. 2013, Vollset et al. 2014). One potential explanation of the low recapture rates is the increased potential for dispersal with longer migrations. For instance, fish released further from the outer estuary may disperse more and, consequently, select different migration paths to a greater extent (e.g. through Radfjorden or Hjeltefjorden). Another possibility is that the groups with the longest migration distance have a higher mortality. Acoustic studies on cultivated smolts from the Vosso River (Vollset et al. 2016) suggest a high estuarine mortality. These studies also demonstrate that smolts that migrate slowly are less likely to survive through the estuary and that cod *Gadus morhua* and trout *Salmo trutta* feed on salmon during the estuarine migration. Similar patterns of high estuarine mortality have been observed elsewhere (Lacroix 2008, Thorstad et al. 2012a) and have also been linked to predation (Hvidsten & Lund 1988, Thorstad et al. 2012a). Consequently, a large part of the mortality of cultivated salmon smolts occurs before the salmon are severely affected by salmon lice.

Concluding remarks

The modelled arrival time and capture of wild post-smolts suggest that post-smolts from the largest river in the inner fjord migrate past the outer fjord systems, the most likely area of salmon lice exposure, from mid-May throughout June. By coupling ecological data on behaviour of smolt with modelled infestation pressure from fish farms, we have demonstrated the importance of detailed local knowledge on migration of wild salmon when designing effective management to alleviate disease transfer to wild fish. This study has demonstrated that local mitigation plans should at the very least include local knowledge on the migration times of wild salmon smolt from the largest rivers in the region.

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