

From the fjords to the rivers: Evaluating the spatial distribution of escaped farmed salmon to inform ecologically relevant management strategies

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Scientific environment

The work of this doctoral thesis was carried out under the partnership between NORCE Norwegian Research Centre (NORCE) and the University of Bergen (UiB, Department of Biological Sciences). The candidate, Shad Mahlum, was affiliated with the Ecological and Environmental Change Research Group (EECRG) at UiB and the Laboratory for Freshwater Ecology and Inland Fisheries (LFI) at NORCE. Funding was provided by UiB, NORCE, and Norwegian Environment Agency.



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Abstract

Over the last 40 years, the relatively fast expansion of Atlantic salmon aquaculture has created new obstacles for the persistence of wild Atlantic salmon stocks where the two overlap. Now, the greatest threat to existing wild Atlantic salmon populations is the unintended release of domesticated Atlantic salmon from aquaculture sites. Once escaped, domesticated Atlantic salmon can migrate into rivers and spawn with wild salmon populations. Overall, the hybridization of wild and domesticated salmon has negative impacts that threatens the long-term viability of many salmon populations. However, researchers have limited knowledge into the mechanics that promote the direct overlap between the two conspecifics and thus stakeholders lack robust and effective mitigation strategies and are largely dependent on reactive measures to control escaped Atlantic salmon.

This thesis was focused on the spatial distribution and overlap of wild and escaped farmed Atlantic salmon and identifying ecologically sound mitigation and management strategies to control the abundance of escaped Atlantic salmon in nature. To accomplish this, the thesis is divided into four objectives: 1) evaluate the movement patterns of acoustically tagged wild adult Atlantic salmon throughout the estuaries and connected fjords where salmon directly overlap with aquaculture sites. 2) validate the spawning count data collected during fall snorkel surveys to quantify the abundance of wild and escaped salmon during active spawning activities. Finally, using validated data from the spawning count surveys, assess the 3) among- and 4) within river distribution of wild and escaped Atlantic salmon.

My results demonstrated the direct spatial overlap of wild and escaped Atlantic salmon and fills the following knowledge gaps necessary for the effective management of escapees in rivers: 1) when relying on reactive mitigation efforts (e.g., active removals from the river), monitoring and removal methods that fail to account for the within river spatial variation of escaped Atlantic salmon can be limited in their effectiveness to quantify and remove escapees and should only be used when alternate mitigation efforts fail (e.g., proactive management strategies), 2) to implement effective marine protected areas, it is necessary to either incorporate a) the habitat

where direct interactions between wild and escaped farmed salmon are most likely to occur or b) the spatial scopes that aquaculture concessions has the greatest effect on escapee abundance (75 km from important rivers), and 3), it is recommended that the current regulation of aquaculture production (e.g., traffic light system) should be expanded to include regulating concession limits to reduce the number of escaped farmed salmon in important Atlantic salmon rivers. This thesis highlights the importance of understanding spatial distribution and the mechanisms that drive the direct overlap of wild and escaped farmed salmon so that robust ecologically based tools can be developed for resource managers to help regulate the abundance of escaped Atlantic in the wild.

List of Publications

Paper I

Mahlum, S. K., Skoglund H., Wiers T., Norman E.S., Barlaup B.T., Wennevik, V., Glover, K. A., Urdal K., Bakke G., Vollset K.W (2019). Swimming with the fishes: validating drift diving to identify farmed Atlantic salmon escapees in the wild. *Aquaculture Environment Interactions* **11**: 417-427.

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Paper III

Mahlum, S. K., K. W. Vollset, B. T. Barlaup, H. Skoglund, G. Velle (*in review*). Salmon on the lam: Drivers of escaped farmed fish abundance in rivers.

Paper IV

Mahlum, S. K., K. W. Vollset, B. T. Barlaup, H. Skoglund, G. Velle (*submitted*). The last stop: Longitudinal distribution of farmed escaped Atlantic salmon in rivers.

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Author Contributions

	Paper I	Paper II	Paper III	Paper IV
Research Design	SM , KV, BB, HS, EN, TW, KG, VW, GB	BB, TW, KV	SM , BB, KV, HG, GV	SM , BB, KV, HG, GV
Data collection	SM , HS, EN, TW, VW, GB, KU	TW	BB, HG, KV, GV	BB, HG, KV, GV
Data Analysis	SM	SM	SM	SM
Data Interpretation	SM , HS, KV, KG, VW	SM , KV, GV, BB	SM , KV, GV, HS, BB	SM , KV, GV, HS, BB
Manuscript Writing and Preparation	SM	SM	SM	SM
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Note: SM = Shad Mahlum, KV = Knut Vollset, GV = Gaute Velle, BB = Bjørn

Barlaup, HS = Helge Skoglund, EN = Eirik Norman, TW = Tore Wiers, KG = Kevin

Glover, VW = Vidar Wennevik, GB = Gunnar Bekke, KU = Kurt Urdal

List of Abbreviations

AE – Arna Estuary

ANCOVA – Analysis of Covariance

ANOVA – Analysis of Variance

CI – Credibility Interval

CL – Capture Location

db-RDA – Distance-based Redundancy Analysis

DE – Dale Estuary

DEM – Digital Elevation Map

CPUE – Catch Per Unit Effort

EFS – Escaped Farmed Salmon

ID – Intensity Distribution

IF – Inner-Fjord

IQR – Interquartile Range

MCMC – Markov Chain Monte Carlo

MKDE – Movement-based Kernel Density Estimation

MPA – Marine Protected Area

MSE – Mean Squared Error

MSP – Marine Spatial Planning

NSP – National Salmon Program

NSF – National Salmon Fjord

OF – Outer-Fjord

OURO – Oppdrettsnæringens sammenslutning for utfisking av rømt oppdrettsfisk

SHQ – Spawning Habitat Quality

SW – Sea Winter

TPR – True Positive Rate

UCC – Upstream Cell Count

VE – Vosso Estuary

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1. INTRODUCTION

Many of the world's socially and economically important species of salmonids have been subjected to numerous anthropogenic pressures, such as river regulation, fish farms, and diseases (Reid et al. 2019) and the interactions between humans and the surrounding ecosystem has warranted the need to evaluate their ecological impacts (Costanza et al. 2014). In turn, the importance of spatial planning to mitigate and maximize the ecosystem services of the environment has gained considerable attention (Douvere 2008, Foley et al. 2010, Qiu and Jones 2013). A particular focus of spatial planning is the interface between human needs and aquatic environments (e.g., dams, drinking water, sports fishing; Carter 2007, Jager et al. 2015) and more recently in the coastal regions (e.g., energy production and aquaculture; Douvere 2008).

The domestication of aquatic species as a food source is a major global industry (~66 million tons in 2012; FAO 2014). Finfish species, particularly salmonids, are cultivated in net pen facilities in marine environments where current efforts are focused on creating an environmentally sustainable industry. Environmental sustainability is broadly defined as the requirement to development aquaculture to meet the needs of the current generation while at the same time maintaining the capacity to meet the needs of future generations (page 112 - 113; Pillay 2008). This requires identifying the carrying capacity of aquaculture sites in an area given the limitations of the environment to absorb the adverse effects from aquaculture, the current technology to mitigate adverse effects, and an equilibrium between aquaculture and the wide array of ecosystem services (Gentry et al. 2017). To do this, it is important to directly assess how different habitats, flora, and fauna are affected by aquaculture activities and to incorporate ecologically relevant metrics into current and future management and planning strategies to help develop an environmentally sustainable aquaculture sector.

1.1 Atlantic salmon

Atlantic salmon (*Salmo salar*) is an anadromous species that has a dynamic life history with considerable within- and among population variation (Birnie-Gauvin et al. 2019). They range from mid North American (northern United States) and southern Europe

(Portugal) to northern latitudes (e.g., northeastern Canada, Greenland, and northwestern Russia; Parrish et al. 1998). Perhaps the most critical aspect of the salmon lifecycle is their anadromous migrations between the freshwater and marine habitat where important history functions are carried out. Today, Atlantic salmon has become one of the most studied fish species due to the complex interactions between their environment and anthropogenic stressors and the need for information to mitigate the anthropogenic influences (Birnie-Gauvin et al. 2019).

Atlantic salmon begin their lifecycle in river habitats and after several years in natal rivers as parr (1 – 8 years), Atlantic salmon undergo smoltification (i.e., physiological and morphological changes for marine ecosystems; Folmar and Dickhoff 1980, McCormick et al. 1998) and begin their journey to the marine environment for feeding and growth. During this transition under natural conditions, migrating smolts experience increased mortality that often results in > 90 % reduction in numbers during their out-migration to the sea (Thorstad et al. 2011). Here, even small compounding anthropogenic disturbances are likely to impact the recruitment of future generations (e.g., navigation of multiple hydropower facilities; Nyqvist et al. 2017). Once in the marine environment, less is known about Atlantic salmon distribution and behavior. However, the development of new technology and analytical techniques have allowed researchers to better assess the marine migration of Atlantic salmon (see Strøm et al. 2018 as a recent example).

Depending on the genetic disposition and growth conditions at sea, adult Atlantic salmon usually migrate back to their natal rivers after 1 to 3 years in the sea to spawn. Arrival to their natal rivers usually occurs in the early spring and summer months and in some instances the previous year prior to spawning (Quinn et al. 2015). Their return spawning migration has two distinct marine phases (Hansen et al. 1993), the first, is a course scale movement from the feeding ground to the coast. The second is more focused movement that is directed in identifying natal rivers through the use of olfactory cues (Hansen et al. 1993), environmental determinates (Jonsson and Jonsson 2011), and behavior mechanisms (Berdahl et al. 2016, Berdahl et al. 2017). Atlantic salmon will enter rivers as early as May, but the majority will typically enter in the later portion of the summer or fall (Klemetsen et al. 2003). Several studies have

observed the extended time periods that Atlantic salmon spend in the near shore habitat prior to entering the river (Potter 1988, Priede et al. 1988, Thorstad et al. 2003). However, limited information is available on the behavior and habitat use of estuaries and fjords of Atlantic salmon and the mechanism that promote extended marine residence (Quinn et al. 2015). Such information can be particularly advantageous as we expand the use of the marine habitats for a variety of recreational, economical, and mitigation functions (e.g., fishing, aquaculture, and marine protected areas [MPA]; Bishop et al. 2017).

Once in the river, Atlantic salmon display several distinct phases of river migration (Økland et al. 2001). The first phase is a direct upstream migration followed by a search phase for the desired spawning habitat. Here, salmon enter an extended holding or residence phase where limited movement occurs. The final phase is active spawning that typically occurs in October and November. Suitability of a spawning habitat is dependent on the geomorphology, temperature regimes, and flow characteristics of the river (Armstrong et al. 2003) and dictate the spatiotemporal distribution of Atlantic salmon in the riverscape and thus can have important implications on population success (Finstad et al. 2010). Once spawned, Atlantic salmon are termed kelts and migrate back to the ocean soon after spawning or the following spring depending on energetic reserves (Haltnunen et al. 2013) and can potentially return in successive years to spawn as repeat spawners (Bordeleau et al. 2019).

The dynamic life history of Atlantic salmon is dependent on vastly different habitats throughout their life. The broad spatial extent that they occupy can present challenges for researchers who study salmonids and the various factors that can impact them. Aquaculture is one of the most important anthropogenic factors facing Atlantic salmon (Forseth et al. 2017) and is an important area of research. However, studying these interactions often requires long-term datasets that allows researchers to detect trends associated to population changes (Diserud et al. 2019, Glover et al. 2019) or the use of new technologies that can directly quantify how wild Atlantic salmon and aquaculture spatially interact (e.g., remote telemetry; Lennox et al. 2018).

1.2 Aquaculture

Wild fish stocks were once abundant and the thought of depleting the different populations seemed to be impossible. In the past 70 years, we have seen a shift from a mostly stable fishery that consists of high trophic level species, which are long-lived, to a lower trophic level-based fishery, which are short-lived (Pauly et al. 1998). As a result of the improper management of important fisheries (e.g., Atlantic cod closures in northeastern North America), fish populations began to depreciate below sustainable thresholds that results in a population collapse and subsequent closure (Pauly et al. 1998, Pinsky et al. 2011). To supplement the stagnation of fish biomass harvest over the last 30 years (Figure 1) and to provide a new source of economic stability to local economies, the fishing industry has shifted to the domestication and cultivation of popular fish species to supplement declining wild stocks and to provide society with a high-quality food source (Yucel-Gier et al. 2019).

The use of cultivated fish for food production has been a common practice at small scales for centuries (FAO 2014). However, since the 1950's, with the steady increase in the global population, we have seen corresponding increases in fish production for food. With the development of key innovations, the viability of aquaculture on a broad scale became a real possibility and in the late 70's and early 80's. Now, aquaculture is a major source of fish production for food consumption and averages approximately 8% growth per year (Olsen and Hasan 2012) and overtook commercial fisheries in 2014 as the main source of aquatic based food for human consumption (Clavelle et al. 2019). Today, about 567 species are used in aquaculture (FAO 2016), with roughly 112 million tons produced globally and consisting of roughly 54 % of the global fisheries in 2017 (Figure 1) with the expectation that aquaculture will continue to increase to meet the global demand for low cost protein.

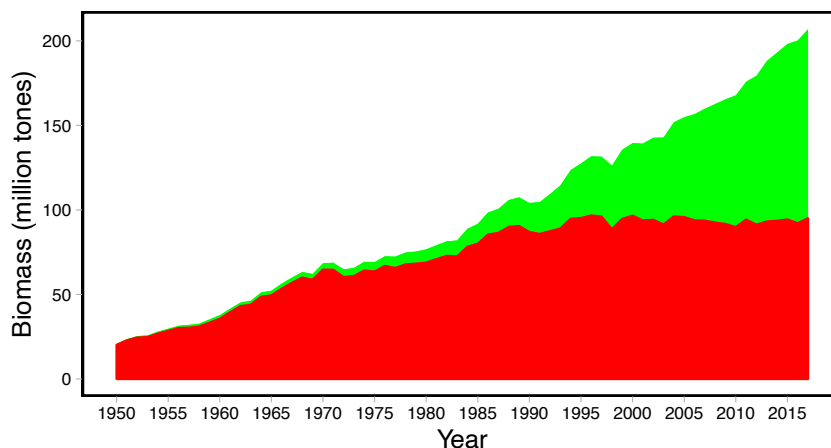


Figure 1. The total global harvest of fisheries (red) and aquaculture (green, excluding Atlantic salmon) from 1950 to 2017 (<http://www.fao.org/fishery/statistics/en>).

Atlantic salmon is a widely used salmonid in aquaculture with Norway, Chile, and Great Britain producing the most Atlantic salmon (Figure 2). The cultivation of salmonids is primarily used for two different purposes. The first is to directly supplement a fishery or a stock that has shown declines in abundance due to anthropogenic influences (Myers et al. 2004). The second, is for economic gain to provide society with what is regarded as a quality fish that can no longer be captured sustainably in the wild. Norwegian aquaculture dates to the 1850's with the land-based domestication of brown trout (*Salmo trutta*) and in the early 1900's a shift to rainbow trout (*Oncorhynchus mykiss*; FAO 2005) as a means to supplement or create new fisheries. In the 1960's and 70's, the large-scale production of domesticated Atlantic salmon began with breakthroughs in cultivation success in marine environments (Tilseth et al. 1991). In the early 90's, individual owners were allowed to maintain multiple concessions and this shifted aquaculture from numerous small independent companies to several large conglomerates owning the majority of the domesticated Atlantic salmon production (Asche et al. 2013, Olaussen 2018). Currently, Atlantic salmon is the main aquaculture product in Norway accounting for ~ 80 % of the total production nationally and 54 % of the global market of domesticated Atlantic salmon in 2017 (Figure 2, Asche et al 2013). Still, Norway has an ambitious plan to increase domesticated salmon production from 1.24 million tonnes in 2017 (Figure 2) to 5.0

million tonnes by 2050 (based on the potential industrial growth projections from Olafsen et al. 2012). Yet, the production of Atlantic salmon has stalled over the last 10 years due to the frequent occurrences of parasites and disease (e.g., Chile; Osmundsen et al. 2017, Kim 2018) and through the increase in regulations (e.g., production limits to control the impacts of sea lice and wild fauna; Osmundsen et al. 2017).

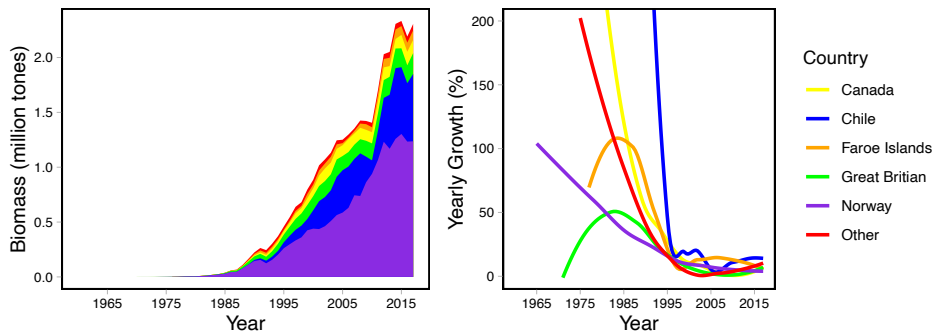


Figure 2. Top producers of Atlantic salmon from 1960 to 2017 (left) and the percent yearly growth from 1960 to 2017 (right, loess smoothers used for trend lines; <http://www.fao.org/>).

1.3 Conflicts between wild Atlantic salmon and aquaculture

Wild populations across their spatial extent have been declining since the late 20th century as a result of numerous anthropogenic factors (e.g., climate change, habitat degradation, invasive species, and aquaculture; Parrish et al. 1998, Forseth et al. 2017, Nicola et al. 2018, Soto et al. 2018, Lehnert et al. 2019), and in some instances, populations have been extirpated from the landscape (Parrish et al. 1998). With the increase of salmon farm production over the last 5 decades, the magnitude of farmed fish relative to their wild conspecifics has increased (domesticated salmon account for ~ 98 % of Atlantic salmon biomass; Parrish et al. 1998). Moreover, during the development of the aquaculture industry, multiple unintended issues have appeared that impact the ecological integrity of the ecosystem (Taranger et al. 2014, 2015, Forseth et al. 2017). Therefore, understanding the potential interactions between industry and the environment is critical in developing the industry in a sustainable way.

The high density of domesticated salmon in the fjords serves as source populations for parasites and disease. A common ectoparasite associated with aquaculture are salmon lice (*Lepeophtheirus salmonis*). Sea lice are naturally found in regions that support salmonids, however, locations with increased salmon aquaculture have artificially inflated the density of sea lice around migration routes that out-migrating salmon smolts depend (Vollset et al. 2015). Also, the potential for disease transmission from aquaculture sites through the direct interface with wild salmonids (Garseth et al. 2013) can also have negative implications for Atlantic salmon. Viral diseases constitute the dominate disease vector affecting aquaculture. However, direct evidence of disease transfer from aquaculture to wild conspecifics is limited (but see Nylund et al. 2019). Yet, horizontal transmissions have been documented to be introduced via aquaculture farms and subsequently detected in wild populations (Nylund et al. 2019) and recaptured escaped farmed salmon have been observed with high densities of pathogens in or near rivers (Madhun et al. 2017). Still, broad scale infection rates are largely unknown due to the difficulty of detecting infected individuals as they tend to be less catchable and more susceptible to predation events (Bakke and Harris 1998).

The introgression of domesticated Atlantic salmon genotypes in wild stocks is regarded as the main threat to the persistence of wild Atlantic salmon populations in Norway (herein the unintentional release of domesticated Atlantic salmon from aquaculture sites will be referred to as escaped farmed Atlantic salmon, escapees, or escaped salmon; Forseth et al. 2017). The strong artificial selection of genetic traits in aquaculture has resulted in a distinct genetic signature significantly different from the wild stock they were originally based (Karlsson et al. 2011). In addition, escapees from fish farms can also lead to resource competition (Fleming and Einum 1997, Fleming et al. 2000, Robertsen et al. 2018) and the establishment of invasive species (e.g., escapees from farmed rainbow trout; Taranger et al. 2015). In Norway, Karlsson et al. (2016) found that approximately 50% of the wild salmon populations exhibit significant levels of introgression. The consequences of introgression in Atlantic salmon are population dependent (Fraser et al. 2010, Glover et al. 2013, Heino et al. 2015, Bolstad et al. 2017, Wringe et al. 2018), but the overall impacts of introgression from escaped salmon include decreases in survival (Fleming and Einum 1997,

McGinnity et al. 2003), reduced smolt production (Fleming et al. 2000, Skaala et al. 2019), and overall reductions in the fitness of wild populations (McGinnity et al. 2003), which together may lead to the extirpation of vulnerable Atlantic salmon populations (McGinnity et al. 2003, Castellani et al. 2018).

To help improve the management of these interactions, it is important to first understand how wild salmon use their environment and at what spatiotemporal scales they interact with aquaculture and their by-products. Therefore, to develop an environmentally sustainable aquaculture industry, it is necessary to identify the problems and to what extent aquaculture sites interact with the environment and limit the long-term viability of both industry and nature.

1.4 Mitigating the impacts of escaped farmed Atlantic salmon

The introduction of domesticated Atlantic salmon in the marine environment was a necessary step into an economically sustainable industry and it is essential to continue to develop aquaculture while maintaining various ecosystem processes. Often with new technologies, economic progress frequently outpaces the necessary knowledge needed to understand what impact they have on the environment. While regulations have helped limit the escapement of individuals from farms (e.g., standardization of net pen construction; Jensen et al. 2010, Høyli 2016), incidences of escaped events still occur at levels that pose a threat to the persistence to wild salmon (see Wringe et al. 2018 as a recent example). To help mitigate and reduce the negative impact of aquaculture, stakeholders use a range of management strategies to reduce the threat of genetic introgression from escaped farmed Atlantic salmon.

Reactive strategies to recapture escaped farmed salmon after release from the farm site is perhaps the most widely used method to mitigate the potential interactions with wild Atlantic salmon (Diserud et al. 2019, Glover et al. 2019). For instance, where available, recaptures with nets in the marine environment is the most effective method to reduce the number of escapees directly post-release (Skilbrei 2010, Chittenden et al. 2011). However, initial efforts to recapture escaped salmon must be taken immediately (within 24 hours), otherwise recaptures will be unlikely (Chittenden et al. 2011,

Dempster et al. 2018). In addition, removal efforts in rivers is another commonly used method in Norway to mitigate the interactions of escaped salmon with wild fauna (Glover et al. 2019). However, this occurs close to or during spawning activities and can potentially have limited benefits if escaped farmed salmon spawn prior to removal.

A better alternative is a proactive management strategy that directly inhibits the abundance of escaped salmon that are able to interact with wild fauna (Atalah and Sanchez-Jerez 2020). Marine spatial planning (MSP) is one proactive tool that can help resource managers make informed decisions on the spatial distribution of activities in the sea that humans dependent, while promoting a healthy marine ecosystem for current and future activities (Foley et al. 2010, Qiu and Jones 2013). A core postulate of many MSP actions is centered around an ecosystem-based management approach that is based on scientific methodologies to support sound policies decisions (Crowder and Norse 2008, Sørensen et al. 2008). However, it is not guaranteed to be the foundation within the decision-making process (Foley et al. 2010). For instance, while it is a stated goal of the various MSP actions in Norway to protect important populations from introgression (Aasetre and Vik 2013), their effectiveness to buffer against introgression has not been rigorously tested. Furthermore, the necessary biological understanding of how wild and escaped farmed Atlantic salmon interact across the landscape is limited and thus prevents stakeholders from acquiring the necessary information to effectively manage the threat of introgression (Guttormsen 2015).

2. OBJECTIVES

This thesis was motivated by the current lack of proactive management strategies against escaped farmed salmon in Norway. However, the biological understanding of how industry and ecosystems interact is still limited (e.g., escapee dispersal) and it is essential that research is directed towards understanding these interactions. Therefore, the overarching goal is to 1) assess the dispersal of wild salmon near farming sites (**Paper II**), 2) determine the environmental variables that influence escapee dispersal among- (**Paper III**) and within rivers (**Paper IV**). However, as a precursor to **Papers III** and **IV** it was necessary to 3) test the effectiveness of the sampling method to distinguish between wild and escaped Atlantic salmon *in situ* (**Paper I**). Subsequently, the focus of this synopsis will be to discuss the spatial overlap of wild and escaped Atlantic salmon and the relevancy of these results to mitigate the abundance of escaped salmon in rivers through different reactive and proactive management strategies.

3. SUMMARY OF PAPERS

Paper I

Swimming with fishes: Validating drift diving to identify farmed Atlantic salmon escapees in the wild

Shad K. Mahlum, Helge Skoglund, Tore Wiers, Eirik Straume Norman, Bjørn T. Barlaup, Vidar Wennevik, Kevin Glover, Kurt Urdal, Gunnar Bakke, Knut W. Vollset

Escaped farmed Atlantic salmon *Salmo Salar* interbreeding with wild conspecifics represents a threat to the genetic integrity and viability of wild populations. Therefore, it is necessary to accurately quantify escapees in riverine systems to monitor and mitigate interactions with wild conspecifics. Drift diving surveys are presently used in Norway to quantify the number of wild and farmed escaped salmon in rivers. However, limited information is available on the validity of the method to distinguish escapees from wild conspecifics. Comparing the proportion of escapees calculated from drift diving (mean = 8.5 %) and net captures (mean = 8.6 %), we found that drift diving was well correlated with net captures ($\text{adj.}r^2 = 0.79$). Furthermore, scale analysis from an independent dataset demonstrated a 98 % true positive rate when identifying and capturing farmed escapees during drift diving. The results of this study indicate that drift diving is an accurate and robust method to quantify farmed escaped salmon, at least in rivers where observation conditions are adequate for snorkeling. In general, drift diving can be a valuable tool for stakeholders to quickly assess broad spatial extents with limited time and resources.

Paper II

Where the salmon roam: Fjord habitat use of adult Atlantic salmon

Shad K. Mahlum, Knut W. Vollset, Bjørn T. Barlaup, Gaute Velle, and Tore Wiers

The habitat use of adult Atlantic salmon was evaluated in a fjord complex in western Norway. A representative sample of 9 wild and 29 hatchery origin Atlantic salmon were tagged with acoustic tags and tracked with 28 stationary receivers from June 2012 to river entry. Using a movement-based kernel density estimation, we identified near shore habitat use in relation to a National Salmon Fjord (NSF) and adjoining aquaculture sites. Furthermore, we compared progression rates and vertical distributions among habitat units. Mean residence time for salmon with acoustic tags from marking to river entry was 30 days (range 3–83 days). Moreover, recaptures of individuals with T-bar anchor tags supported the long residency of Atlantic salmon within the fjord (0–63 days). The main habitat use occurred outside the NSF (68%), with 62% of the individuals overlapping with one or more aquaculture sites. Median progression rates ranged from 15kmd⁻¹ up to 42kmd⁻¹ among the different sections of the fjord with a mean vertical distribution <2m from the surface. Whereas direct implications from the overlap with aquaculture are unclear, the results illustrate the challenge encountered when evaluating the effectiveness of marine protected areas in close proximity to aquaculture sites.

Paper III

Salmon on the lam: Drivers of escaped farmed fish abundance in rivers

Shad K. Mahlum, Knut W. Vollset, Bjørn T. Barlaup, Helge Skoglund, Gaute Velle

The production of Atlantic salmon in aquaculture has grown substantially over the last 40 years. The unintentional release of domesticated salmon poses a significant risk in the long-term persistence of wild Atlantic salmon populations through ecological interactions and genetic introgression. Our ability to link aquaculture production to farmed escaped salmon in rivers is still limited and hinders identifying the appropriate carrying capacity of the environment to mitigate unwanted interactions between wild and escaped Atlantic salmon. Here, we use a 14-year dataset of farmed escapee abundance in rivers along with a priori selected covariables to identify factors that affects the abundance of escapees in 54 watersheds. In addition, we evaluate the predictive strength of the model to assess the risk of individual rivers to introgression. We found that the abundance of farmed escaped Atlantic salmon in rivers is not a random process and directly relates to the production limits for aquaculture facilities when controlling for biotic (abundance of wild Atlantic salmon) and abiotic mechanisms (mean yearly discharge). The model performed moderately well when predicting the abundance of farmed escaped salmon in rivers (40% success rate) and improved when categorizing into management thresholds (75 % success rate). This study provides important links between aquaculture production and the abundance of farmed escaped Atlantic salmon in rivers so that governmental agencies can provide ecological relevant production values for an environmentally sustainable aquaculture industry. Understanding these relationships are beneficial in areas with an established aquaculture industry and for potential new aquaculture sites where domesticated and wild Atlantic salmon will overlap. In addition, these methods could be applied to other species of domesticated fish (e.g., rainbow trout), that share similar life histories that also pose an ecological threat to wild fauna.

Paper IV

The last stop: Longitudinal distribution of farmed escaped Atlantic salmon in rivers

Shad K. Mahlum, Knut W. Vollset, Bjørn T. Barlaup, Helge Skoglund, Gaute Velle

The interaction between wild and escaped farmed salmon is a significant threat to the long-term persistence of wild Atlantic salmon populations. Risk assessments of the impacts by escaped farmed fish are normally done at the watershed level, although interactions between wild and farmed fish is likely dependent on the spatial distribution of the species within rivers, and how they use the available spawning grounds in the river. Therefore, the focus of this study is to assess the spatial distribution of wild salmonids and escaped Atlantic salmon in rivers using data from spawning counts. We found that 1) in contrast to earlier studies, escaped Atlantic salmon generally distribute in the same parts of the river as wild salmonids, but are more variable among year in their distribution. 2) Densities of sea trout and salmon was correlated to the distribution of spawning habitat, whereas, escaped salmon densities lacked statistical clarity to any of the riverscape metrics. 3) Using a distance-based redundancy analysis we identified that sea trout, wild Atlantic salmon, and escaped Atlantic salmon appeared to segregate according to the slope, elevation, and spawning habitat quality, where fish size categories appeared to be segregated by watershed placement. Our study indicates that the spatial overlap between wild and farmed salmon are dependent on the watershed characteristics and the size distribution of wild and escaped farmed fish, and that a risk assessment evaluating the impact of farmed fish must take these factors into account.

4. SYNTHESIS AND GENERAL DISCUSSION

In the following sections, I summarize the key findings from these four papers relative to the spatial overlap of wild and farmed escaped Atlantic salmon. Then, discuss six management strategies, their potential benefits for wild salmon populations, and the implications for promoting an environmentally sustainable industry (Figure 3): 1) no mitigation, 2) river monitoring and active removal (current management strategy; **Paper I and IV**), 3) regulating escapees with production limits based on environmental carrying capacities (“Traffic light system”; **Paper III**), 4) maintaining existing protected areas (National Salmon Fjord [NSF]; **Paper II**), 5) ecological relevant protected areas (**Paper II & III**), and 6) the incorporation of new technologies (e.g., triploid salmon).

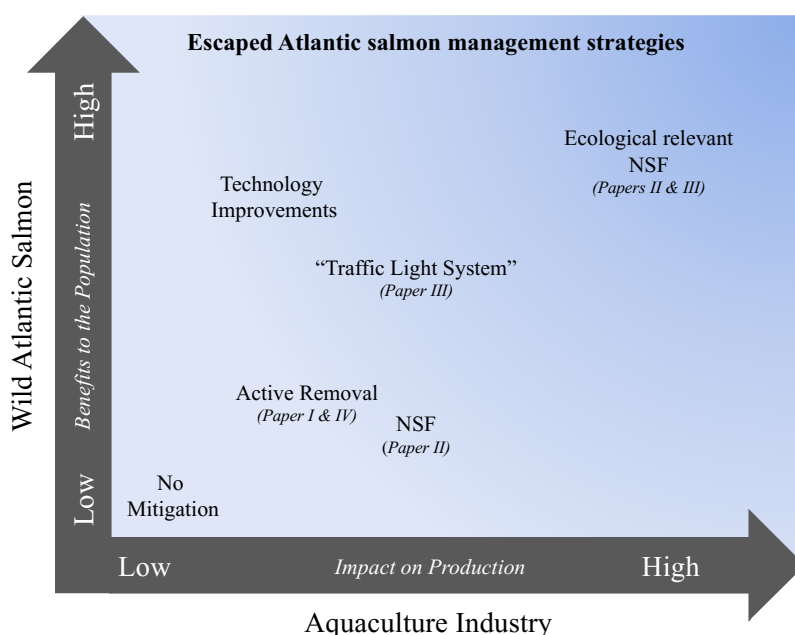


Figure 3. Current and potential management strategies to mitigate the impacts of escaped Atlantic salmon on wild Atlantic salmon (NSF = National Salmon Fjord).

4.1 The spatial overlap of wild and escaped Atlantic salmon

The spatiotemporal overlap of wild and escaped farmed Atlantic salmon can result in competition for mates and habitat (Robertsen et al. 2018). However, of greater concern is the long-term genetic degradation of wild Atlantic salmon stocks (Bolstad et al. 2017, Skaala et al. 2019). For introgression to occur, wild and escaped Atlantic salmon must overlap in space and time. Therefore, to understand the threat of introgression and how to best mitigate interactions between conspecifics, it is necessary to first understand the underlying mechanisms that contribute to the direct spatial overlap between wild and escaped farmed salmon.

After escape, the overlap of wild and escaped farmed Atlantic salmon starts in the marine environment. Unlike wild salmon, escaped farmed Atlantic salmon lack imprinted natal cues to specific rivers (Jonsson and Jonsson 2011), and if present, are thought to be more general to a given area (Skilbrei et al. 2015). Thus, escaped Atlantic salmon require secondary navigational strategies to find rivers to spawn (e.g., collective migration hypothesis; Berdahl et al. 2016). For example, a key factor that determined the abundance of escaped Atlantic salmon in rivers and spawning sites is the abundance of wild salmon (i.e., it seems evident that farmed fish are found in the same places as wild fish independent of the habitat; **Paper III**, **Paper IV**, Jonsson et al. 2003). With the high affinity of wild salmon to congregate for extended periods of time in spatially distinct areas just prior to river entry (**Paper II**), the probability increases that escaped salmon can locate groups of wild salmon via pheromones and other biological cues (Bett and Hinch 2015). Escaped salmon may then follow wild salmon into their respective rivers (**Paper III**) and spawning sites (**Paper IV**; Berdahl et al. 2017). Social mechanisms, like the collective migration theory (Berdahl et al. 2016), likely play an active role in the distribution of wild and escaped Atlantic salmon and managing escaped farmed Atlantic salmon within this context can improve our ability to mitigate the threat of escaped salmon (e.g., 4.2.4 National Salmon Fjords).

River specific distributions can have important implications for the success of introgression. The distribution of the spawning population of salmonids along the riverscape continuum provides an important insight into how populations are affected

and potentially allow managers to identify bottlenecks that affect the productivity of the river (Atlas et al. 2015). For instance, juvenile salmonids have limited ability to disperse after emergence from the gravel. Consequently, aggregations of nests can result in density-dependent effects, such as reduce individual growth from increased competition (Einum et al. 2006, Einum et al. 2008) and decreased survival (Einum and Nislow 2005, Einum et al. 2008). One might envision that such density-dependent mechanisms can help buffer the population against the effects of introgression. For example, offspring of escaped farmed fish are inferior competitors compared to their wild conspecifics in river settings (Fleming and Einum 1997), and the inclusion of domesticated- and hybrid origin individuals increases the competition for resources and reduces the river capacity of wild smolt production (Skaala et al. 2012, Skaala et al. 2019). Yet, results from the Guddal River, Norway, indicates that rivers sites that display increased density-dependency also have a greater difference in survival between wild and escaped framed Atlantic salmon (Skaala et al. 2019).

Although a small dataset, comparing data on the distribution of escapees from this thesis to introgression rates suggests that sites with small unimodal distributions of wild spawning salmon (e.g., River Granvinselva mean 68 wild salmon per year, **Paper IV**) also have a greater population level introgression rates (10 % probability of being wild; supplementary material in Karlsson et al. 2016). However, in rivers with more robust populations (e.g., Eidfjordvassdraget has mean yearly abundance of wild salmon = 151, **Paper IV**), population level introgression was shown to be more resilient even though distributions of spawners are also lumped together (92 % probability of being wild; supplementary material in Karlsson et al. 2016). Clearly, the robustness of the wild population is an important buffer against introgression. However, this effect is most likely affected by the distribution of escapees within the river and following local density-dependent completion between wild and farmed fish.

River fragmentation may also play an important role in limiting the rate of introgression. The distribution within the watercourse is dependent on the connectedness of the habitat patches (Parry et al. 2018). For instance, Sylvester et al. (2018) found that the hybridization rates decreased with the number of obstructions within the river. Furthermore, while anthropogenic barriers are easily definable in

space and time, natural fragmentation is less obvious in the context of partial barriers (e.g., flow dependent structures that are only passable to the most fit individuals). By identifying natural barriers within a river, (Enqvist 2020) found that escaped salmon passed significantly less barriers than wild Atlantic salmon and sea trout. While fragmented rivers often have detrimental effects to wild populations (Mahlum 2014), in some instance (e.g., invasive species), natural and anthropogenic barriers can help protect species at risk, such as the interbreeding of wild and escaped Atlantic salmon.

Understanding the distribution of escaped farmed salmon relative to wild salmon outside (**Paper II**), among (**Paper III**), and within rivers (**Paper IV**) is an important first step into developing robust ecological advice to resource managers. The distribution of escaped salmon is dependent on the behavioral mechanisms (e.g., collective migration hypothesis) and the geomorphological attributes of the river. However, the risk of introgression is likely more complex and depends on the ability of the wild population to absorb the yearly abundance of escaped salmon and to minimize long-term introgression rates (e.g., density-dependency relationships; section 4.1). It is therefore necessary to build upon existing knowledge to continue to identify the mechanisms that affect introgression to better refine effective management strategies (e.g., density-dependent relationships of wild and escaped farmed salmon at broad spatiotemporal scale; Osmundsen et al. 2017).

4.2 Mitigation of escaped farmed Atlantic salmon

Mitigating the risk of introgression should be a principle objective when recommending future aquaculture sites or when evaluating current production limits. The development and implementation of different MSP tools can alleviate the pressure of escaped Atlantic salmon on wild conspecifics and build a sustainable industry. Here, I will discuss current management strategies, their limitations, and how the new insights from this thesis might impact how we mitigate escaped farmed salmon populations and manage aquaculture production in the future (Figure 3).

4.2.1 No mitigation

The absence of mitigation of escaped salmon was largely relevant at the early onset of the aquaculture industry when the industry benefited from high growth rates (Figure 2). However, in the late 80's and early 90's, researchers became concerned over the potential genetic degradation of wild populations (Gausen and Moen 1991). Then, with advances in genetic analysis at population levels to track the rate and degree of introgression (Karlsson et al. 2011), it became evident that the interbreeding between wild and escaped Atlantic salmon was eroding the unique genetic signature of wild salmon populations (McGinnity et al. 1997, Karlsson et al. 2016) with clear ecological impacts on the population (Bolstad et al. 2017, Skaala et al. 2019). Because of the negative consequences of introgression, long-term mitigation strategies are required to preserve the existing populations of wild Atlantic salmon from further degradation.

4.2.2 Monitoring and active removal

Active removal of escaped farmed salmon is a reactive management strategy that is widely used only after an escape event occurs. Tracking escapees in rivers can be difficult and a range of methods are used to try and quantify and remove escaped Atlantic salmon. Norway has over 400 salmon populations (Anon 2016) and the monitoring of escapees within these rivers has been conducted across Norway since 1989 (Diserud et al. 2019). The National Salmon Program (NSP) in Norway has evolved into a broad scale collaboration of five research institutes surveying 241 rivers in 2017 (Glover et al. 2019). Here, the primary directive of the NSP is to quantify the proportion of escaped salmon in important salmon rivers (Glover et al. 2019). The NSP uses several sampling methods to track and provide mitigation advice for stakeholder to reduce the impacts of escaped farmed salmon (utfisking.no). Then, based on advice from the NSP, the "Oppdrettsnæringens sammenslutning for utfisking av rømt oppdrettsfisk" (OURO) distributes funds for the active removal of escaped Atlantic salmon in rivers. Through this mitigation program, escapee abundances are reduced to levels that are believed to be within limits to prevent long-term impacts from introgression (Næsje et al. 2013, Skoglund et al. 2019).

The differences in the spatial and temporal distribution of conspecifics can produce biased estimates of escaped farmed Atlantic salmon. The quantification of escaped farmed Atlantic salmon is primarily accomplished through either the direct visual observations based on distinctive morphological characteristics (e.g., video analysis and drift diving, **Paper I**, Svenning et al. 2017) or through the evaluation of growth rings of scales obtained during captures (primarily based on rod and reel captures; Diserud et al. 2019). Monitoring of a single river can occur in the course of a day (e.g., drift diving), several weeks (e.g., autumn fishing surveys), or even months (e.g., summer sports fishing). The methods that have extended sampling periods risk the increased likelihood that populations non-randomly change over time and result in biased estimates (Kendall 1999, Maunder and Punt 2004). For example, escaped Atlantic salmon enter rivers later than wild salmon and may create a sampling mismatch between wild and escaped salmon (e.g., seasonal closures of sports fishing; Jonsson et al. 1990, Heggberget et al. 1993, Erkinaro et al. 2009) and can result in the two conspecifics exhibiting large differences in catchability (Harvey et al. 2017, Svenning et al. 2017). In addition, the spatial distribution of escaped farmed Atlantic salmon has a high degree of variability among years (**Paper IV**) and many of the commonly used removal methods (e.g., snorkeling and net captures) are constrained to sites that can be effectively sampled, which have limited efficiency in large river systems (**Paper I and IV**). Failure to account for changes in variation and sites with limited sampling capabilities can produce biased estimates (Moe et al. 2016) and limit the effectiveness of active monitoring and removals.

Active sampling methods can also have negative impacts on wild salmon. Sampling of adult Atlantic salmon occur close to or during spawning activities. This can be a sensitive time and invasive sampling techniques that capture and remove individuals may induce unnecessary stress on individuals, which alters their behavior (Lennox et al. 2017, Lennox et al. 2019), and in some instances can result in greatly depreciated successive spawning events (e.g., brood stock fishing; Bordeleau et al. 2018). Repeat spawners constitutes less than 10 % of the population, but plays an important role in supporting the populations during low recruitment years (Bordeleau et al. 2019). Therefore, continued active monitoring of escaped farmed fish (e.g. rod

fishing) during or close to spawning may have unintended consequences in the long-term persistence of the population.

To ensure representative abundance estimates of escaped salmon while minimizing the impact on wild fauna, it is necessary to promote methods that are characteristic of the entire anadromous reach (e.g., drift diving) or all individuals returning to spawn (e.g., whole river fish traps or video analysis; Svenning et al. 2017, Glover et al. 2019). For instance, drift diving has been shown to have minimal bias when quantifying wild salmon (**Paper I**, Orell and Erkinaro 2007, Orell et al. 2011) and is a robust method when estimating the proportion of escaped salmon (**Paper I**). By sampling the entire anadromous reach in a single event, drift diving can compensate for both the potential disparity in catchability seen in capture methods and provide representative estimates of abundance. Furthermore, drift diving allows for the passive observation of Atlantic salmon populations with limited or no short- or long-term impacts that are seen in active sampling methods (Snyder 2003).

The continued monitoring and removal strategy should be considered a secondary measure of mitigating escapee impacts when primary measures fail (e.g., structural failures of net pens). The unknown biases among sampling methods could result in recommendations to OURO that are limited when mitigating interactions between wild and escaped salmon. Surprisingly, potential biases associated with catch statistics have not been addressed and future research is needed to explore the catchability dynamics of escaped and wild Atlantic salmon to understand the limitations of the different methods. Consequently, it is difficult to determine how and to what extent estimates of escaped salmon based on catch statistics are biased and how limitation of the sampling and removal methods impacts our ability to effectively provide sound management advice to policy makers. Taken together, i.e. the uncertainty of sampling methods and the inefficiency of removal strategies in some rivers, more proactive strategies, such as production limits, new technologies or implantation of ecological relevant MPA's, should be relied upon to reduce the risk of escapees directly interacting with wild fauna.

4.2.3 Regulating escapees with production limits (traffic light system)

Acknowledging the need to refocus the management of salmon aquaculture based on an ecosystem-based approach, the Norwegian government mandated that future growth of the industry will be directly linked to the ecological impacts on the environment (Guttormsen 2015). To address this need, a new regulatory framework, termed the traffic light system, was implemented in 2017 and requires that industry growth will be conditional on minimizing their ecological footprint. Within this framework, the coast is divided into 13 production zones where production levels are based on key environmental indicators. Currently the implementation of the traffic light system is based on the predicted mortality of out migrating smolts from sea lice pressure within a production zone (Vollset et al. 2017). However, to incorporate an avenue within the current regulatory framework to include escaped salmon as an indicator (Guttormsen 2015), it is necessary: 1) that the impact is measurable (e.g., escaped salmon abundance) and closely linked to aquaculture production (e.g., concessions) and 2) to identify the carrying capacity of the system (e.g., abundance of wild Atlantic salmon) to buffer against the long-term impacts from escaped salmon in rivers (e.g., critical thresholds of escapee abundance relative to wild salmon abundance; Næsje et al. 2013, Diserud et al. 2019).

The production of aquaculture is directly related to the abundance of escaped farmed salmon in rivers. By assessing a range of metrics (e.g., reported escapees and *in situ* production values) across spatial scales (up to 100 km from the river mouth), **Paper III** linked the concessions allotted to aquaculture sites (within a 75 km buffer from the river mouth) to the abundance of escaped farmed Atlantic salmon in rivers. Surprisingly, few studies have attempted to link aquaculture production to the abundance of escaped salmon in rivers and the studies that have explored mechanism of escapee abundances in rivers often focused on the reported number of escapees (**Paper III**, Walker et al. 2006, Green et al. 2012, Skilbrei et al. 2015). However, this has yielded disappointing results, which is believed to be from a chronic underreporting of escape events (up to two- to four-fold underreporting; Skilbrei et al. 2015). Directly linking aquaculture production to escaped salmon in rivers provides stakeholders a

valuable tool to proactively regulate the threat of escaped salmon in rivers towards desired thresholds.

The ability of the environment to absorb escaped salmon with minimal long-term impacts on wild Atlantic salmon is dependent on the size of the wild population. Several studies have found a correlation between the abundance of wild and escaped farmed Atlantic salmon (**Paper III**, Jonsson et al. 2003). If escaped salmon are drawn to rivers with more robust populations that can withstand long-term introgression, then it is necessary to take steps to preserve these populations to maintain their resiliency. However, the wild salmon abundance of many Norwegian rivers is often less than 100 wild individuals (**Paper III**, Gausen and Moen 1991), and in such cases, even low abundances of farmed escaped salmon (> 4 individuals) can increase the risk of long-term genetic impacts (Diserud et al. 2019). It is therefore necessary to ensure that wild populations are robust to help buffer against introgression and thus increase the production potential of natural systems (**Paper III**).

The regulation of aquaculture production based on the abundance of escaped salmon in rivers will provide a strong long-term management tool in mitigating introgression (Figure 3). Furthermore, regulating based on known relationships of escapee abundance and aquaculture production is important when assessing future aquaculture sites and the potential risk of introgression between conspecifics. By understanding the relationship between the abundance of wild and escaped salmon, resource managers can continually adjust the production limits based on the population status of wild salmon stocks. This will likely result in decreasing production in areas where wild salmon populations are low with limited capacity to buffer against introgression (e.g., Hardangerfjord, **Paper III**), but indicate an increase in production in areas with more robust salmon populations and an increased capacity to buffer against introgression (Ryfylke, **Paper III**). This would provide added industrial incentives to maintain and improve regional salmon populations to increase aquaculture production and thus capitalize on improved regional carrying capacities.

4.2.4 Marine Protected Areas

The implementation of MPA's is a special type of MSP action used to reduce the ecological impacts of human influences. Marine protected areas are primarily established to protect sensitive habitats or species or for the management of restoring commercially important fisheries (Sørensen et al. 2008). Often, MPA's range in protective status with no-take reserves regarded as the strictest to partially protected areas that allow various forms of activity (e.g., sports fishing; Agardy 2000, Lester and Halpern 2008). In Norway, MPA's are used to buffer wild populations from the side effects of aquaculture.

Current National Salmon Fjords

The implementation of the NSF's, a partially protected MPA, were designed to buffer important wild salmon producing rivers from disease, parasites, and introgression connected to aquaculture sites (Aasetre and Vik 2013). The current structure of the NSF's is based on the implementation of 52 temporary protected zones in 1989. Then in 2002, twenty-one permanent NSF's were established (DKMD 2002a, b) with an additional 8 NSF's included into the regulatory structure in 2007 (DKMD 2006) to a total 29 NSF's.

Many of the current NFS's have limited success in meeting their stated regulatory goals. Several studies have assessed the effectiveness of NSF's and found that they had minimal impacts in protecting salmonids against sea lice (Bjørn et al. 2011, Serra-Llinares et al. 2014). **Paper II** determined that the current size of the NSF failed to encompass the habitat that is used by returning wild Atlantic salmon and that salmon directly overlapped with aquaculture sites. This echoes' previous studies indicating that the effectiveness of the current NSF is site- dependent and that smaller NSF's provide minimal protection (Bjørn et al. 2011, Serra-Llinares et al. 2014). Furthermore, after accounting for the wild population size, Hindar et al. (2018) found that the percentage of escaped salmon was consistently lower in rivers located in protected areas. However, no clear difference in genetic introgression was observed between rivers located within and outside the NSF (Hindar et al. 2018).

Ecological Relevant National Salmon Fjords

Ecologically relevant NSF's need to account for the biological attributes of the species of interest. To function properly, protected areas need to be large and encompass the habitat that is routinely used by the target species. Otherwise, it may result in a mismatch between the MPA boundary and the habitat that the species occupies (Lennox et al. 2018). Therefore, to buffer against introgression, NSF's need to inhibit the initial spatial overlap of wild and escaped Atlantic salmon in the marine environment. This can be accomplished through either the protection of habitat that is routinely used by wild Atlantic salmon (**Paper II**) or by buffering rivers based on the spatial scales that escapees act (**Paper III**).

Effective MPA's to buffer rivers against introgression need to have ecological relevant spatial extents to be effective. Studies that assessed escaped salmon distribution, found that escapees entered rivers within 150 km from release with most observing escaped salmon entering rivers within 90 km from release (Heggberget et al. 1993, Jonsson et al. 2003, Hansen and Youngson 2010, Quintela et al. 2016). In addition, within this spatial extent, the rivers with the more robust populations attract more escaped salmon (**Paper III**, Jonsson et al. 2003). Potentially, two different spatial extents can be used to create ecologically relevant NSF's. First, because returning wild Atlantic salmon have long residence periods (**Paper II**, Thorstad et al. 2003) in spatially distinct areas of the marine habitat (**Paper II**), excluding the production of domesticated salmon from areas where wild salmon reside prior to river entry, can help reduce the risk of escaped salmon finding and following wild salmon to spawning rivers (see section 4.1). However, this is predicated on a strong understanding of habitat use by wild salmon, and such information is often absent or requires extensive remote telemetry methods to acquire (Lennox et al. 2018). Alternately, the "scale of effect" that aquaculture production is related to the abundances of escaped salmon in rivers can be used to create ecologically relevant NSF's boundaries (Jackson and Fahrig 2012). For example, **Paper III** found that the concessions allowed within 75 km from the river was the best predictor of aquaculture production related to the number of escaped salmon in the rivers. Because active monitoring is more common in rivers compared to extensive remote telemetry studies, resource managers would likely be

more successful using the “scale of effect” in designing ecological relevant MPA’s. Implementing ecologically relevant MPA’s would reduce the likelihood of escapees inhabiting areas of high salmon abundance and subsequently migrate into the rivers to spawn.

Effective MPA’s will always directly impact the production of aquaculture by decreasing the already constrained allowable habitat that can be used (Sanchez-Jerez et al. 2016). In extreme cases, if the protected areas are implemented based on the spatial scope that aquaculture acts on the abundance of escaped salmon in rivers (75 km buffer from rivers), this could effectively close the existing aquaculture industry. While broad scale exclusion zones would potentially be very beneficial to the wild salmon population, it will have detrimental impacts to the local economies that depend on aquaculture. Therefore, the use of MPAs should be used sparingly when other mitigation strategies fail to protect important populations of Atlantic salmon.

4.2.5 New Technologies

Aquaculture is a dynamic industry (Osmundsen et al. 2017) and the relationships between aquaculture and escapee abundance among and within rivers is conditional on the current technology (e.g., farm retention measures) and the legal guidelines that regulate it. However, evolving technologies can have profound impacts on the industry and the long-term viability. The most notable was the initial development net pen facilities that allowed for aquaculture to move to the marine environment. Below, I briefly discuss some recent technological developments and how they may allow industry to continue to grow while minimizing the threat of introgression.

First, improvements in site retention will result in increases in carrying capacity of the system. For example, in 2004, universal net-pen construction regulations resulted in decreases in reported escaped events despite increases in production (Jensen et al. 2010). Continued technological improvements (e.g., self-contained or land-based aquaculture sites) would result in increases of the carrying capacity of the ecosystem and thus parallel increase in aquaculture production. Retention is the most important factor that can help mitigate the genetic interactions between wild and escaped farmed

fauna. In addition, the improved retention of salmon will directly result in increases in production that is otherwise lost when individuals escape.

Second, the degree of the impact from escapees is dependent on the competitive ability of escaped Atlantic salmon relative to wild salmon and how they interact in space and time (Houde et al. 2017). The abundance of escaped Atlantic salmon are still at levels deemed as high risk for introgression and one way to potentially reduce the risk is to use sterile fish. Of the methods to sterilize individuals (see Benfey 2016 for a review), the use of triploids females presents the most robust avenue. Unlike triploid males (Fjelldal et al. 2014), females have inhibited spawning behaviour and are less likely to migrate to freshwater to spawn (Glover et al. 2016). Overall triploid fish display similar qualities to their diploid counterparts. However, concerns have been raised regarding their robustness to disease and parasites and their ability to seek reservoirs for pathogens (Benfey 2016). Still, by eliminating the ability for introgression to occur, the direct interactions with wild fauna will likely have minimal long-term effects on wild populations.

The development of offshore aquaculture can potentially reduce the direct interaction of aquaculture with wild fauna. Aquaculture is predominantly located within nearshore habitats where refugia from the open ocean is best. However, it is believed that large scale increases in aquaculture production will need to capitalize on the new habitats such as the open ocean (see Gentry et al. 2017 for a recent review). Shifting new production sites to offshore habitat can reduce the pressure and potentially separate some of the mechanisms that are important for escaped salmon to find rivers (section 4.1, **Paper III**). In addition, relocating aquaculture to offshore environments can potentially also have important secondary benefits that are critical for sustainable aquaculture (e.g., reduction of disease and parasite transmission pathways).

The discovery and implementation of new technologies will likely have the greatest impacts on limiting the negative interactions between aquaculture and the surrounding environment. New technologies often have steep initial cost during development, however, once established and tested, can result in increased industrial growth. While the previous strategies will help alleviate the symptoms that impact the environment (e.g., concession limits and MPA's), only improvements in the retention

of domesticated salmon or directly inhibiting introgression will instil long-term environmental stability to the industry.

4.3 Conclusion

The main objective of my thesis was to evaluate the spatial overlap of wild and escaped farmed salmon and the potential implementation of effective management policies to mitigate introgression. Following Atlantic salmon from the fjord to the river with the use of fine scale data (remote telemetry and snorkel estimates), I was able to help clarify how both wild and escaped Atlantic salmon interact across the landscape. Moreover, I outlined how understanding these mechanisms is critical when applying ecological relevant management strategies (e.g., concession limits) and understanding their strengths (e.g., proactive strategies) and weaknesses (e.g., reactive strategies).

Important information was ascertained from this thesis pertaining to the spatial overlap of wild and escaped farmed Atlantic salmon. However, less attention has been shown to the increased risk of intraspecific introgression between sea trout and escaped Atlantic salmon. Natural introgression between Atlantic salmon and sea trout can occur but is considered rare (see Adams et al. 2013 and references therein) and natural introgression between salmonid species is restricted based on spatiotemporal differences in spawning. The spatial overlap (**Paper III**) and early spawning of escaped salmon (Lura and Sægrov 1993) may indicate that sea trout have an increased risk of mating with escaped Atlantic salmon (Hindar and Balstad 1994). Studies that have focused on introgression rates between escapees and sea trout found interspecific introgression frequencies range from < 1% up to 41 % (Youngson et al. 1993, Jansson and Öst 1997, Hórreo et al. 2011), which can result in the suppressed growth of wild fauna (Oke et al. 2013). Therefore, the potential for increased interspecific introgression rates, future research should also be directed into the broad scale impacts of the interspecific hybridization of sea trout populations and the potential ecological effects.

This thesis fills important knowledge gaps needed to help incorporate ecologically pertinent metrics into current and future management strategies. It is

recommended that stakeholders shift focus on limiting the interactions of wild and escaped farmed salmon through the use of 1) technological advances that inhibit the potential for introgression (e.g., closed systems, or triploid females) or 2) the use of proactive strategies, such as concession limits (e.g., traffic light system) or through complete closures of ecologically relevant protected areas (e.g., NSF). Furthermore, reactive mitigation efforts (e.g., active removals within rivers) should be used as a last resort when primary mechanisms fail (e.g., net failures). Therefore, incorporating metrics that allow for robust wild salmon populations to persist, my thesis will help propagate the salmon aquaculture sector in an environmentally sustainable manner while also promoting the continued economic success of the industry.

Source of data

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Papers

Paper I



Swimming with the fishes: validating drift diving to identify farmed Atlantic salmon escapees in the wild

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ABSTRACT: Escaped farmed Atlantic salmon *Salmo salar* interbreeding with wild conspecifics represents a threat to the genetic integrity and viability of wild populations. Therefore, it is necessary to accurately quantify escapees in riverine systems to monitor and mitigate interactions with wild conspecifics. Drift diving surveys are presently used in Norway to quantify the number of wild and escaped farmed salmon in rivers. However, limited information is available on the validity of the method for distinguishing escapees from wild conspecifics. Comparing the proportion of escapees calculated from drift diving (mean = 8.5%) and net captures (mean = 8.6%), we found that drift diving was well correlated with net captures (adj. $r^2 = 0.79$). Furthermore, scale analysis from an independent data set demonstrated a 98% true positive rate when identifying and capturing farmed escapees during drift diving. The results of this study indicate that drift diving is an accurate and robust method for quantifying escaped farmed salmon, at least in rivers where observation conditions are adequate for snorkeling. In general, drift diving can be a valuable tool for stakeholders to quickly assess broad spatial extents with limited time and resources.

KEY WORDS: Snorkeling · Domesticated salmon · Aquaculture · Bayesian · Method comparison · Escaped farmed salmon · Mitigation

1. INTRODUCTION

The introduction of exotic species is a well-known risk to the ecological integrity of many ecosystems (Wilcove et al. 1998). Less known is the impact of introduction of non-native genotypes into a population from conspecifics through restocking programs, which has resulted in reductions in overall population fitness (Champagnon et al. 2012). The expansion of aquaculture over the last century has resulted in the unintentional introduction of domesticated animals to regions that they would not have otherwise inhabited (Naylor et al. 2001). Aquaculture facilities have provided source populations that can inadvertently escape into the surrounding biome and produce self-sustaining populations—or in some cases,

interbreed with existing wild conspecifics, thereby introducing deleterious domesticated genetic attributes into the wild population (Glover et al. 2017).

Over the last several decades, declines in wild Atlantic salmon *Salmo salar* populations have been reported throughout their historic range (Parrish et al. 1998, Friedland et al. 2003, Chaput 2012, Soto et al. 2018). During the same time period, there has been an increase in the production of domesticated *S. salar* (Gross 1998, Bostock et al. 2010). One of the biggest environmental challenges related to salmonid aquaculture is the escape of farmed individuals that disperse from cultivation sites and migrate into rivers to spawn (Taranger et al. 2015, Forseth et al. 2017). Retention of farmed fish within net pen facilities has greatly improved with time (Jensen et al.

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2010), yet escape events still occur at levels that pose a significant threat to wild populations of salmon (see Wringe et al. 2018 for a recent example). To circumvent the ecological ramifications of escaped farmed salmon, various stakeholders have increased awareness and efforts to monitor the presence of escapees in wild populations (Glover et al. 2019) and to mitigate the effects that can occur between wild and farmed salmon.

Introgression of domesticated escapees is considered to be one of the most significant threats to native *S. salar* populations in countries where salmon aquaculture is practiced (Taranger et al. 2015, Forseth et al. 2017). This phenomenon has been documented in the wild for decades (Diserud et al. 2019, Glover et al. 2019), and extensive introgression and hybridization has been observed in areas where aquaculture and wild *S. salar* overlap (Clifford et al. 1998, Glover et al. 2013, Karlsson et al. 2016, Wringe et al. 2018). While consequences arising from escaped salmon are likely to be population-dependent (Fraser et al. 2010, Glover et al. 2013, Heino et al. 2015, Wringe et al. 2018), the offspring of domesticated salmon, and their hybrids with wild salmon, display reduced survival in the wild (McGinnity et al. 1997, Fleming et al. 2000, Skaala et al. 2012, 2019). Therefore, introgression of domesticated escapees in native *S. salar* populations, if extensive enough, may ultimately lead to the extirpation of vulnerable populations (McGinnity et al. 2003, Castellani et al. 2018). It is therefore imperative to be able to quantify escaped salmon in relation to specific populations so that management strategies (e.g. escapee removals and improved retention within net pens) can be implemented or improved to minimize the risk of further introgression. However, river systems where *S. salar* reside often encompass broad spatial scales that can be time-consuming and costly to manually survey and difficult to attain a representative sample.

Quantifying escaped farmed salmon in a river can be challenging. Common survey techniques (e.g. mark–recapture or electrofishing) can incur undue stress on wild individuals at critical times in their life cycle (Snyder 2003), require releasing escaped salmon back into the system (e.g. mark–recapture), or are subject to limitations due to variation in the catch per unit effort (CPUE), which is beyond the changes in abundance (e.g. recreational fishing estimates; Maunder & Punt 2004). Similar to other observational methods (e.g. video surveillance and camera traps), drift diving represents a relatively non-invasive method to directly survey the abundance of different species (Pilliod & Peterson 2001, Ebner et al.

2015) in a range of habitat types (e.g. freshwater and marine ecosystems; St. John et al. 1990, Beauchamp et al. 1994, Toft et al. 2007), with extensive use in lotic ecosystems to monitor salmonids (Thurrow et al. 2006, Orell et al. 2011, Vollset et al. 2014). Although drift diving has been used for several decades to assess salmonid populations in rivers, some concerns exist (Dolloff et al. 1996). For instance, the accuracy and precision of drift diving may vary according to various factors, such as individual fish size (Slaney & Martin 1987, Hillman et al. 1992, Thurrow et al. 2006), density across various habitats (Hankin & Reeves 1988), habitat complexity (O’Neal 2007), and the tendency of individuals to seek specific habitat types (Orell & Erkinaro 2007). Although visual estimates may incur uncertainties with regards to precision, drift dive estimates can save time and expenses (Dolloff et al. 1996, Thurrow et al. 2006, Orell et al. 2011) and potentially increase the total habitat sampled, thus improving the overall abundance estimates of a system (Hankin & Reeves 1988).

Drift diving is one of the main sampling methods used to quantify the number and proportion of escaped farmed *S. salar* throughout rivers in Norway (data from 133 rivers included in the national monitoring program in 2017; Glover et al. 2019). In order to identify farmed salmon escapees through drift diving, it is necessary to be able to distinguish them from wild conspecifics by identifying variations in several phenotypic traits (e.g. spotting patterns; Jørgensen et al. 2018). However, in contrast to other methods implemented in the Norwegian monitoring program that involve capture and subsequent determination of origin through scale reading, the accuracy of drift diving in differentiating between escaped farmed and wild salmon is still to be investigated. Therefore, the overall aim of this study was to (1) assess the accuracy of quantifying the proportion of escaped farmed salmon using the abundance approximations from drift diving validated against net captures, and (2) establish the accuracy of identifying escaped farmed salmon (i.e. true positive rate; TPR) in rivers during drift diving when applying commonly used removal methods (e.g. harpoon).

2. MATERIALS AND METHODS

This study consists of 2 independent datasets to assess the accuracy of drift diving in identifying escaped farmed salmon. Dataset 1 is a comparison of the proportion of escapees at sites observed during drift diving and subsequent net captures. Dataset 2

quantifies the TPR of drift diving as a mitigation method to removed escapees from spawning sites.

2.1. Study sites

The rivers in which the methods were tested were located in 3 fjords in western Norway (Fig. 1). The rivers originate in alpine systems where steep gradients dominate the upper reaches of the watersheds and lower gradients dominate the lower reaches; hydropower is a prevalent feature in the landscape (6 of the 9 streams). Atlantic salmon *Salmo salar* and anadromous brown trout *S. trutta* represent the dominant salmonid species within the anadromous reaches of these rivers. The presence of aquaculture is variable among the 3 fjords with at least one National Salmon Fjord in each fjord complex that restricts aquaculture activities in these defined zones (Aasetre & Vik 2013). The rivers were chosen based on the frequent observations of escaped farmed salmon in previous years, and because they were suitable for catching and sampling fish to validate drift diving counts.

Sampling occurred from 2016 to 2018 in October and November when salmon returned to spawn. To directly compare salmon drift dive estimates, each site needed to have stream conditions that were conducive to the use of a beach seine or gill nets (e.g.

low flow velocities and limited in-stream structures such as large boulders and large woody debris). A total of 26 comparisons were conducted at 19 different sites among 9 watersheds (Table 1). Capture sites consisted of pools ranging in size from 716 to 15 179 m² that were chosen based on previous experience indicating that these locations were spawning and/or holding pools for salmon. One site was excluded from the comparison analysis based on unrepresentative net captures (<25% of the observed population during drift diving and an unequal CPUE towards escaped farmed salmon; Site 3 in Table 1).

2.2. Dataset 1: drift diving and net captures

Drift diving was conducted before the removal of fish (both wild and farmed) at a sampling site (~10 to 15 min). Prior to drift diving, underwater visibility (effective visibility; in m) was estimated as the distance at which features of the fish could be observed to assign the origin of the individual (e.g. wild vs. farmed). This was done by assessing objects with enough clarity to identify detailed characteristics (e.g. the facial features of a drift dive partner) and estimating the distance to those objects. A single downstream pass was used to count fish with experienced drift diving personnel, in accordance with Norwegian standards (NS 9456:2015). To maintain visual coverage of the stream width during sampling, the number of personnel (1 to 4 divers) was adjusted to the stream width and the effective visibility of the site. Only fish that passed upstream of the dive team were counted to avoid double counting of fish moving downstream. Upon encounter, fish were visually identified to species (i.e. *S. salar* or *S. trutta*), rearing origin (wild, hatchery, or farmed; see below), and size class (small: <3 kg; medium: 3 to 7 kg; large: >7 kg). For the purposes of this study, the offspring of wild salmon produced and reared in a hatchery and deliberately released into the river as juveniles for the purpose of supportive breeding were classified as wild (identified by lack of adipose fin, which was removed prior to release as smolts). Morphological differences were used to distinguish between the different conspecifics. Specifically, escaped farmed *S. salar* were distinguished based on differences in body proportions, fin erosion, morphology of operculum, behavior, and pigmentation (Lund et al. 1991, Walker et al. 2006, Erkinaro et al. 2010, Jørgensen et al. 2018).

To remove salmon from the site immediately following drift diving, we used either gill nets (length =

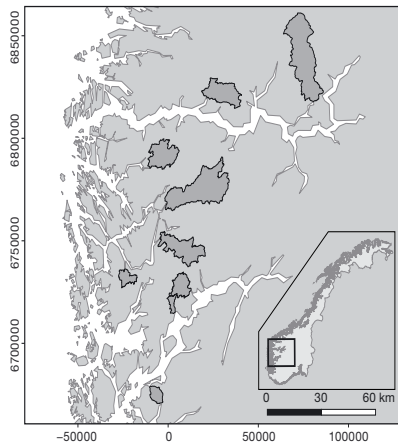


Fig. 1. Study area. Dark grey polygons: watersheds where comparison sampling occurred; black box: location in Norway (WGS84 / UTM zone 33N)

Table 1. Site, net captures, and drift dive observations of Atlantic salmon for each sampling year. First number: total captures; second number: total number of escaped farmed salmon (EFS). %EFS_m: mean proportion of escaped salmon for each year (bottom row) and site (column); **bold** %EFS_m numbers indicate the mean for each method. Site 3 was removed from the overall analysis due to biased sampling during net captures

Site	Net captures				Drift dive				Area (m ²)
	2016	2017	2018	%EFS _m	2016	2017	2018	%EFS _m	
Arnaelva									
Site 1	–	–	13/3	23.1	–	–	10/3	30.0	1054
Åroyelva									
Site 2	179/15	267/9	174/2	4.3	186/7	231/4	196/6	2.9	2482
Site 3	–	–	10/3	30.0	–	–	45/3	6.7	2894
Daleelva (Høyanger)									
Site 4	–	–	4/1	25.0	–	–	4/1	25.0	716
Site 5	–	–	10/1	10.0	–	–	12/1	8.3	1254
Site 6	14/1	7/0	17/1	5.3	15/1	8/1	23/1	6.5	2016
Site 7	7/1	–	–	14.3	11/2	–	–	18.2	2283
Site 8	–	11/0	–	0.0	–	15/0	–	0.0	4603
Site 9	9/2	4/0	–	15.4	10/2	5/0	–	13.3	871
Site 10	8/1	–	–	12.5	12/2	–	–	16.7	760
Site 11	–	8/0	–	0.0	–	9/0	–	0.0	3042
Daleelva (Vaksdal)									
Site 12	14/1	–	–	7.1	28/2	–	–	7.1	2905
Site 13	30/1	30/0	24/0	1.1	34/1	26/0	31/0	1.0	2803
Ekso									
Site 14	–	–	17/0	0.0	–	–	18/2	11.1	15179
Site 15	–	49/2	–	4.1	–	54/2	–	3.7	6609
Matreelva									
Site 16	–	–	9/2	22.2	–	–	9/2	22.2	1236
Steinsdalselva									
Site 17	–	–	5/1	20.0	–	–	5/1	20.0	1794
Strandadalselva									
Site 18	–	–	10/0	0.0	–	–	11/0	0.0	1500
Uskedalselva									
Site 19	18/0	–	–	0.0	18/0	–	–	0.0	1035
% EFS _m	9.4	1.1	12.5	8.5	9.4	2.6	11.9	8.6	

30 m, depth = 2 m, half mesh size = 45 to 75 mm), a beach seine (length = 40 m, depth = 6 m, half mesh size = 15 mm), or both during the capture process (referred to as net captures throughout). All nets were constructed of nylon. Prior to drift diving, the net was positioned at the back of the pool to prevent individuals from escaping downstream during drift diving. Once drift dive transects were completed, several personnel guided salmon into position to encircle them with the net. To limit accidental escape after capture, entanglement with the net, and to reduce stress during sampling, fish were removed from the capture area and placed in holding cages until processing (30 mm half mesh nylon; 100 × 50 × 50 cm). For each individual, we measured total length (cm), sex, noted the presence of an adipose

fin, and collected scales to determine the origin (described below). Fish identified as farmed escapees were killed upon capture, as the work, in part, was organized to reduce the incidence of farmed fish in the populations. In sites with more than 50 captured individuals, Finquel vet. (100 mg l⁻¹) was used to sedate the fish during workups; they were then placed in the cages to recover from the anesthetic (10 to 15 min from anesthesia to release).

In addition to comparing relative abundance of escapees between the 2 methods, we also assessed the accuracy of drift diving to differentiate among size classes. Correct size classification of salmon is important when assessing the impact of farmed fish, as fecundity is strongly size-dependent (Fleming 1996). Because no weights were taken and due to a lack of length–weight regressions specific to the different populations sampled, we categorized size classes of net captures based on the sea winter age (calculated from scale reading; SW) and length of wild *S. salar* caught in the net. We classified the SW stages as 1, 2, and 3+ SW age classes. Then, we calculated the 25 and 75% quartile (interquartile range; IQR) of length for

each SW and divided the difference in length of the IQR between adjacent SW by 2. This created breaks at 70.5 cm between 1 and 2 SW fish and 88.5 cm for 2 and 3+ SW fish (horizontal lines in Fig. 2). To compare to drift dive size classifications, net-captured salmon <70.5 cm were classified as small, 70.5 to 88.5 cm were classified as medium, and >88.5 cm were classified as large.

2.3. Dataset 2: removal of escaped farmed salmon during drift diving surveys

A secondary independent dataset was incorporated to supplement the study and to compare the TPR (proportion of positively identified farmed

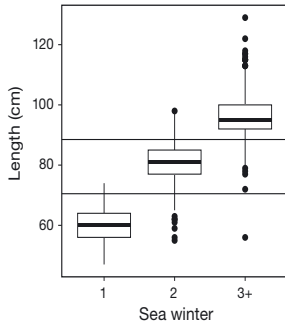


Fig. 2. Size classification of Atlantic salmon net captures based on sea winter age. Solid horizontal lines: length breaks into small, medium, and large size classifications. Boxes: interquartile range (IQR); horizontal lines in the boxes: median values; whiskers: 1.5 times the IQR; solid circles: outliers

escaped salmon) of identifying escapees during routine removals of escapees from rivers with drift diving. Significant resources are diverted throughout Norway to mitigate potential introgression with wild fish, and drift diving is one method used to identify and actively remove escaped farmed salmon from the watercourse where introgression is prone to occur. Removals included in this study are located throughout western Norway among 35 rivers (8 of 9 rivers from data set 1) and involved data from 2016 to 2018. Consistent with drift diving protocols described above, the removals were carried out by the Norwegian Research Center (NORCE). Once visually identified as farmed escaped salmon, harpoons were used to remove individuals. The total length (cm), wet mass (kg), sex, and maturity stage (visual inspection of gonads) were recorded, and scale samples were collected to confirm the individual was of aquaculture origin.

2.4. Origin classification based on scale readings

To verify the visual identity of each fish captured with nets and removed with harpoons, scales were taken just posterior of the dorsal fin directly above the lateral line. Origin was based on variations of seasonal growth rings as described in Fiske et al. (2005). Consistent with Diserud et al. (2019), the origin for net-captured individuals with unidentifiable scales was based on visual identification at capture ($n = 46$; see Table 2). Individuals with missing or un-

readable scales from dataset 2 were removed when calculating the TPR ($n = 2$; see Table 2). Scale readings were performed by NORCE, the Institute of Marine Research, and Rådgivende Biologer AS.

2.5. Analysis

We first used a generalized linear model (Poisson error) to regress the abundances of the 2 methods to determine their precision and any indication of unwanted bias (e.g. outliers signifying an unrepresentative sample for either method). To account for left skewedness of the data distribution, relative abundances were log transformed. A strong relationship with small variance would indicate that the methods had equivalent performances when sampling the populations of interest, and deviations would indicate a potential sampling bias between the 2 methods. A Bayesian inference was implemented to compare the proportion for each size category (small, medium, large) and the proportion of farmed escapees observed between drift diving (explanatory variable) and net captures (response variable). No information was available for a prior distribution for the Bayesian inference; therefore, we used a diffuse normal prior for the intercept and slope (uninformative). Because of violations of model assumptions (non-normally distributed residuals), the failure of model outputs with a binomial distribution to fit the data, and an expected linear relationship between methods, we deferred to a Gaussian distribution instead of the preferred binomial distribution for proportion data. Furthermore, to control for the impact of increased deviations in the proportion of farmed escapees at sites with small counts, we weighted each sample by the sample size of net captures, thereby giving more weight to larger catches. We ran 5000 burn-in iterations across 3 chains before running the 15 000 Markov chain Monte Carlo samplings (45 000 total iterations). Model convergence was achieved based on the low variance between chains (Gelman-Rubin diagnostic test < 1.05 ; Gelman & Rubin 1992) and visual inspection of the posterior distributions. In addition, 2 data points indicated a large difference in the proportion of farmed escapees between the 2 methods (extreme outliers). Therefore, we compared the goodness-of-fit (adj. r^2) of the model that included all sampling points (primary model) and a model excluding the 2 data points which were believed to be outside the ability to accurately identify and quantify individuals at a site (i.e. observed escape of salmon during capture from the

Table 2. Net captures, drift dive observations, and harpoon removals of Atlantic salmon. Rearing origin was determined from scale readings, and individuals were classified as wild (W), escaped (E), or unknown (U). Scales were classified as unknown if they were missing, damaged, or new (i.e. lacking an entire growth cycle). Size was categorized by weight for drift diving (small [S]: <3 kg; medium [M]: 3 to 7 kg; large [L]: >7 kg) and by mean length (cm) for net captures and harpoon removals

	Total	Rearing origin			Size			Sex		Mature	
		W	E	U	S	M	L	M	F	Yes	No
Drift diving											
2016	314	297	17	–	36	169	109	–	–	–	–
2017	348	241	7	–	43	177	128	–	–	–	–
2018	364	344	20	–	83	160	121	–	–	–	–
Seine											
2016	279	252	21	6		84		98	179	–	–
2017	376	352	11	13		86		137	239	–	–
2018	288	250	13	25		82		151	137	–	–
Harpoon											
2016	91	0	89	2		78		50	40	66	25
2017	48	0	48	0		77		25	20	38	9
2018	46	1	45	0		75		29	17	42	4

site; open circles in Fig. 5). All analyses were done within the statistical programs R v.3.5.2 (R Core Team 2018) and JAGS v.4.3.0 (Plummer 2003).

3. RESULTS

A total of 1026 salmon were counted and identified through drift diving; of these, 943 were subsequently captured and verified through scale analysis (Table 2). Among the captured individuals, 45 were classified as true escaped farmed salmon and 854 were classified as true wild salmon based on the results from the scale analysis (Table 2). The origin of the 44 individuals with unreadable scales was determined by visual identification. For individuals whose origin could be verified during scale readings, the accuracy of the visual identification on land for net captures was very high (96 and 99% for farmed escaped and wild origin, respectively).

3.1. Dataset 1:
drift diving and net captures

Comparison of the abundances between the 2 methods demonstrated that drift diving and net captures were very highly correlated ($r^2 = 0.99$; Fig. 3) with a near 1:1 relationship between the methods (slope = 1.06, $z = 37.202$, $n = 25$, $p < 0.001$; Fig. 3). The overall trend showed that net captures of Atlantic

salmon were lower compared to drift dive counts of Atlantic salmon, which was likely due to difficulties in obtaining all fish in a site, as some fish were observed to escape during capture attempts.

Overall, drift diving classified salmon into different size categories relatively well compared to net captures (small: adj. $r^2 = 0.5$; medium: adj. $r^2 = 0.37$; large: adj. $r^2 = 0.55$) with no significant deviation from the expected 1:1 relationship (small: mean = 0.96, lower CI = 0.75, upper CI = 1.16; medium: mean = 1.27, lower CI = 0.85, upper CI = 1.7; large: mean = 1.03, lower CI = 0.88, upper CI = 1.18; Fig. 4).

The proportion of farmed escapees estimated from drift diving and net captures was also well correlated (adj. $r^2 = 0.79$; Fig. 5a) with a significant relationship between the 2 methods (mean = 0.77, lower CI = 0.52, upper CI = 1.01). Furthermore, no statistical difference was seen between a 1:1 relationship and the current predicted relationship (dashed line in Fig. 5a). However, 97% of the values of the posterior distribution fell below a 1:1 relationship, suggesting that a small difference potentially exists between drift diving and net captures. This was further supported after removing the 2 outliers, where we observed an improved goodness-of-fit for the model (adj. $r^2 = 0.93$; mean = 0.85, lower CI = 0.64, upper CI = 1.06; Fig. 5b) and a high proportion (92%) of the posterior distribution below the expected 1:1 trend line.

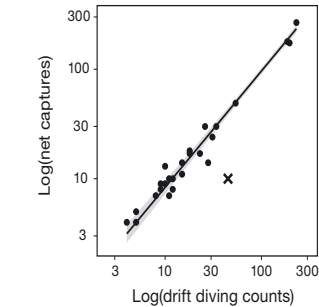


Fig. 3. Generalized linear regression of the total Atlantic salmon counts observed in drift diving and net captures. Solid line: fitted line; shaded area: 95% confidence intervals. The x is a point that was removed from the analysis due to an unrepresentative and biased net capture

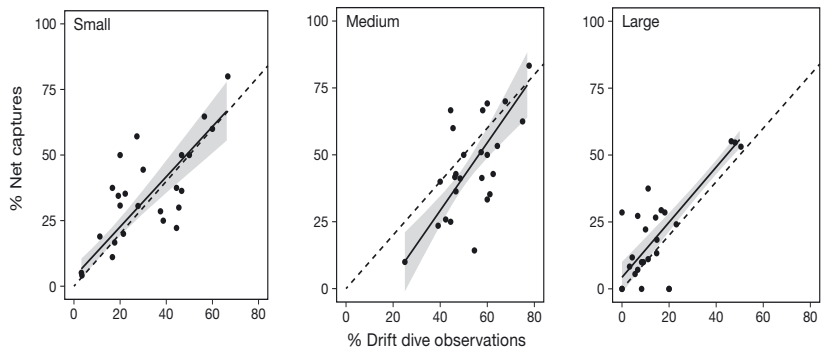


Fig. 4. Comparison of the proportion of size categories (small, medium, and large) of Atlantic salmon between drift diving and net captures. Solid line: fitted line; dashed lines: 1:1 line; shaded areas: 95 % credibility intervals

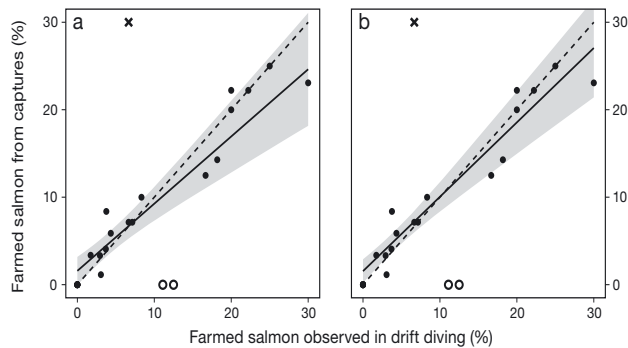


Fig. 5. (a) Bayesian inference comparing the proportion of escaped Atlantic salmon observed in drift diving and captured with nets; (b) the same relationship after removing 2 outliers (open circles). Solid line: fitted line; dashed line: 1:1 relationship; shaded area: 95 % credibility intervals (CI). Fitted line and CIs were calculated from all points — solid and open circles in (a) ($r^2 = 0.79$). Outliers removed due to limitations outside of individual identification, e.g. escape during net capture (b) ($r^2 = 0.93$). The \times in both panels indicates a point that was removed from the analysis due to an unrepresentative and biased net capture

3.2. Dataset 2: removal of escaped farmed salmon during drift diving surveys

Independent drift diving sampling of 35 rivers during routine removals of farmed salmon escapees identified 185 individuals as escapees (Table 2). Scale analysis verified that 182 were indeed escapees (TPR = 98 %) and 1 individual was identified as a wild *S. salar*. Two individuals had unreadable scales and could not be verified as either escaped or wild.

4. DISCUSSION

Accurate identification is pivotal when monitoring proportions of farmed salmon escapees in rivers and assessing the effectiveness of mitigation efforts against the potential interbreeding of domesticated conspecifics (e.g. improved aquaculture retention and removal efforts). Here, for the first time, we validated that drift diving represents a robust method that can accurately classify Atlantic salmon *Salmo*

salar into size categories and determine their origin (i.e. wild vs. farmed). Furthermore, results from individual removal data (TPR = 98% with harpoon captures) demonstrates that drift divers rarely identified wild fish as escaped farmed salmon (1 out of 183 individuals). Similar to previous studies (Orell & Erkinaro 2007, Orell et al. 2011), we also found drift dive abundances to be highly correlated with net captures of Atlantic salmon, even at large densities (>150 ind.). Based on these findings, we conclude that drift diving represents a robust method, when observation conditions are adequate, to effectively assess the numbers, size categories, and proportions of farmed vs. wild *S. salar*.

While previous studies on drift diving quantified the number of *S. salar*, few have evaluated the precision of this method to quantify differences in population structure (but see Orell & Erkinaro 2007 as an example of distinguishing between sex of *S. salar*) and particularly, the identification of farmed escaped salmon in rivers. In general, there was a good fit between the proportions of escapees identified between the 2 methods (adj. $r^2 = 0.79$), demonstrating that visual identification of escapees by snorkeling was, in most cases, highly accurate. However, some deviation from the expected relationship was observed, likely caused by biases in either of the sampling methods. Firstly, some error is likely to arise due to limitations in catch efficiency of net captures. For instance, we were unable to verify that all individuals were captured at a site, as some fish escaped during net captures. For example, small 1 SW fish (<50 cm) were, in some cases, observed to swim through or under the net and are therefore likely to be underrepresented in those catches. Because we were unable to verify the origin of missed individuals, these were not included in the calculations of proportions and hence could potentially result in the differences observed between drift diving and net captures. Furthermore, degraded scale quality limited our ability to verify the origin of some individuals. Finally, many of the sample locations had relatively few fish (<20 ind. observed in 18 of 26 locations). Consequently, small deviations in counts between the 2 methods will, in such cases, create large discrepancies in the observed proportions.

Secondly, some deviance from the 1:1 relationship in the present study may arise due to identification error during drift diving. As characterizations of farmed salmon escapees during snorkeling is based on visual identifications, it requires that the snorkeler is able to observe each fish well enough to correctly distinguish escapees and wild fish. This likely de-

pends upon several factors, such as visual conditions underwater (i.e. water clarity and light conditions), the distance between the observer and the fish, the length of time the observer has to observe each fish, and the experience of the observer. Furthermore, farmed fish may vary in distinctiveness, with the typical 'farmed' features being more expressed in some individuals than in others. For example, fish that escape as smolts are likely to have fewer distinguishing characteristics than recently escaped fish and may thus be more difficult to differentiate from wild fish (Jørgensen et al. 2018). Also, repeat spawners of wild fish may, in some cases, exhibit abrasions and fin erosion commonly seen in farmed escaped salmon (Fleming et al. 1997) and be miss-identified as escapees, particularly by inexperienced observers. However, in those instances where escapees were removed and verified with scale analysis (dataset 2), only 1 wild fish was misidentified as a domesticated salmon, indicating that such misidentification of previously spawned salmon are rare. Yet in most cases, identification error is likely to be towards misidentifications of farmed fish as wild fish, and consequently, cause an underestimation of the proportion of farmed salmon escapees in the sample or river. This was not apparent in our study, and in fact, drift diving appeared to potentially overestimate the proportion of farmed fish compared to the net catches, as 97% of the posterior distribution fell below the predicted 1:1 line for the comparison of the 2 methods. Still, for most locations, both the total number and proportion of farmed fish coincided well between the 2 methods and, while some bias may be present, it will likely have little effect on the overall management decisions.

Drift diving has only recently (since 2014) been included as a standard method used in the Norwegian monitoring program of farmed escaped salmon (Glover et al. 2019), supplementing the traditional method based on validation of fish gathered from angling (Diserud et al. 2019, Glover et al. 2019). Compared to angling-based methods of assessing the number and proportions of farmed escaped salmon (e.g. net captures and fishing), drift diving offers several advantages. For example, the variation in the CPUE is one of the main challenges when incorporating fishing statistics to quantify farmed escaped salmon. In Norway, fishing for *S. salar* primarily occurs during summer when salmon enter the river or are holding in estuaries until optimal stream conditions for upstream migration (e.g. adequate water discharge). This could result in a mismatch between sampling and the effective spawning population

(Harvey et al. 2017). It has also been shown that the angling catch efficiency is quickly reduced after river entry (Harvey et al. 2017), suggesting that variation in time of river entry (Erkinaro et al. 2010, Svenning et al. 2017) may cause different catch probabilities between wild and escaped salmon.

Furthermore, differences within the river in the distribution of escaped and wild salmon and variations in spatial CPUE during fishing may further underestimate or overestimate the proportion of escaped farmed salmon in the spawning populations (Moe et al. 2016). For example, sampling in areas where escapees or wild fish are spatially aggregated may give a biased sample. In addition, without prior knowledge of the spatial distribution of the fish in the river, it is almost impossible to know how to design a representative sampling design. Drift diving, on the other hand, is less susceptible to many of these issues. For instance, the spatial CPUE is less variable during drift diving when the entire anadromous reach (~5 to 10 km) of moderately sized rivers can be sampled in a single day with 1 to 3 divers. Because of the quick assessment of the river and the downstream direction of the sampling, drift diving can also capture differences in distribution between conspecifics while minimizing effects from fluctuations in population density during sampling (e.g. immigration or emigration). Finally, drift diving estimates are usually conducted close to or during active spawning and therefore the mismatch between sampling and effective spawning population is limited and can provide a better representation of the proportion of farmed escaped salmon in the period that is most relevant in terms of risk for genetic effects on the population (i.e. spawning).

Another important advantage of drift diving is the relatively limited time and expense needed to sufficiently survey broad spatial extents (Dolloff et al. 1996, Thurow et al. 2006, Orell et al. 2011). For instance, to obtain a comparable sample with net captures for this study, additional time (on average 1 to 2 h), personnel (5 to 7), and equipment (e.g. capture nets, holding pens) were needed to capture the same representative sample that took 2 divers only 10 to 15 min to sample. In addition, drift divers are able to sample habitats that are impractical to sample with conventional methods or are prohibited (e.g. streams that are closed to fishing). Drift diving is also less invasive compared to other methods that would require the physical removal of the individual to determine whether it was an escaped or wild salmon.

While the current study provided valuable information on the accuracy of drift dive estimates to

quantify farmed escaped salmon, limitations exist. Orell et al. (2011) saw a decrease in the precision of drift diving estimates of *S. salar* abundance when assessing more complex habitats. While routine sampling of the spawning population includes a range of conditions in terms of river size, depth, and water clarity, we focused on sites that allowed for a congregation of salmon while also allowing for the use of net captures to validate observations. This necessitated us to focus predominantly on habitat units consisting of pools. As a result, it is likely that estimates and the ability to identify farmed escaped salmon will fluctuate as habitat complexity (e.g. riffle vs. pools or the inclusion of boulders and debris) and sampling conditions (e.g. water turbidity and clarity) vary. Furthermore, while not assessed in this study, the experience of the diver is an important factor in being able to distinguish between conspecifics (Orell et al. 2011), and it is necessary to develop training protocols to improve the skill level of inexperience personnel while maintaining the integrity of the sampling method.

In conclusion, the implementation of drift diving in rivers where escaped farmed and wild *S. salar* coexist was determined to be a robust tool that will allow managers to quickly and accurately identify areas of potential introgression and focus removal efforts. This study demonstrates the usefulness to assess the proportion of escaped farmed salmon in a system via drift diving and provides stakeholders with a valuable tool that is not limited by changes in CPUE nor does it inflict unnecessary stress at a sensitive time in a salmon's life history (e.g. spawning). Future applications should focus on assessing how changes in habitat affect the accuracy of correctly identifying escaped salmon.

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