



Fisheries and Oceans  
Canada

Pêches et Océans  
Canada

Ecosystems and  
Oceans Science

Sciences des écosystèmes  
et des océans

## Canadian Science Advisory Secretariat (CSAS)

---

Research Document 2019/074

Newfoundland and Labrador Region

### Evaluation of potential direct genetic effects of the proposed Atlantic salmon (*Salmo salar*) aquaculture site expansion in southern Newfoundland

Ian Bradbury<sup>1</sup>, Steve Duffy<sup>1</sup>, Sarah Lehnert<sup>1</sup>, Ragnar Johannsson<sup>2</sup>, Jon Hlodver Fridriksson<sup>2</sup>, Marco Castellani<sup>3</sup>, Ingrid Burgetz<sup>4</sup>, Emma Sylvester<sup>1</sup>, Amber Messmer<sup>1</sup>, Nicholas Kelly<sup>1</sup>, Ian Fleming<sup>5</sup>

<sup>1</sup>Science Branch  
Fisheries and Oceans Canada  
80 East White Hills Rd.  
St. John's, NL A1C 5X1

<sup>2</sup>Marine and Freshwater Research Institute  
Skulagata 4  
101 Reykjavik, Iceland

<sup>3</sup>Department of Mechanical Engineering  
University of Birmingham  
Birmingham, UK

<sup>4</sup>Fisheries and Oceans Canada  
200 Kent Street  
Ottawa, Ontario K1A 0E6

<sup>5</sup>Department of Ocean Sciences  
Memorial University of Newfoundland  
230 Elizabeth Ave  
St. John's, NL A1C 5S7

---

## Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

### Published by:

Fisheries and Oceans Canada  
Canadian Science Advisory Secretariat  
200 Kent Street  
Ottawa ON K1A 0E6

[http://www.dfo-mpo.gc.ca/csas-sccs/  
csas-sccs@dfo-mpo.gc.ca](http://www.dfo-mpo.gc.ca/csas-sccs/csas-sccs@dfo-mpo.gc.ca)



© His Majesty the King in Right of Canada, as represented by the Minister of the  
Department of Fisheries and Oceans, 2022

ISSN 1919-5044

ISBN 978-0-660-38624-9 N° cat. Fs70-5/2019-074E-PDF

### Correct citation for this publication:

Bradbury, I., Duffy, S., Lehnert, S., Johannsson, R., Hlodver Fridriksson, J., Castellani, M., Burgetz, I., Sylvester, E., Messmer, A., Kelly, N., and Fleming, I. 2022. Evaluation of potential direct genetic effects of the proposed Atlantic salmon (*Salmo salar*) aquaculture site expansion in southern Newfoundland. DFO Can. Sci. Advis. Sec. Res. Doc. 2019/074. iv + 21 p.

### *Aussi disponible en français :*

Bradbury, I., Duffy, S., Lehnert, S., Johannsson, R., Hlodver Fridriksson, J., Castellani, M., Burgetz, I., Sylvester, E., Messmer, A., Kelly, N., et Fleming, I. 2022. Évaluation des possibles effets génétiques directs du projet de création de nouveaux sites d'aquaculture de saumon de l'Atlantique (*Salmo salar*) dans le sud de Terre-Neuve-et-Labrador. Secr. can. de consult. sci. du MPO, Doc. de rech. 2019/074. iv + 24 p.

---

---

## TABLE OF CONTENTS

ABSTRACT.....	IV
INTRODUCTION .....	1
METHODS.....	1
PROPAGULE PRESSURE .....	2
INDIVIDUAL-BASED MODELING OF DIRECT GENETIC IMPACTS.....	2
DISPERSAL MODELING OF ESCAPEES .....	3
Distribution of Rivers and Wild Population Size .....	3
Production Data and Proportion of Escapees .....	4
RESULTS .....	6
PROPAGULE PRESSURE .....	6
INDIVIDUAL-BASED MODEL PREDICTIONS .....	6
DISPERSAL MODELING OF ESCAPEES .....	10
SENSITIVITY ANALYSIS.....	12
DISCUSSION.....	15
INDIVIDUAL-BASED MODELING.....	15
ESCAPEE DISPERSAL PREDICTIONS .....	16
SUMMARY .....	17
ACKNOWLEDGEMENTS .....	18
REFERENCES CITED.....	19

---

## ABSTRACT

In 2019 a proponent applied for aquaculture licenses at various sites located on the south coast of Newfoundland and the request was referred to DFO for siting advice including examination of the potential for genetic interactions with wild Atlantic salmon. Here we examine the potential genetic interactions resulting from the proposed finfish expansion involving thirteen sites (1M individuals/site) in southern Newfoundland using a combination of empirical data, and both individual-based and dispersal modeling. We use an eco-genetic individual-based Atlantic salmon model (IBSEM) parameterized for southern Newfoundland populations, with regional environmental data and field-based estimates of aquaculture parr survival, to explore how the proportion of escapees relative to the size of wild populations influences genetic and demographic change in the wild. Our simulations suggest that both demographic decline and genetic change are predicted when the proportion of escapees relative to wild population size exceeds 10% annually. The occurrence of escapees in southern Newfoundland rivers (estimated population size ~22,000 individuals), both at present and under the proposed expansion scenario were predicted using river and site locations, simple models of dispersal for early and late escapees, and the best available data from Canada and Europe. Model predictions of escapee dispersal suggest that under the present regime, rivers characterized by the largest proportion of escapees relative to wild population size are located in the head of Fortune Bay and Bay d'Espoir (19 rivers total > 10% escapees, max 15.6%) consistent with recent empirical evidence of escapees and hybridization. Under the proposed expansion, the number of escapees in southern Newfoundland rivers is predicted to increase by 49% (1.5X) and the rivers characterized by the greatest proportion of escapees relative to wild population size are predicted to occur in the Bay d'Espoir area (20 rivers total >10% escapees, max 24%).

---

## INTRODUCTION

Genetic interactions (i.e. hybridization) between wild and escaped farmed Atlantic salmon, *Salmo salar*, have been documented across the natural range of the species where the two co-occur (Diserud et al. 2019, Glover et al. 2017, Keyser et al. 2018), and at distances of up to 200 km from the nearest aquaculture site; although distant occurrences at sea have also been reported (Hansen and Jacobsen 2003, Hansen et al. 1993, Hansen et al. 1997, Jensen et al. 2013). As a consequence, hybridization between wild and domestic salmon can be spatially extensive (Glover et al. 2013, Glover et al. 2017, Heino et al. 2015, Sylvester et al. 2018, Wringe et al. 2018) and wild population decline and genetic change are the likely outcomes (Castellani et al. 2015, 2018, Hindar et al. 2006, Sylvester et al. 2019). Recent genetic studies have documented widespread hybridization between wild salmon and aquaculture escapees both in southern Newfoundland (Sylvester et al. 2018, Sylvester et al. 2019, Wringe et al. 2018) and the Maritimes (DFO 2018a, Lehnert et al. 2019, O'Reilly et al. 2006). Across the North Atlantic, the magnitude of genetic impacts due to escaped farmed salmon on wild populations has been correlated with the biomass of farmed salmon in nearby cages and the size of wild populations (Glover et al. 2013, Glover et al. 2017, Keyser et al. 2018, Sylvester et al. 2018, Wringe et al. 2018).

In 2019 a proponent applied for aquaculture licenses at various sites located on the south coast of Newfoundland and the request was referred to DFO for siting advice. In conjunction with the proposed expansion, the potential exists for increased genetic interactions between escaped farmed and wild Atlantic salmon in southern Newfoundland. Our goal here was to apply model-based approaches in conjunction with recent empirical data on genetic interactions to examine the potential for genetic and demographic change as a result of this proposed expansion in southern Newfoundland. Specifically, the population impacts (i.e., demographic and genetic) of farm escapees were examined using an individual-based modelling approach, which explored how the proportion of escapees present in wild rivers influences genetic and demographic change. This modeling exercise utilized a recently developed Atlantic salmon individual-based eco-genetic model and extended recent work completed both in Norway (Castellani et al. 2015, 2018) and Canada (Sylvester et al. 2019). Secondly, we modelled the distribution of escapees in the wild under the current and proposed production regime using a spatial model of dispersal and survival recently implemented in Iceland (Jóhannsson et al. 2017). In both the individual-based and spatial modelling exercises, the data used represented the best currently available, and we identified sources of uncertainty when present. Salmon populations in southern Newfoundland have been classified as threatened by the Committee on The Status of Endangered Wildlife In Canada (COSEWIC 2011) with record lows of abundance reported in recent years (DFO 2018b, 2019). Accordingly, this work directly supports Fisheries and Oceans Canada's obligations under the Fisheries Act and the Species at Risk Act with respect to the proposed expansion in southern Newfoundland.

## METHODS

Model-based approaches to explore escape events from net-pens and their impacts on wild populations allow the opportunity to evaluate escape scenarios and management decisions and are currently under development both for salmonids as well as marine species (e.g., Baskett et al. 2013). In Atlantic salmon, several models of genetic and demographic interactions among wild and farm escapees have been developed and/or applied including OMEGA (International 2012), IBSEM (Castellani et al. 2015), and that of Hindar et al. (2006). Of these models, IBSEM has been most extensively used to date and is an individual-based eco-genetic Atlantic salmon

---

life history model. IBSEM has been used to understand how the proportion of escapees scales with demographic and genetic impacts in Norway (Castellani et al. 2015, 2018), how natural straying may mitigate these impacts (Castellani et al. 2018), and how varying the strength of selection against aquaculture offspring in the wild influences population outcomes (Sylvester et al. 2019). Despite these recent advances in modeling, empirical estimates of many key parameters are still required to inform modeling efforts. In particular, the strength of selection against aquaculture offspring in the wild appears to be a key parameter in predicting population level impacts (Sylvester et al. 2019). Overall, these model-based explorations of potential impact provide an unprecedented opportunity to inform management and policy decisions related to genetic impacts resulting from escaped farmed Atlantic salmon.

## PROPAGULE PRESSURE

To first explore the potential changes in genetic interactions between wild and domestic salmon associated with the proposed expansion we calculated propagule pressure following Keyser et al. (2018) for both the existing and proposed production regimes. Propagule pressure was calculated for each river using maximum stocking allowable (see below), divided by the distance to that site, and summed across all sites. That is:

$$(1) \text{ Propagule pressure for a given river } (R) = \sum_{i,y=1}^S \frac{F_{i,y}}{LCD(S_{i,y} \text{ to } R)}$$

where  $S_{i,y}$  represents an aquaculture site in a given year ( $y$ ),  $R$  represents a given river,  $F_{i,y}$  is the number of fish at site  $S_i$  and  $LCD$  represents the least-cost distance function. This metric has been shown to correlate with both the occurrence of escapees and genetic interactions between wild and farm escapees in Atlantic Canada (Keyser et al. 2018).

## INDIVIDUAL-BASED MODELING OF DIRECT GENETIC IMPACTS

To explore the population effects of various levels of invasion in southern Newfoundland we used an individual-based salmon eco-genetic model (IBSEM) developed by Castellani et al. (2018). Detailed modeling methods are described in Castellani et al. (2015, 2018) and Sylvester et al. (2019). IBSEM models wild population changes in abundance, genotype, and individual size in response to the introduction of domesticated individuals. The model considers the duration of invasion, wild population size, number of invaders, environmental conditions, individual size and genotypic and phenotypic differences between individuals of farm and wild origin. Growth and survival are simulated by stochastic processes that are influenced by genotype, fish size and age, temperature and population density at three life stages: embryo, juvenile and adult. Simulated loci are unlinked with possible gamete recombination and random inheritance, and a range of influences on phenotype and therefore suitability to the environment. The sum of the genetic effects is linearly related to phenotype, such that genotypic values approaching 1 are associated with growth and survival rates typical of wild salmon, and values approaching zero are associated with rates observed in farm escapees. Reproductive success of farm escapees is reduced relative to the wild, and the success of both is sex-specific, with female fertility dependent upon weight, and male reproductive success dependent upon length, with the possibility of precocial sexual maturation. A full list of parameters representative of Newfoundland salmon and environmental conditions in the region can be found in Sylvester et al. (2019).

Simulations build on those of Sylvester et al. (2019) that utilized estimates of feral fry and parr survival calculated from genetic analysis of individual cohorts following an escape event in southern Newfoundland in 2013 (Sylvester et al. 2019, Wringe et al. 2018). Estimates of survival

---

used here from southern Newfoundland populations are lower than most previous estimates of relative survival of feral parr (Fleming et al. 2000, McGinnity et al. 2003, McGinnity et al. 1997, Skaala et al. 2019) and increasing survival in freshwater has been shown to increase both genetic and demographic impacts (Sylvester et al. 2019). We examined the population consequences of invasion over a 50-year period in a wild population of 500 individuals with the proportion of invaders varying from 0-100% that of the wild population annually. We compared the change in adult population abundance (both wild and escaped farmed fish) and sum of the genetic effects across the adult set of genes included in the simulation to observe changes in the genetic fitness of the population. All models were run for 100 years prior to invasion to ensure model stability and for 100 years after the 50-year invasion period ceased. All other parameters remained consistent across model runs.

## **DISPERSAL MODELING OF ESCAPEES**

To model the distribution of farm escaped salmon and to allow scenario testing we have applied a simple dispersal model that incorporates best information on local levels of production, rates of escapees, survival, behavior, environment, and size of wild populations. Details on the dispersal model can be found in Jóhannsson et al. (2017) but a summary is included below. Three main categories of data were considered in the model. First, the production data was considered and included locations, biomass, size and age, and average proportion of escapees per unit harvest. Second, geographic factors considered include distribution of rivers along the coast, and any directionality of local currents. Finally, the model included any existing life history data and behavioral differences between wild and farmed salmon. Two independent models were used, one for early escapees (i.e., smolts), and one for late escapees (i.e., adults) to allow for differences in behavior and survival among life stages. The model was implemented in R with a web-based interface.

### **Distribution of Rivers and Wild Population Size**

For this analysis we have focused on 76 rivers (scheduled and non-scheduled rivers) known to have wild Atlantic salmon populations distributed along the south coast of Newfoundland spanning the region from Bear Cove Brook to Renews River (Figure 1). This region has been demonstrated previously to encompass genetic impacts following escape events in the region (Keyser et al. 2018, Wringe et al. 2018). Information is generally lacking on the size of wild populations in the majority of these rivers (DFO 2013, 2018b, Porter et al. 1974), and as such estimates of population size were derived using an established relationship between river size and wild population size for Newfoundland following Wringe et al. (2018). River size was calculated as axial length to complete obstruction using data from Porter et al. (1974) and the relationship was developed using abundance data (i.e., counting fence data) from 2009-2014 where available, or another six representative years for rivers lacking contemporary data. However, as this relationship is based on habitat, these estimates may not reflect declines experienced over recent decades (COSEWIC 2011, DFO 2018b) and therefore may over-estimate the current population size and underestimate the proportion of escapees. In the event of any error in our initial parameters, the estimates of escapees would be more conservative than would likely be the case in the field. Nonetheless they represent the only available estimates of stock size for most of these systems.

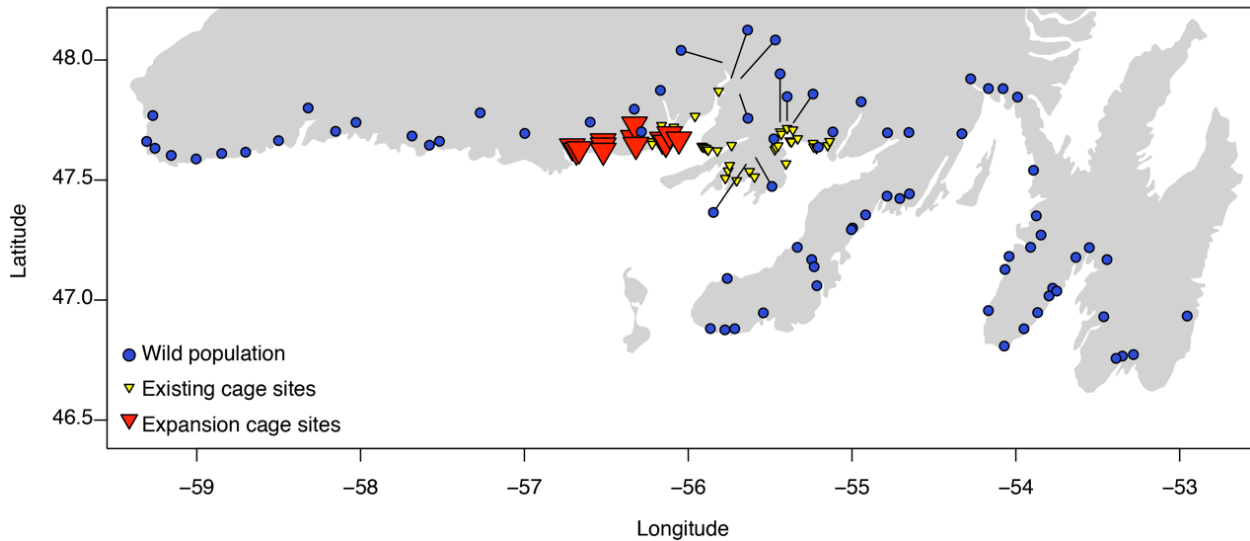


Figure 1. Map of southern Newfoundland rivers known to contain Atlantic salmon (blue circles), existing aquaculture sites (yellow triangles), and proposed expansion sites (red triangles).

## Production Data and Proportion of Escapees

Reported stocking, harvest information, and licensed maximum stocking allowable were obtained for all existing aquaculture locations in southern Newfoundland 2013-2017 from Aquaculture Management of Fisheries and Oceans (C. Hendry, Aquaculture Management, Fisheries and Oceans Canada, *pers. comm.*). For consistency among existing and proposed sites, we used the maximum licensed stocking numbers. Numbers of fish were converted to harvest biomass using an individual fish weight of 3 kg, reducing by 25% to account for fallow periods and the production/fallow cycle, and finally multiplying by 0.65, a ratio estimated from a comparison of stocking and harvest that excludes sites with catastrophic losses. The expected number of escapees per unit production is required to estimate escapees in the environment. In the absence of an extensive escapee monitoring program in southern Newfoundland, we rely on Norwegian statistics of annual production and escape events for the period 2009-2016 to estimate the expected number of escapees per ton of fish production (Norway 2019). However these estimates of escapees have been shown to be an underestimate (Glover et al. 2017, Skilbrei et al. 2015), therefore they were adjusted following Skilbrei et al. (2015) as per Jóhannsson et al. (2017). As a result, the estimate is ~0.8 fish per ton of production but given uncertainty in this value for Newfoundland, extensive sensitivity analyses were conducted for exploration of other values.

The proportion of escapees that enter estuaries and could ascend rivers was estimated to be 17% based on Hamoutene et al. (2018) with correction for estuaries without receivers. This calculation assumes escapees detected in estuaries will enter adjacent rivers, and although this number is actually unknown, escapees have been detected in rivers throughout the region (Hamoutene et al. 2018, Keyser et al. 2018). Nonetheless, this represents the best information at present. The proportion of escapees that are reproductively mature during freshwater entry has been estimated for the Garnish system as 63% calculated using the counting fence data for the years 2015-2017. This is however based only on individuals phenotypically identified as escapees (i.e., late escapees) at the counting fence, and as early escapees could be undetected this is likely an underestimate. Overall, based on the best available data, we estimate that the proportion of escapees that enter freshwater and mature is ~11%. This is



---

comparable to a value of 15% currently in use in similar modeling exercises in Iceland (Jóhannsson et al. 2017).

Two models of dispersal were calculated, one for early (i.e., smolts) and one for late escapees (i.e., adults) and we assumed an equal split between the two in absence of data on early escapees. The number of late escapees from a single site that arrive at rivers (EG) was calculated based on Equation 2, where P is aquaculture production, SG is the escapees per ton of production, and M is the likelihood that an escapee becomes sexually mature and enters freshwater.  $\frac{R}{T}$  represents the proportion of total time in the cages (T) that an individual could escape, survive, and sexually mature. We estimated this ratio at 0.66 as it is unlikely an escapee would survive beyond this time (i.e. 1 year) in the wild (Hamoutene et al. 2018, Hansen and Youngson 2010).

$$(2) \quad E_G = PS_G \frac{R}{T} M$$

The total number of early escapees from a single site that make it to local rivers was calculated based on Equation 3, where P is the production, S<sub>s</sub> is the escapees per ton of production, L represents the proportion of smolts that survive at sea in the wild, and  $\frac{L_f}{L_w}$  is the ratio of farmed to wild smolt survival.

$$(3) \quad E_s = PS_s L \left( \frac{L_f}{L_w} \right)$$

At present the marine survival (smolt to adult) of Atlantic salmon in monitored rivers of Newfoundland varies from ~4 to 8% (DFO 2018b), therefore we set a value of 6% for this exercise. The relative survival of farm to wild smolts was set at 0.37 following Hindar et al. (2006).

To simulate the dispersal of escapees from cage sites to rivers we use a Weibull distribution shaped by two parameters, representing both the width and the shape or skewness of the distribution. To estimate the width of the distribution or the distance escapees may disperse along the coast, we used a combination of experimental release data (Hamoutene et al. 2018), escapee recaptures (Keyser et al. 2018), and genetic estimates of hybridization (Sylvester et al. 2018, Wringe et al. 2018). Similarly, Morris et al. (2008) reported escaped farmed salmon occurring in 56 of 62 Maritime rivers within 300 km of aquaculture operations. We set a maximum distance at 200 km which is smaller than used elsewhere (i.e., Jóhannsson et al. 2017) but still larger than both tagging and genetic indications of escapee dispersal in southern Newfoundland. Modifying the shape or skewness of the distribution can allow projections to account for the influence of ocean currents which can influence distribution patterns (Hansen and Youngson 2010). Ocean currents in the region are largely wind driven, and predominately from the northeast in winter and spring and southwest in summer and fall. Recent tagging work (Hamoutene et al. 2018) suggests no obvious east or west bias in movements along the coast. Therefore, we used a symmetrical distribution for the dispersal of both early and late escapees.

Sensitivity analyses were conducted by varying several parameters and examining the resultant number and distribution of escapees in rivers under the proposed expansion scenario. First the number of escapees per unit harvest was varied from 0.2, 0.4, 0.8, to 1.2 fish per ton. Second, we varied the proportion of early to late escapees from all early, equal portions of both, and all late escapees. Finally, we varied the proportion of late escapees that mature and enter rivers from 0.06, 0.11 and 0.16.

---

## RESULTS

### PROPAGULE PRESSURE

Our calculation of propagule pressure under the current magnitude and distribution of production indicates that the areas of highest expected propagule pressure are located in the head of Fortune Bay (Figure 2A). Under the proposed expansion scenario (Figure 1), this area is predicted to expand to include the Bay d'Espoir area as well (Figure 2B). Here the propagule pressure is expected to increase by at least 2X in seven rivers including Conne River, Little River, and Southeast Brook (Figure 2C).

### INDIVIDUAL-BASED MODEL PREDICTIONS

Individual-based model simulations allowed trends in population abundance and allele frequency to be examined in response to varying levels of invasion by escaped farmed salmon. The annual levels of invasion were varied from 0 to 100% of the size of the wild population. All runs stabilized near a population size of 500 individuals pre-invasion and all levels of invasion ranging from 20% to 100% displayed evidence of demographic decline (Figure 3) and genetic change (Figure 4) in the wild population. Overall, the magnitude of demographic decline and genetic change increased with increasing proportions of farm escapees present (Figure 5). The magnitude of demographic decline observed ranged from ~0% under no invasion to ~25% decline under 100% annual invasion (Figure 3, 5). The amount of genetic change predicted varied from <1% to ~3% (Figure 4, 5). The time to recover both population size and allele frequency once invasion has ceased increased with level of invasion and varied from a few years to 50+ years (Figure 3, 4). Overall, the simulations suggest that both demographic decline and genetic change are predicted when the proportion of escapees relative to wild population size exceeds 10% annually (Figure 5). As such, a threshold of 10% escapees relative to the wild population of a given river was used as a threshold for subsequent simulations, see below.

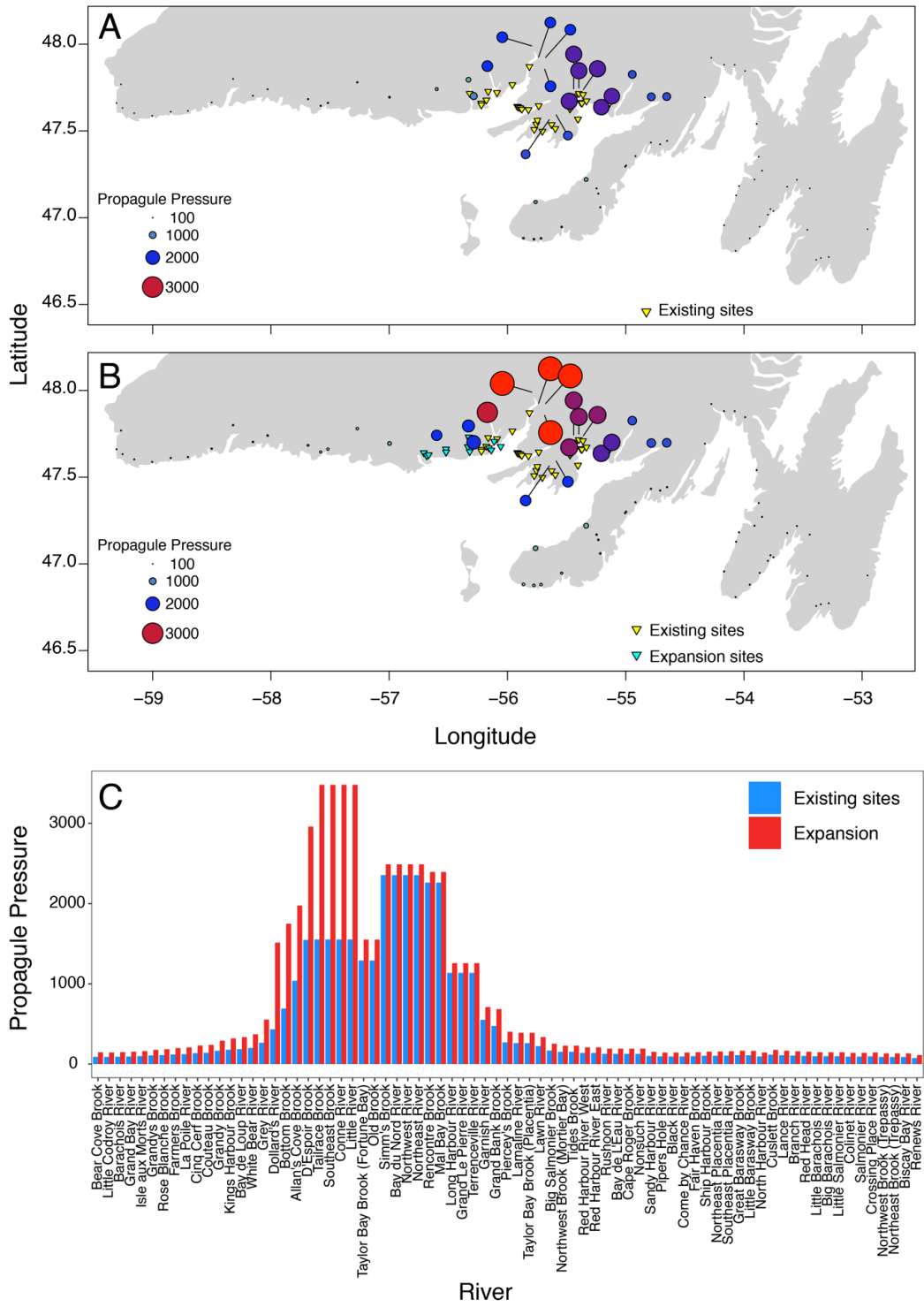


Figure 2. Propagule pressure calculated following Keyser et al. (2018) for southern Newfoundland under the existing production regime (A, C) and the proposed expansion scenario (B, C). See methods for details.

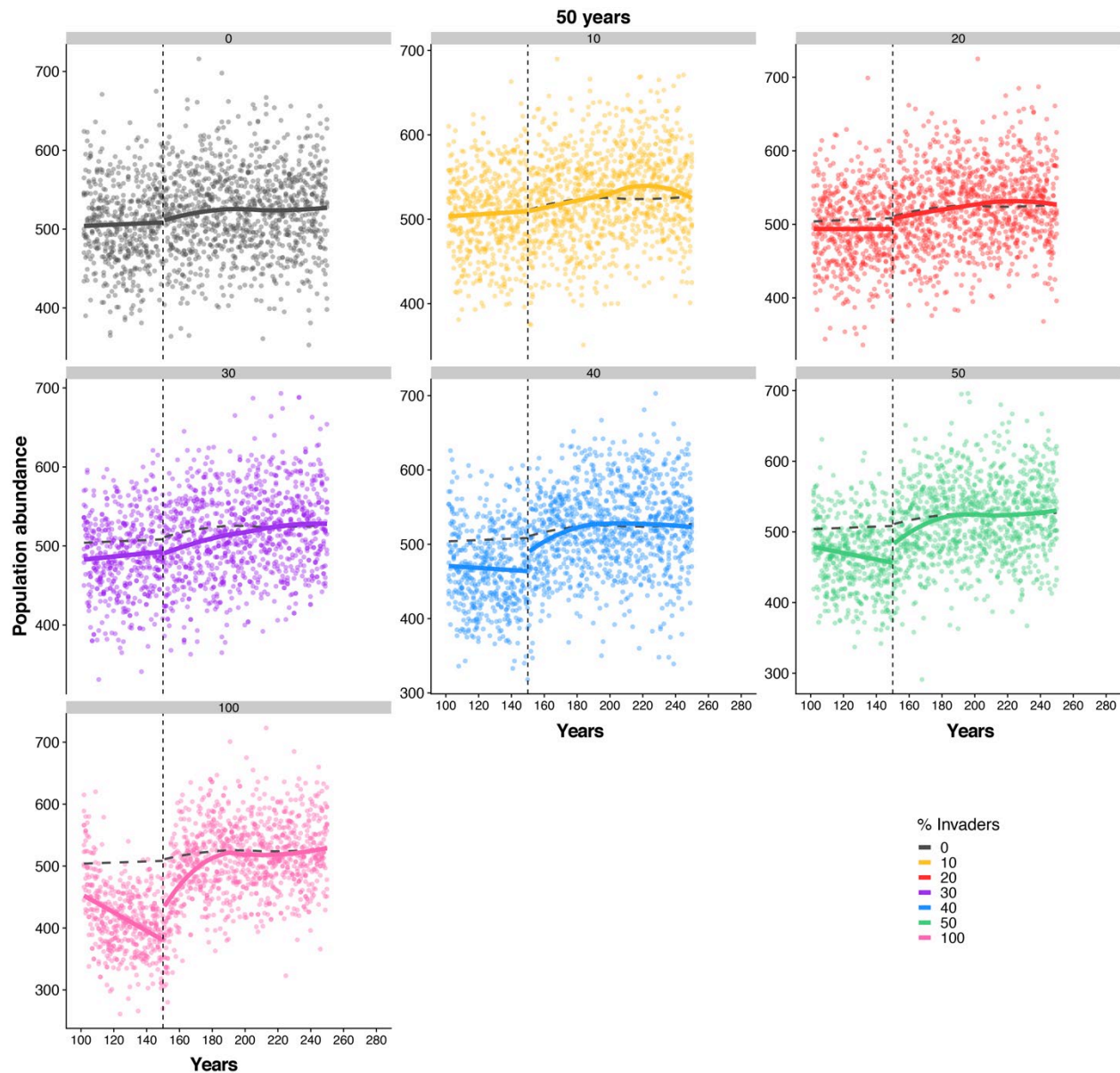


Figure 3. Demographic changes over time (years) during and following 50 years of invasion by farm escaped salmon. Levels of annual invasion vary from 0% to 100% of the wild population. All simulations were conducted using IBSEM, see methods and Castellani et al. (2015, 2018), Sylvester et al. (2019) for details. Horizontal dashed line represents the mean of the zero-invasion simulation, vertical dashed line represents the end of simulated invasion of escaped farmed salmon.

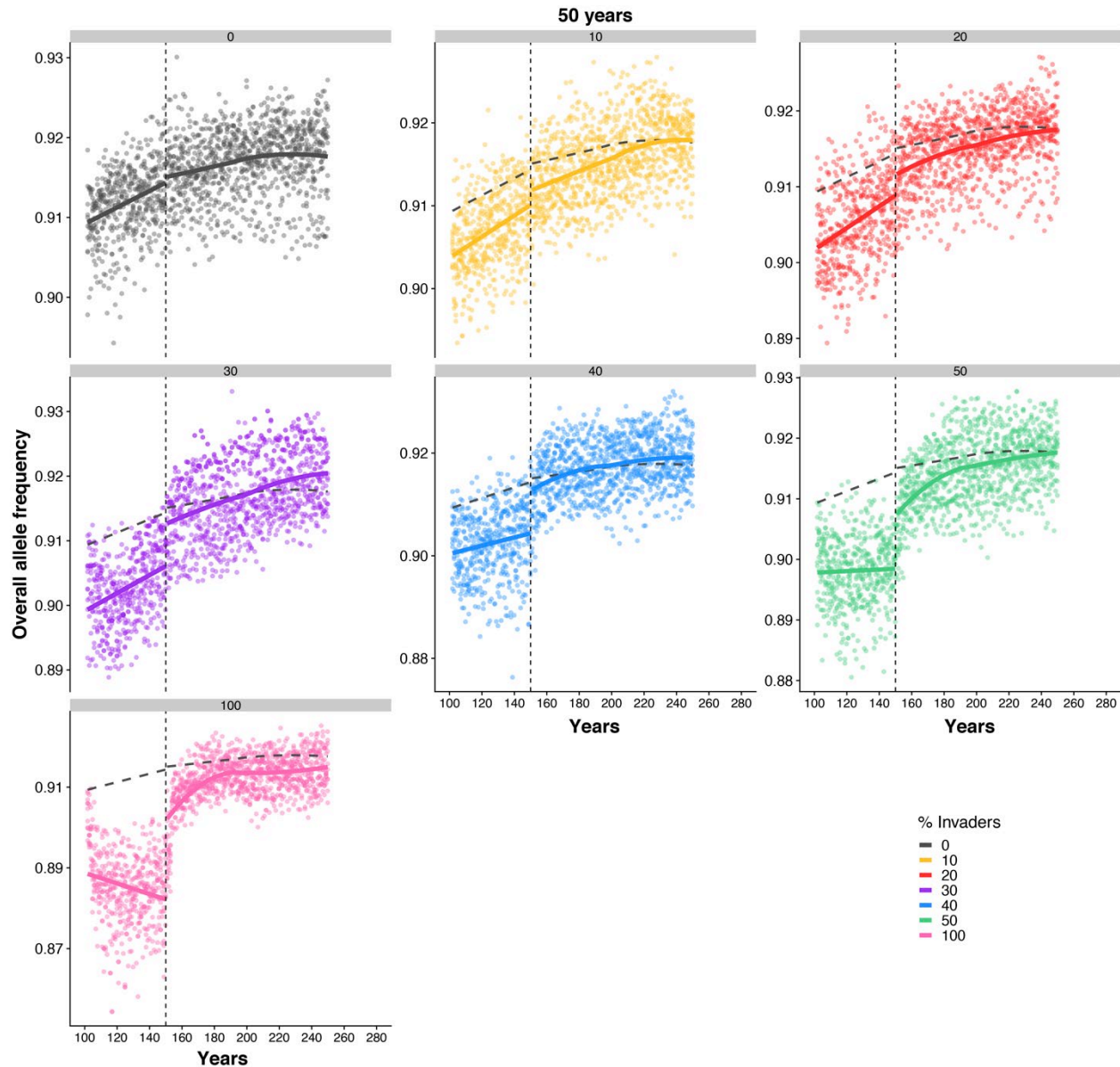


Figure 4. Changes in overall allele frequency over time (years) during and following 50 years of invasion by escaped farmed salmon. Levels of annual invasion vary from 0% to 100% of the wild population. Wild populations characterized by an allele frequency of 1 and aquaculture populations an allele frequency of 0. All simulations were conducted using IBSEM, see methods and Castellani et al. (2015, 2018), Sylvester et al. (2019) for details. Horizontal dashed line represents the mean of the zero-invasion simulation, vertical dashed line represents the end of simulated invasion of escaped farmed salmon.

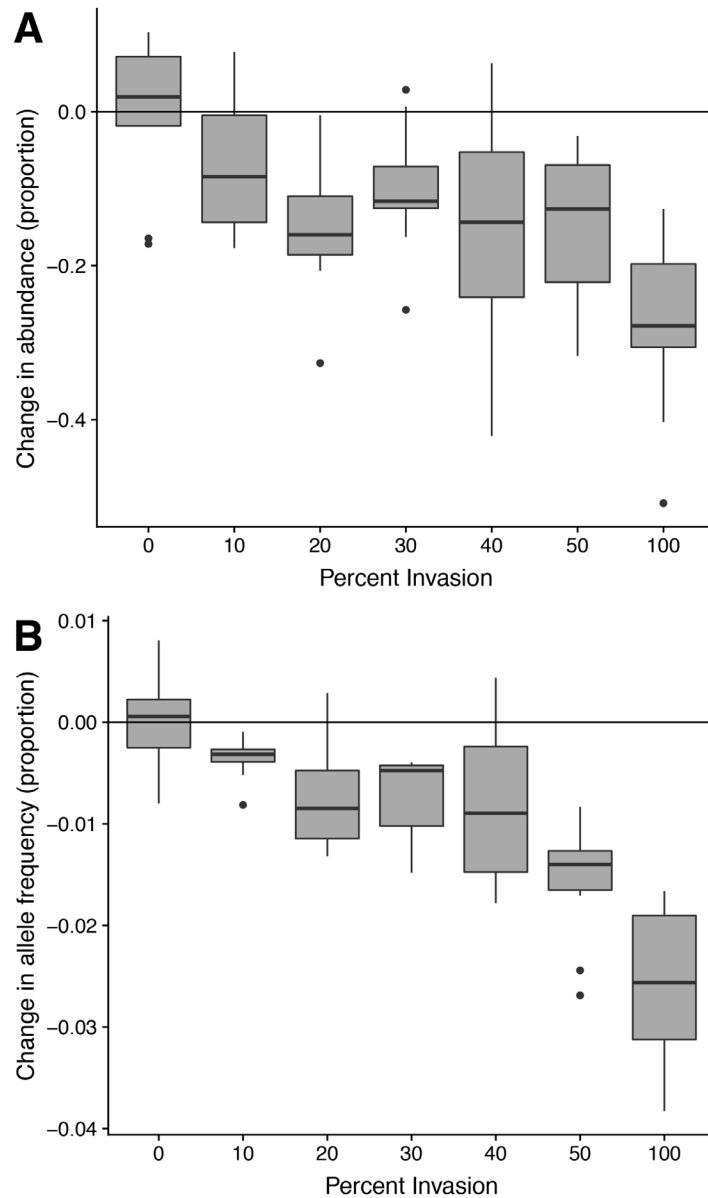


Figure 5. Magnitude of demographic decline (A) and genetic change (B) observed over 50 years of invasion by escaped farmed salmon into a wild population. Annual levels of invasion vary from 0-100% that of the wild population. Changes were calculated by comparing each scenario (and iteration) against the mean of the zero-invasion scenario at the end of the invasion period.

## DISPERSAL MODELING OF ESCAPEES

Under the current level and distribution of production, the total number of escapees was predicted to reach rivers is estimated at 1278 escapees annually. Under this existing regime, 19 rivers would meet or exceed the 10% threshold with a maximum value of 15.6% (Figure 6). Escapees are predicted to occur in all but eleven rivers in Fortune Bay and west with numbers ranging from 1 to 150 escapees per river. Rivers characterized by the largest proportion of escapees are concentrated in Fortune Bay including Taylor Bay Brook, Old Bay Brook, Simms Brook, Bay du Nord River, Northwest and Northeast Rivers, as well as a few Bay d'Espoir rivers (Figure 6). Model predictions for the Garnish River suggested 13 escapees annually, which is

comparable to the average 6 escapees detected at the counting fence during the summer months annually (June to Sept).

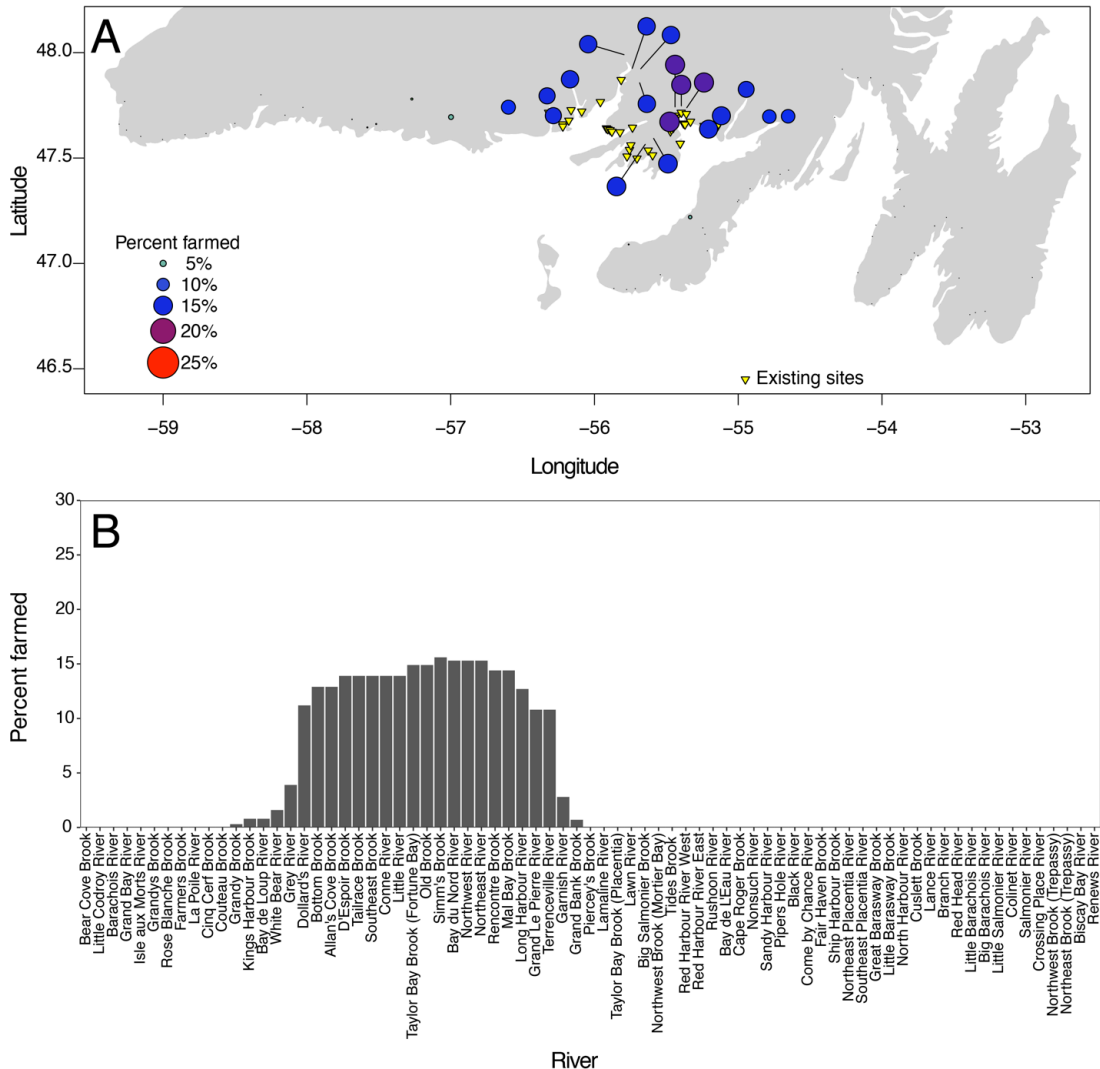


Figure 6. Predicted spatial distribution (A) and relative proportion of escaped farmed salmon to wild salmon (B) in rivers of southern Newfoundland under the present production regime. See methods for details regarding simulations.

Under the proposed expansion scenario, the total number of escapees predicted to reach rivers was estimated at 1915 annually which represented an increase of 1.5X of the number of escapees predicted in rivers along the coast (Figure 7). Twenty rivers were predicted to meet or exceed the 10% threshold with eight rivers exceeding 20% escapees and a maximum value of 24% (Figure 7). Escapees were predicted to occur in all but eight rivers in Fortune Bay and west with numbers ranging from 1 to 275 escapees per river. Under the proposed expansion the rivers characterized by the largest number of escapees shifts to the head of Bay d’Espoir (i.e., Conne River, Little River, Southwest Brook, Tailrace River) and to the west (i.e., Bottom Brook, Dollards River, and Allans Cove Brook) (Figure 7).

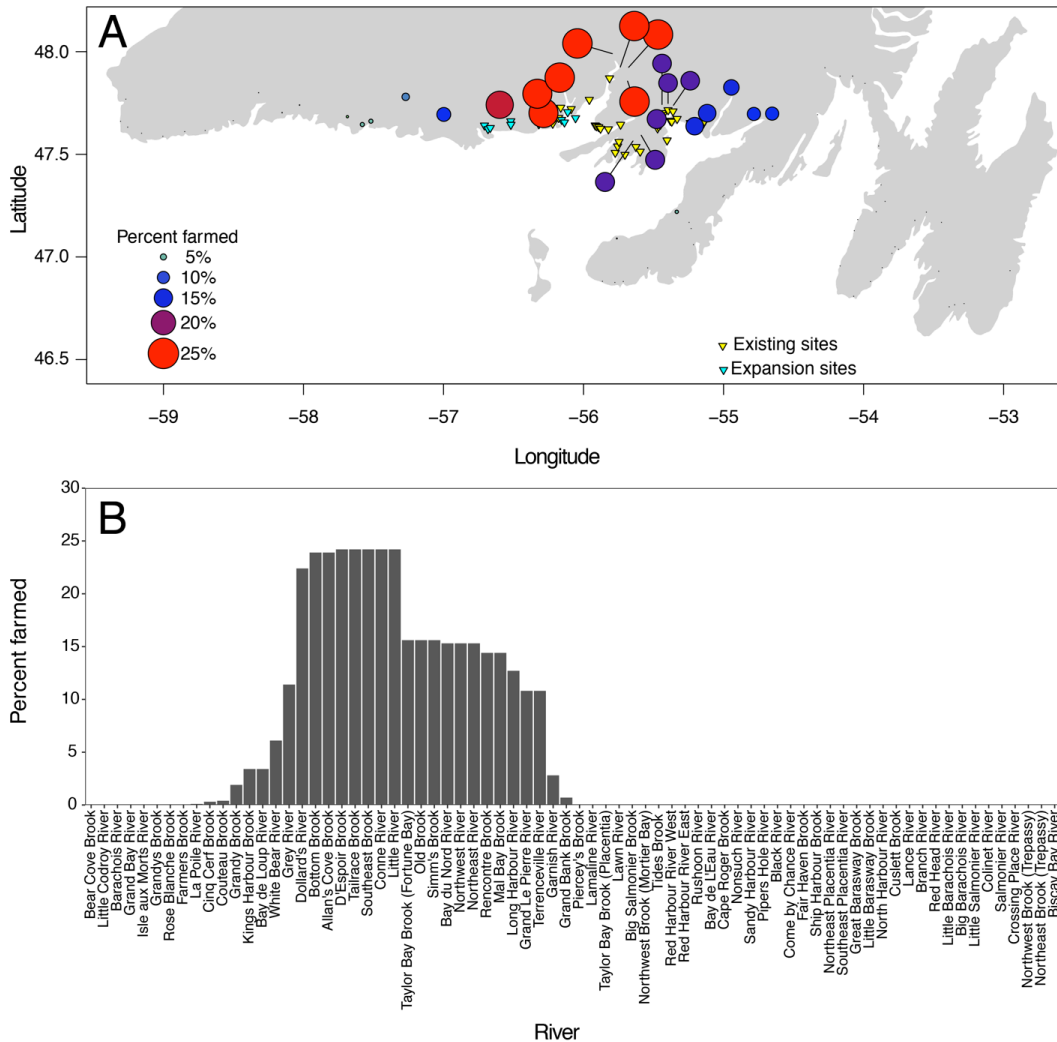


Figure 7. Predicted spatial distribution (A) and relative proportion of escaped farmed salmon to wild salmon (B) in rivers of southern Newfoundland under the proposed expansion scenario. See methods for details regarding simulations.

## SENSITIVITY ANALYSIS

We explored the sensitivity of the model predictions to changes in several key parameters. Research using simulated escape events in Norway suggests the actual proportion of escapees per ton is likely between 0.4 and 0.8 (Skilbrei et al. 2015). The number of escapees per ton of harvest was varied from 0.2 to 1.2. The total number of escapees doubled with each doubling of the number of escapees per harvest (Figure 8A).

We also examined how varying the proportion of late or early escapees per ton influenced model predictions (Figure 8B). Interestingly, we observed a 2.75X increase in the proportion of escapees predicted to occur when only late escapees are considered versus early escapees with estimates ranging from 2860 (late only) to 970 escapees (early only). For the late only escape scenario, escapees were also distributed across more locations with higher proportions of escapees compared with only early escapees (Figure 8B).



Varying the proportion of late escapees that mature and enter rivers had a significant influence on the number of escapees in rivers with estimates ranging from 1265 to 2565 escapees (Figure 8C). However even under the lowest probability examined (e.g., 0.06), 14 rivers were still predicted to exceed 10% escapees under the proposed expansion scenario (Figure 8C).

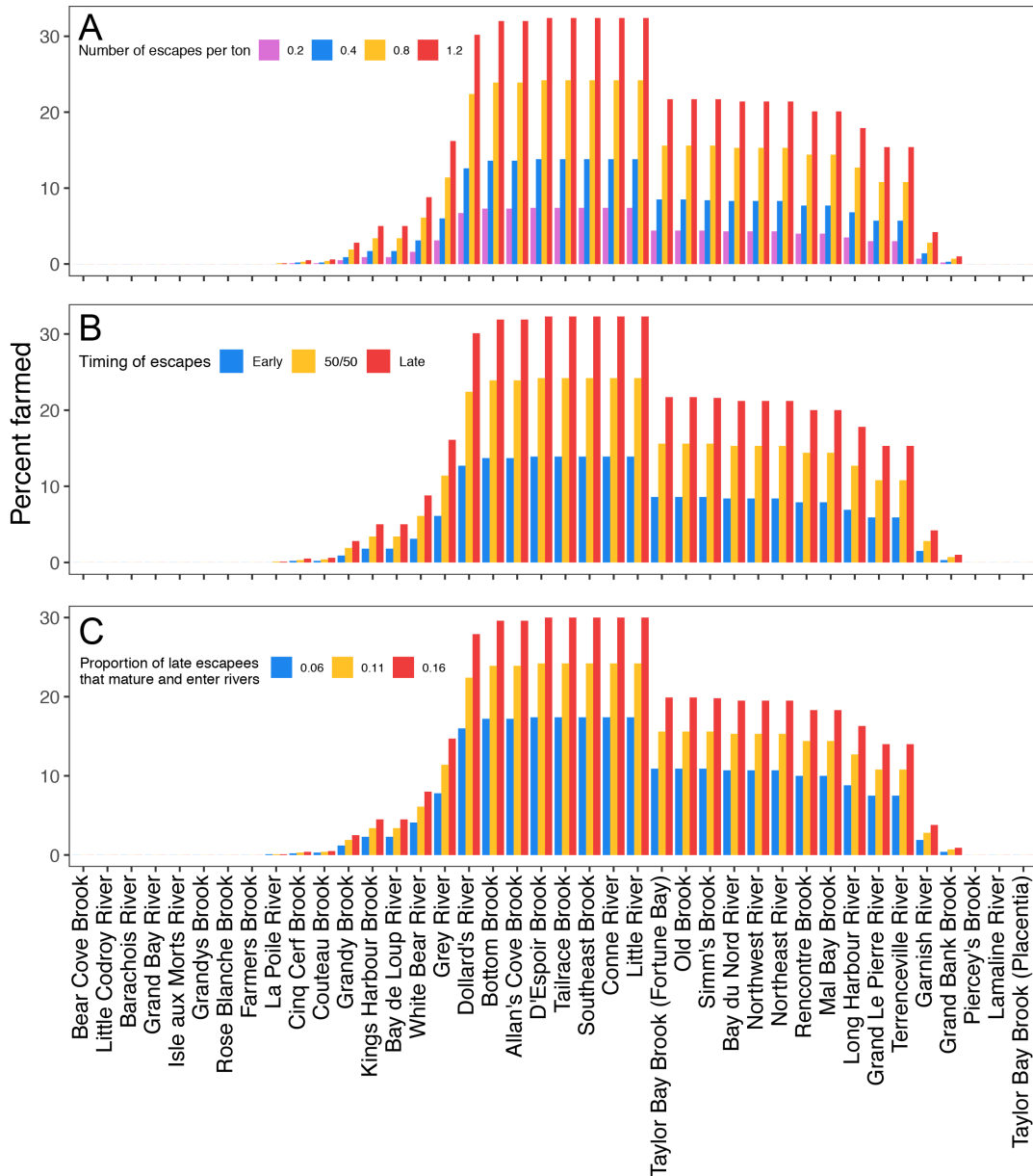


Figure 8. Predicted relative proportion of escaped farmed salmon to wild salmon in rivers of southern Newfoundland under the proposed expansion scenario varying (A) the number of escapees per unit harvest (0.2, 0.4, 0.8, 1.2 fish per ton), (B) varying the proportion of early to late escapees (all early, 50:50, or all late), and (C) varying the proportion of late escapees that mature and enter rivers (0.06, 0.11, 0.16). See methods for details regarding simulations.

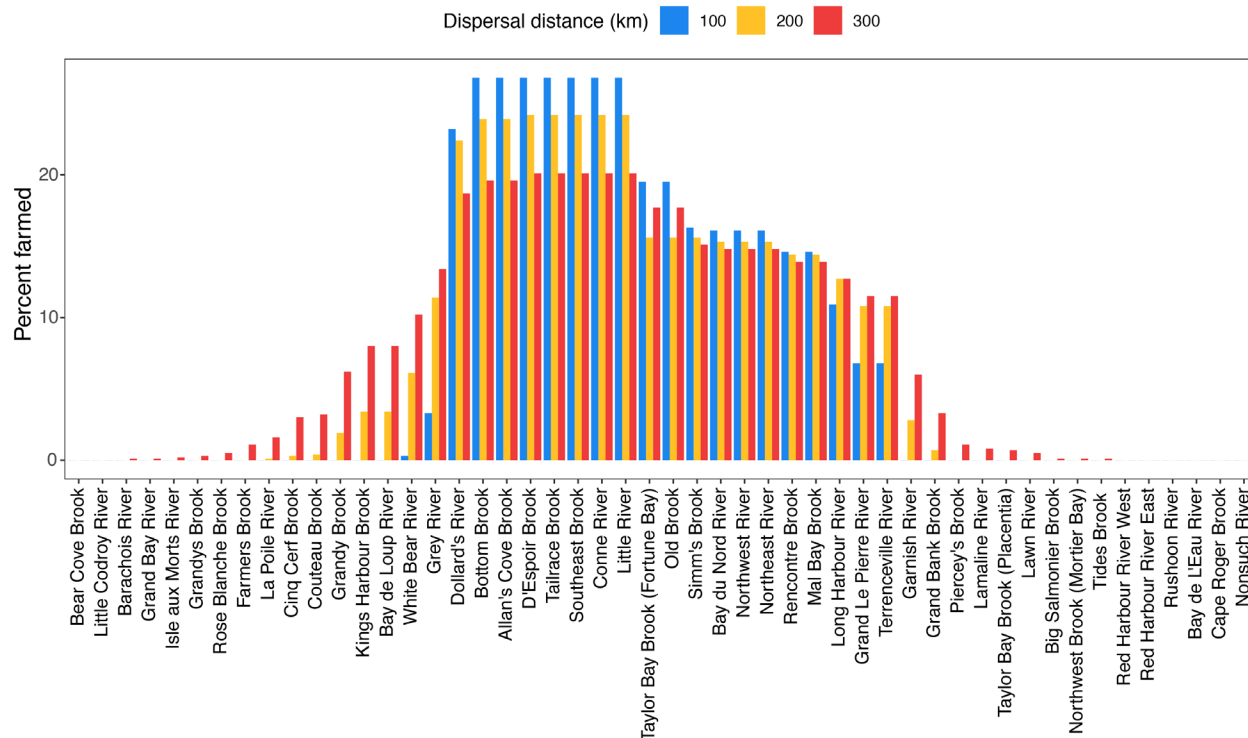


Figure 9. Predicted relative proportion of escaped farmed salmon to wild salmon in rivers throughout southern Newfoundland under the proposed expansion scenario varying the maximum dispersal distance for escapees (100, 200, 300 km). See methods for details regarding simulations.

Modifying the maximum dispersal distance did not significantly alter the number of escapees found in rivers, only the distribution of escapees across rivers (Figure 9). For a maximum dispersal distance of 100 km, escapees were only predicted to occur in 21 rivers with a maximum proportion of escapees of 25.4%. A maximum dispersal distance of 200 km resulted in 29 rivers predicted to receive escapees and a maximum proportion of 23.3% escapees (Figure 9). Finally, using a dispersal distance of 300 km, 37 rivers with escapees were predicted with a maximum proportion of 19.6% escapees to wild individuals (Figure 9).

---

## DISCUSSION

In 2019 a proponent applied for aquaculture licenses at various sites located on the south coast of Newfoundland and the request was referred to DFO for siting advice. Our goal here was to explore the potential genetic interactions resulting from the proposed finfish site expansion involving fourteen sites (1 M individuals per site) in southern Newfoundland using a combination of empirical data, and both individual-based and dispersal modeling. Our individual-based simulations suggest that as the proportion of escapees within a population increases, both population decline and genetic change are expected, and thus allow an assessment of the risk of various levels of escapees to wild populations. Our analysis of propagule pressure, and simulations of escapee dispersal into southern Newfoundland rivers (estimated population size ~22,000 individuals) suggest increased numbers of escapees (49% or 1.5X increase) and westward shifts in the predicted distribution of escapees associated with the proposed expansion. Our results directly build on previous modeling and empirical studies (Castellani et al. 2018, Glover et al. 2017, Hindar et al. 2006, Keyser et al. 2018, Sylvester et al. 2019), directly inform management decisions regarding the transfer of salmon to net-pens, and supports Fisheries and Oceans Canada's obligations under the Fisheries Act and the Species at Risk Act with respect to the proposed expansion in southern Newfoundland.

### INDIVIDUAL-BASED MODELING

Population impacts of hybridization with escaped farmed salmon have been shown to vary (Glover et al. 2017, Sylvester et al. 2018) and as such predicting the population responses to the presence of escaped farmed salmon remains a challenge. Our individual-based eco-genetic simulations suggest that demographic decline and genetic change are apparent once the proportion of escapees in rivers increases beyond 10%, and that the observed impacts increase with the proportion of escapees (Figure 5). These predictions are consistent with empirical estimates of reduced aquaculture offspring survival (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2012, Sylvester et al. 2019) and reductions in wild population productivity resulting from hybridization with farm escapees (Castellani et al. 2018, Fleming et al. 2000, Sylvester et al. 2019). For example, Fleming et al. (2000) report reductions of >30% in productivity of wild populations experiencing hybridization. The magnitude of the predicted demographic changes observed here varied with the proportion of escapees present in the river but ranged from <10% to > 50% decline but were generally less than 30% for most simulations over the modelled 50-year period. The predicted genetic changes are consistent with both local evidence of hybridization and introgression (Sylvester et al. 2018, Wringe et al. 2018) and recent studies suggesting significant changes to key life history traits due to introgression (Bolstad et al. 2017, Skaala et al. 2019). As these impacts scale with the proportion of escapees present, the ultimate impact to wild populations experiencing escapees may be significantly greater in small or depressed populations and existing empirical data supports this hypothesis (Heino et al. 2015, Sylvester et al. 2018, Wringe et al. 2018).

Estimates of the proportion of escapees occurring in rivers have been used as a management or conservation tool elsewhere and model predictions of population impacts of escapees can directly inform siting decisions and mitigation action. In Norway extensive summer and autumn surveys for escapees are used to estimate an index of the proportion of escapees in rivers (Diserud et al. 2019, Glover et al. 2019, Svenning et al. 2017). Based on these surveys, the incidence of escapees in rivers are designated as high (>10%), moderate, or low (<10%) and this designation is used to prioritize rivers for mitigation action such as the active removal of escapees from rivers (Glover et al. 2019). Similarly, a recent risk assessment in Iceland has opted for a 4% threshold for the proportion of escapees in rivers to provide a precautionary approach to siting as the industry develops (Jóhannsson et al. 2017). These values are

---

consistent with both levels of straying in the wild (<10%, Stabell 1984, Thorstad et al. 2010) and our observations here that demographic and genetic change are likely when the proportion of escapees exceeds 10%.

Ultimately, although the best available regional data were used to parameterize the individual based model, improved empirical estimates of several key parameters may both improve these model predictions and any subsequent management advice. Here population specific life history and environmental data considered were from the Conne River, which represents the best studied population/river in southern Newfoundland. Although this is likely representative of the region, additional data from other populations would allow regional variation in demography, life history, and environmental features to be considered in model predictions. Similarly, potential key variables such as stage specific survival of aquaculture escapees and offspring have been shown to be both spatially and temporally variable (Skaala et al. 2019). Moreover, recent work suggests that population outcomes may be highly influenced by differences in the survival of escapees and hybrids (Sylvester et al. 2019) as well as rates of straying among wild populations (Castellani et al. 2018). As such, further refinement of empirical estimates of these interactions are needed to improve predictions of population outcomes.

## **ESCAPEE DISPERSAL PREDICTIONS**

The spatial extent of hybridization between wild and domestic escapees will likely be dependent on the number of escapees, the scale of escapee dispersal in the wild, and the status of wild populations. Field detections of aquaculture salmon indicate regional as well as both season and size-specific dispersal patterns (Glover et al. 2019, Keyser et al. 2018, Morris et al. 2008). Nonetheless, the consensus for Atlantic Canada is that escapees are usually found in rivers at moderate to small distances (i.e., 10s to 100s km) from escape locations (Keyser et al. 2018, Morris et al. 2008). These observations are supported by experimental releases conducted by Hamoutene et al. (2018) in southern Newfoundland indicating maximum dispersal distances of 80 km, with most salmon remaining in the embayment of release. Moreover, genetic identification of hybrids following a single escape event in southern Newfoundland detected first generation hybrids at distances of up to 100 km from the escape event (Sylvester et al. 2018, Sylvester et al. 2019, Wringe et al. 2018). Similarly, Morris et al. (2008) reported escaped farmed salmon occurring in 56 of 62 Maritime rivers within 300 km of aquaculture operations. Our use of a simplified dispersal kernel informed by all available data on the dispersal of escapees suggests that under the existing distribution of production in the region, the heads of Fortune Bay and Bay d'Espoir are likely to be characterized by the highest numbers of mature escapees entering rivers. Under the proposed expansion plan, the number of escapees is predicted to increase by 1.5X (49%) and the area of the highest number of mature escapees entering rivers shifts to the head of Bay d'Espoir. This shift is entirely consistent with our estimates of propagule pressure, the proposed increases in production (~50%), and the shift in location to the area west of Fortune Bay.

It is important to note when considering these predicted proportions of escapees to wild individuals, that there is uncertainty in both the estimates of predicted escapees but also in the estimates of wild population size. The estimates of escapees per unit production used here are based on Norwegian statistics and there is uncertainty as to their applicability to Newfoundland. Also, the estimates of wild population size used here are the best currently available for many of the rivers considered and based on habitat-abundance associations identified using a larger geographic area. However, as these estimates are based on measures of habitat, they may not adequately reflect recent declines in population size that have occurred in southern Newfoundland (COSEWIC 2011, DFO 2013, 2018b). As such, our predictions of the proportions of escapees in wild populations may be biased low in some instances, particularly in small

---

populations. Improved estimates of wild population size and the presence of escapees for rivers in the region would improve the assessment of genetic and demographic risk. It is also noteworthy that our predictions of escapees at the Conne River under the current production regime significantly exceed detections there to date based on the summer monitoring period. Although escapees and hybrids have been detected in Conne River (Dempson et al. 2004, Wringe et al. 2018), the proportions have generally been low even following significant escape events. The mechanism for this discrepancy is unknown at this time, but it is possible that either escapees are entering the environment undetected, doing so at times outside the limited monitoring period, or are being diverted to the adjacent rivers based on flow patterns in the area.

The dispersal kernels used in our simulations were parameterized to provide predictions consistent with detections of escapees at the Garnish River counting fence which is the nearest monitoring facility regularly detecting escapees in the region. Simulating the observed number of escapees at the Garnish River required using a maximum dispersal distance of 200 km. However, this value exceeds existing empirical estimates for the region, and therefore the model may over estimate dispersal potential in some instances. By comparison, our sensitivity analysis indicated that reducing the maximum dispersal distance to 100 km, reduced the spatial scale of impact but increased the number of escapees predicted to occur in the Bay d'Espoir area under the proposed expansion, with seven rivers predicted to achieve 25% escapees. Also, we assume the influence of ocean currents in the region on the shape of the dispersal kernel is negligible. This assumption is consistent with the dominance of wind driven flow in the area and existing tagging data of escapees in the region (Hamoutene et al. 2018).

Examinations of the sensitivity of the spatial model results were used to explore the influence of varying several parameters including the life stage of escapees, the survival and maturity probability of escapees, and the magnitude of escapees per unit harvest produced. In all three cases the number of predicted escapees varied, but the general trends suggest a higher proportion of late escapees, higher survival or maturity probability, and more escapees per unit harvest all result in predictions of more escapees in rivers. It is notable that in most scenarios tested, the rivers in the Bay d'Espoir area were predicted to be characterized by greater than 10% escapees under the proposed expansion.

## SUMMARY

- Recent work indicates that the magnitude of genetic impacts due to escaped farmed salmon on wild populations is correlated with the biomass of farmed salmon in nearby cages. Given this clear association between cage sites and escapees in Canada and Europe, it is likely that genetic impacts on wild Atlantic salmon populations can be minimized by considering the size and location of wild salmon populations in siting decisions.
- Our individual-based population simulations suggest that as the proportion of escapees within a population increases and exceeds 10%, both demographic decline and genetic change are expected. The magnitude of these changes increases with increasing proportion of escapees present. Improved empirical estimates of escapee and hybrid survival and growth in the wild are needed to refine these estimates.
- Model predictions of escapee dispersal suggest that under the present regime, rivers characterized by the largest proportion of escapees relative to wild population size are located in the heads of Fortune Bay and Bay d'Espoir (19 rivers total > 10% escapees, max 14.9%) consistent with estimates of propagule pressure and recent empirical evidence of escapees and hybridization.

- 
- Under the proposed expansion, the number of escapees in southern Newfoundland rivers is predicted to increase by 49% (1.5X) and the rivers characterized by the greatest propagule pressure and proportion of escapees relative to wild population size are predicted to shift to the Bay d'Espoir area (20 rivers total > 10% escapees, max 23%).
  - Uncertainty exists with respect to: (1) the size of the wild populations in the region which may be biased high underestimating the risk due to genetic interactions, (2) the proportion of escapees per unit production in southern Newfoundland and how this may be reduced through mitigation measures, (3) the scale of escapee dispersal which may be biased high in this analysis also underestimating the risk to certain populations in close proximity to sites, and (4) the proportion of early and late escapees that actually enter freshwater.
  - Spatial predictions could be further improved with data on escapees in the region including, the number and the distribution of escapees in the wild, the proportion of early and late escapees that actually enter freshwater, and the temporal occurrence of escape events across the production cycle.

### **ACKNOWLEDGEMENTS**

The authors thank R. Gregory, B. Dempson, K. Layton, and T. Kess for comments on this manuscript. Funding was provided through the Fisheries and Oceans Program for Aquaculture Regulatory Research. This work has benefited greatly from a three-year Canada-EU Galway Statement for the Transatlantic Ocean Research Alliance Working Group on modelling genetic interactions among wild and farm escaped Atlantic Salmon in the North Atlantic, involving participants from seven countries. The models applied here were evaluated and discussed as part of this working group.

---

## REFERENCES CITED

- Baskett, M.L., Burgess, S.C., and Waples, R.S. 2013. Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. *Evol. Appl.* 6: 1090-1108.
- Bolstad, G.H., Hindar, K., Robertsen, G., Jonsson, B., Sægvog, H., Diserud, O.H., Fiske, P., Jensen, A.J., Urdal, K., Næsje, T.F., Barlaup, B.T., Florø-Larsen, B., Lo, H., Niemelä, E., and Karlsson, S. 2017. Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. *Nat. Ecol. & Evol.* 1: 0124.
- Castellani, M., Heino, M., Gilbey, J., Araki, H., Svåsand, T., and Glover, K.A. 2015. IBSEM: An Individual-Based Atlantic Salmon Population Model. *PLoS ONE* 10(9): e0138444.
- Castellani, M., Heino, M., Gilbey, J., Araki, H., Svåsand, T., and Glover, K.A. 2018. Modeling fitness changes in wild Atlantic salmon populations faced by spawning intrusion of domesticated escapees. *Evol. Appl.* 11(6): 1010-1025.
- COSEWIC. 2011. COSEWIC assessment and status report on the Atlantic salmon *Salmo salar* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa
- Dempson, J.B., Furey, G., and Bloom, M. 2004. Status of Atlantic salmon, *Salmo salar*, in Conne River, SFA 11, Newfoundland, 2003. DFO Can. Sci. Adv. Sec. Res. Doc. 2004/057.
- DFO. 2013. Recovery Potential Assessment for the South Newfoundland Atlantic Salmon (*Salmo salar*) Designatable Unit. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2012/007.
- DFO. 2018a. Review of the Science Associated with the Inner Bay of Fundy Atlantic Salmon Live Gene Bank and Supplementation Programs. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2018/041
- DFO. 2018b. Stock Assessment of Newfoundland and Labrador Atlantic Salmon – 2017. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2018/034. (Erratum: September 2018)
- Diserud, O.H., Fiske, P., Sægvog, H., Urdal, K., Aronsen, T., Lo, H., Barlaup, B.T., Niemelä, E., Erkinaro, J., Orell, P., Lund, R.A., Økland, F., Østborg, G.M., Hansen, L.P., and Hindar, K. 2019. Escaped farmed Atlantic salmon in Norwegian rivers during 1989–2013. *ICES J. Mar. Sci.* 76(4): 1140–1150.
- Fleming, I.A., Hindar, K., Mjølnerød, I.B., Jonsson, B., Balstad, T., and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. *Proc. R. Soc. Biol. Sci. Ser. B* 267: 1517-1524.
- Glover, K.A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M.P., and Skaala, Ø. 2013. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. *BMC Genet.* 14: 74.
- Glover, K.A., Solberg, M.F., McGinnity, P., Hindar, K., Verspoor, E., Coulson, M.W., Hansen, M.M., Araki, H., Skaala, Ø., and Svåsand, T. 2017. Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. *Fish and Fisheries* 18: 890-927.
- Glover, K.A., Urdal, K., Næsje, T., Skoglund, H., Florø-Larsen, B., Otterå, H., Fiske, P., Heino, M., Aronsen, T., Sægvog, H., Diserud, O., Barlaup, B.T., Hindar, K., Bakke, G., Solberg, I., Lo, H., Solberg, M.F., Karlsson, S., Skaala, Ø., Lamberg, A., Kanstad-Hanssen, Ø., Muladal, R., Skilbrei, O.T., and Wennevik, V. 2019. Domesticated escapees on the run: the second-generation monitoring programme reports the numbers and proportions of farmed Atlantic salmon in >200 Norwegian rivers annually. *ICES J. Mar. Sci.* 76(4): 1151–1161.

- 
- Hamoutene, D., Cote, D., Marshall, K., Donnet, S., Cross, S., Hamilton, L.C., McDonald, S., Clarke, K.D., and Pennell, C. 2018. Spatial and temporal distribution of farmed Atlantic salmon after experimental release from sea cage sites in Newfoundland (Canada). *Aquaculture* 492: 147-156.
- Hansen, L.P., and Jacobsen, J.A. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. *ICES J. Mar. Sci.* 60(1): 110-119.
- Hansen, L.P., Jacobsen, J.A., and Lund, R.A. 1993. High numbers of farmed Atlantic salmon, *Salmo salar* L., observed in oceanic waters north of the Faroe Islands. *Aquac. Res.* 24(6): 777-781.
- Hansen, L.P., Reddin, D.G., and Lund, R.A. 1997. The incidence of reared Atlantic salmon (*Salmo salar* L.) of fish farm origin at West Greenland. *ICES J. Mar. Sci.* 54(1): 152-155.
- Hansen, L.P., and Youngson, A.F. 2010. Dispersal of large farmed Atlantic salmon, *Salmo salar*, from simulated escapes at fish farms in Norway and Scotland. *Fish. Manag. Ecol.* 17(1): 28-32.
- Heino, M., Svåsand, T., Wennevik, V., and Glover, K.A. 2015. Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. *Aqua. Environ. Inter.* 6(2): 185-190.
- Hindar, K., Fleming, I.A., McGinnity, P., and Diserud, A. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. *ICES J. Mar. Sci.* 63: 1234–1247.
- International, I. 2012. Offshore Mariculture Escapes Genetic/Ecological Assessment (OMEGA) Model Version 1.0 Model Overview and User Guide. August. (ICF 00613.10.) Seattle, WA. Prepared for NOAA Fisheries, Seattle, WA.
- Jensen, A., Karlsson, S., Fiske, P., Hansen, L., Hindar, K., and Ostborg, G. 2013. Escaped farmed Atlantic salmon grow, migrate and disperse throughout the Arctic Ocean like wild salmon. *Aqua. Environ. Inter.* 3(3): 223-229.
- Jóhannsson, R., Guðjónsson, S., Steinarsson, A., and Friðriksson, J. 2017. Áhættumat vegna mögulegrar erfðablöndunar milli eldislaxa og náttúrulegra laxastofna á Íslandi HV 2017-027. Marine and Freshwater Research Institute, Iceland.
- Keyser, F., Wringe, B.F., Jeffery, N.W., Dempson, J.B., Duffy, S., and Bradbury, I.R. 2018. Predicting the impacts of escaped farmed Atlantic salmon on wild salmon populations. *Can. J. Fish. Aquat. Sci.* 75(4)(4): 1-7.
- Lehnert, S.J., Bentzen, P., Kess, T., Lien, S., Horne, J.B., Clement, M., and Bradbury, I.R. 2019. Chromosome polymorphisms track trans-Atlantic divergence and secondary contact in Atlantic salmon. *Mol. Ecol.* 28(8): 2074-2087.
- McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R.A., Ó Maoiléidigh, N., Baker, N., Cotter, D., O’Hea, B., Cooke, D., Rogan, G., Taggart, J.B., and Cross, T. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proc. R. Soc. Biol. Sci. Ser. B* 270: 2443-2450.
- McGinnity, P., Stone, C., Taggart, J.B., Cooke, D., Cotter, D., Hynes, R.A., McCamley, C., Cross, T., and Ferguson, A. 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES J. Mar. Sci.* 54: 998–1008.



- 
- Morris, M.R.J., Fraser, D.J., Heggelin, A.J., Whoriskey, F.G., Carr, J.W., O'Neil, S.F., and Hutchings, J.A. 2008. Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. *Can. J. Fish. Aquat. Sci.* 65(12): 2807-2826.
- Norway, D.o.F. 2019. Statistics for aquaculture. Available from <https://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemningsstatistikk>.
- O'Reilly, P.T., Carr, J.W., Whoriskey, F.G., and Verspoor, E. 2006. Detection of European ancestry in escaped farmed Atlantic salmon, *Salmo salar* L., in the Magaguadavic River and Chamcook Stream, New Brunswick, Canada. *ICES J. Mar. Sci.* 63(7): 1256-1262.
- Porter, T.R., Riche, L.G., and Traverse, G.R. 1974. Catalogue of Rivers in Insular Newfoundland. Resource Development Branch, Fisheries and Marine Service, Newfoundland Region.
- Skaala, Ø., Besnier, F., Borgstrøm, R., Barlaup, B., Sørvik, A.G., Normann, E., Østebø, B.I., Hansen, M.M., and Glover, K.A. 2019. An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. *Evol. Appl.* 12(5): 1001-1016.
- Skaala, Ø., Glover, K.A., Barlaup, B.T., Svåsand, T., Besnier, F., Hansen, M.M., and Borgstrøm, R. 2012. Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. *Can. J. Fish. Aquat. Sci.* 69(12): 1994-2006.
- Skilbrei, O.T., Heino, M., and Svåsand, T. 2015. Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. *ICES J. Mar. Sci.* 72(2): 670-685.
- Stabell, O.B. 1984. Homing and olfaction in salmonids: A critical review with special reference to the Atlantic salmon. *Biological Reviews* 59(3): 333.
- Svenning, M.-A., Lamberg, A., Dempson, B., Strand, R., Hanssen, Ø.K., and Fauchald, P. 2017. Incidence and timing of wild and escaped farmed Atlantic salmon (*Salmo salar*) in Norwegian rivers inferred from video surveillance monitoring. *Ecol. Freshw. Fish.* 26(3): 360-370.
- Sylvester, E.V.A., Wringe, B.F., Duffy, S.J., Hamilton, L.C., Fleming, I.A., and Bradbury, I.R. 2018. Migration effort and wild population size influence the prevalence of hybridization between escaped farmed and wild Atlantic salmon. *Aqua. Environ. Inter.* 10: 401-411.
- Sylvester, E.V.A., Wringe, B.F., Duffy, S.J., Hamilton, L.C., Fleming, I.A., Castellani, M., Bentzen, P., and Bradbury, I.R. 2019. Estimating the relative fitness of escaped farmed salmon offspring in the wild and modeling the consequences of invasion for wild populations. *Evol. Appl.* 12: 705-717.
- Thorstad, E.B., Whoriskey, F., Rikardsen, A.H., and Aarestrup, K. 2010. Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. Wiley-Blackwell. p. 1-32.
- Wringe, B.F., Jeffery, N.W., Stanley, R.R.E., Hamilton, L.C., Anderson, E.C., Fleming, I.A., Grant, C., Dempson, J.B., Veinott, G., Duffy, S.J., and Bradbury, I.R. 2018. Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. *Communications Biology* 1(1).