Can enrichment improve the post-release survival of hatchery-reared Atlantic salmon fry (*Salmo salar*)? – A field experiment

Thesis submitted in partial fulfilment of the requirements for the degree

Master of Science in Marine Biology

by

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June 2018

Cover photo: A sample of 16 weeks old Atlantic salmon fry, by Martine Røysted Solås.

Acknowledgements

Abstract

Release of captive-reared fish to supplement reduced, wild populations has become a common tool for conservation and management. Such attempted population enhancements have, however, had limited success, and several previous studies provide evidence that one of the main reasons could be high mortality of newly stocked fish. Conventional hatchery-rearing might generate traits and behavioral deficiencies disadvantageous for survival in the wild. Previous experimental studies report that enrichment during rearing promote a more flexible behavioral-repertoire and it has been suggested that enriched rearing could be a way to increase fish survival. Yet there is limited evidence of whether enriched rearing actually does have an effect on survival of released individuals in the wild.

In the present field experiment I have investigated the immediate post-release predation mortality and survival two months after release of Atlantic salmon fry (*Salmo salar*) from two rearing treatments (distinguishable by alizarin marks in their otoliths). One group was reared in a structurally enriched environment and the other in a conventional, plain environment. Predation mortality was investigated by capturing predators and examining their stomach contents for fry. Survival was estimated from electrofishing by sampling the survivors in the river two months later. The predation mortality on the two groups just after release differed only for one of the experimental years, where 60% of the consumed fry were from the plain treatment. Equal numbers of fry from both treatments were recaptured two months later in all except one year, when 63% of the sampled fish originated from the plain treatment. The data also show that enriched rearing reduced the growth of the fish, and that predation was size-selective towards small prey. These novel results suggest that enriched rearing possibly can provide salmon with an enhanced ability to hide from predators immediately after release, but that the enrichment might not be sufficient to promote enhanced survival beyond that. This will be discussed with consideration given to the potential, and limitations, of structural enrichment during rearing and the release procedure. Perhaps future research should take a more detailed look at the effects of different release practices on survival of captive-reared fish

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1.0 INTRODUCTION

The effects of overfishing, habitat altering, pollution and climatic changes are believed to contribute to the reductions of fish populations (Jackson et al., 2001; Myers & Worm, 2003). In attempts to restore and increase the abundance of wild fish, release of hatchery-reared individuals into the natural habitat has become a common practice, using offspring originating from wild counterparts. These attempted population enhancements have, however, shown limited success, and several studies provide evidence that one of the main reasons could be high mortality of newly stocked fish (Henderson & Letcher, 2003; Iglesias et al., 2003; Buckmeier et al., 2005; Støttrup & Sparrevohn, 2007). Several studies suggest that the mortality rate is highest shortly after release, and that a likely main cause of post-release mortality is predation (Henderson & Letcher, 2003; Sparrevohn & Støttrup, 2007).

Previous works suggest that the high mortality rate of released captive-reared fish might be due to the pronounced differences between a traditional hatchery environment, where the fish are reared, and the natural habitat, in which the fish are released (Olla et al., 1998; Brown & Day, 2002). In standard hatchery environments, fish are reared for optimal growth: there are no predators; the temperature and water flow are regulated for optimal conditions; and there is a sufficient food supply – usually in the form of pellets. The tanks are plain; without bottom substrate or any other kinds of structure or shelter, to minimize the time- and production cost of the hatchery. In contrast, the fish' natural environment is constantly changing: predators are present, and the food items available are alive and limited. Increasing amounts of evidence state that the hatchery environment might not provide satisfactory stimuli for developing skills needed for survival after release into the natural habitat (e.g. Suboski & Templeton, 1989; Braithwaite & Salvanes, 2005; Salvanes & Braithwaite, 2005; Ullah et al., 2017). These point out that the rearing environment during early life stages will have a major impact on the development of traits and behaviours needed for survival, and that the plain, standard hatchery-rearing might generate behavioural deficiencies, and traits disadvantageous for survival in the wild.

Since hatcheries offer an environment absent of predators, it has been questioned whether hatcheries offer sufficient stimuli to produce fish with a suitable anti-predator behaviour relevant after they have been released into their natural habitat (Olla et al. 1994; Huntingford, 2004). Experiments indicate that fish with a prior exposure to predator cues, visual or olfactory, have a higher probability of surviving new predator encounters (Berejikian, 1995). An experiment using Atlantic cod (*Gadus morhua*) showed how individuals that lacked

predator experience spent more time on inspection of predators kept behind a glass divider, compared to those that had prior experience with predators (Nødtvedt et al., 1999). Exposure to predator cues did also initiate more risk-averse behaviour like sheltering and shoaling behaviour (Brown & Smith, 1998; Petersson et al., 2015) and can, in brown trout (*Salmo trutta*), be remembered for as long as 4 weeks after exposure (Brown & Smith, 1998). Anti-predator behaviour was also developed from social learning as shown in experiments rearing naïve fish together with predator-experienced fish (Kelley et al., 2003; Vilhunen et al., 2005; Manassa & McCormick, 2012).

It has been discussed whether it is possible to enhance anti-predator behaviour without exposing the fish to real predators or predator cues, and several studies report that including different kinds of enrichment in captive rearing environments can increase the behaviour repertoire of fish (e.g. Gro Vea Salvanes & Braithwaite, 2006; Strand et al., 2010; Ullah et al., 2017). For example, cod reared in a structurally enriched environment developed more flexible behaviour compared to plain-reared cod, and they recovered more quickly from stress caused by a simulated predator attacks (Braithwaite & Salvanes, 2005). Juvenile Atlantic salmon (*Salmo salar*) reared in enriched environments have shown increased spatial learning ability compared to plain-reared counterparts, which is assumed to be a benefit in the natural environment where the ability to adapt to changes becomes fatal (Salvanes et al., 2013). Increased sheltering behaviour also seem to be developed in fish reared in an enriched environment (Salvanes et al., 2007; Roberts & Garcia de Leaniz, 2011; Naslund et al., 2013) supporting the theory that enrichment possibly cause a reduction of maladaptive behaviour, making the individuals better suited for release into the natural habitat.

Structural enrichment has also shown to have a positive effect on fish's ability to transfer from pellets to feed on live prey (Strand et al., 2010) This transition is crucial for the fish to survive, as it otherwise would starve and potentially initiate more risk-taking behaviour as hunger level grows, and this will then make the released individuals become more prone to predation (Godin & Crossman, 1994; Lonnstedt et al., 2012). Hence, evidence from experiments demonstrate that enriched rearing promotes development of anti-predator behaviour in fish reared in captivity. The use of strucural environment could perhaps be a cost-beneficial way to reduce mortality of hatchery-reared fish instead of conditioning the fish with live prey and predators.

A well-studied species group in stocking programmes, are the salmonids. Several species have a long history of stocking due to their high commercial, recreational, cultural and ecological value. One of these species is the Atlantic salmon, a species that spends its early life

stages in freshwater, distributed along native to subarctic and temperate watersheds around the North Atlantic Ocean. Multiple stressors threaten these fish. These include climatic change, overfishing, escaped farmed salmon and habitat altering, which all are suspected to be responsible for the pronounced decrease of wild Atlantic salmon (*Salmo salar*) populations the past years (Parrish et al., 1998; Nicola et al., 2018). In the year 2000, WWF investigated several Atlantic salmon populations, and they found that ~20% of the populations were extinct, or in a critical condition, and another 30% were endangered or vulnerable (WWF, 2001). Additionally, ICES reports an alarming decrease of 90% in reported nominal catches in 40 years (ICES, 2016).

Norway was one of the countries in which WWF categorized several salmon- rivers and populations to be healthy in year 2000, but the Norwegian Institute of Nature Research found in 2016 that the number of returning salmon from the sea have been close to halved since 1980 (NINA, 2017). The salmon strain in the Vosso river system is one of the populations that has struggled the past years. Around 1980 this population experienced a large decrease and almost extinction due to destruction of spawning grounds, high abundance of salmon lice attacking out-migrating smolts, and escaped farmed salmon migrating up the rivers (Sægrov, 1997; Barlaup, 2013). Fortunately, the original wild genes have been "saved" in form of a wild caught brood stock housed in a gene bank. Offspring originating from the wild brood stock has been produced in Voss hatchery and since 1990 have hatchery-reared fish containing the original wild genes have been released as part of a restocking program to restore the original population in the Vosso river system.

Studies in the US and Europa have shown that release of hatchery-reared salmon have little to no effect on increasing the salmon populations (Olla et al., 1998; Brown & Day, 2002). Henderson & Letcher (2003) found evidence of up to 60 % of released salmon fry be predated on by resident brown trout within the first two days after release. Hence, mortality immediately after release may limit effect of releases. Juvenile salmon reared in enriched environments and tested experimentally show enhanced behaviours compared with conventionally-, plain-reared individuals, and it has therefore been suggested that enriched rearing may reduce post-release mortality (Roberts et al., 2011; Naslund et al., 2013; Salvanes et al., 2013). In the present experiment, the hypothesis that enriched rearing generate behaviour beneficial for survival after release is tested using *in situ* field experiments and Atlantic salmon fry.

1.1 Aims and hypothesis

In this Master's project I have studied post-release- predation mortality just after release and survival two months later of hatchery-reared Atlantic salmon from enriched and conventional (plain) rearing treatments. The main hypothesis is that enriched rearing produces salmon with better chance of survival after release than their plain-reared counterparts. To investigate this fry were group marked in their otoliths using alizarin at the egg stage and were reared either in an enriched environment or in a standard, impoverished environment. They were then released in large densities in the river, and at 4 and 48 hours after release predators of the newly stocked salmon were caught and predator stomach contents were examined for consumed salmon fry. Salmon prey were identified to treatment group by examining the otoliths for fluorescent rings. Two months later an electrofishing sampling was done to estimate the proportion treatment groups in the fry remaining in the river.

My hypothesis is that enriched-reared salmon fry have an improved ability to shelter from predators due to their exposure to potential shelter during rearing, and that fish from impoverished rearing might be more active in the water column, hence more prone to predation by piscivorous fish. I also hypothesize that the enriched rearing provided fish with a benefit in relation to stress recovery and the adaptation to live food, and that this will enhance their survival.

For the general predation I expected larger predators to be able to consume larger- and more prey and that most of the predation happened shortly after release. To investigate the latter hypothesis, I developed digestive state categories to evaluate how digested the consumed fry was, where I assumed that less digested individuals had been consumed more recently than those that were more digested.

2.0 MATERIALS AND METHODS

2.1 Experimental release site

The present study was carried out in the years 2015-2017. The stocking of salmon fry took place in a stretch of 100 m in Rasdalselva in Rasdalen (in 2015, 2016 and 2017) and in Teigdalselva in Brekkhus (in 2017), both tributaries of the Vosso river system. (Table 1; Figure 1). Hereafter these two release sites will be referred to by their locality names: Rasdalen and Brekkhus, respectively.
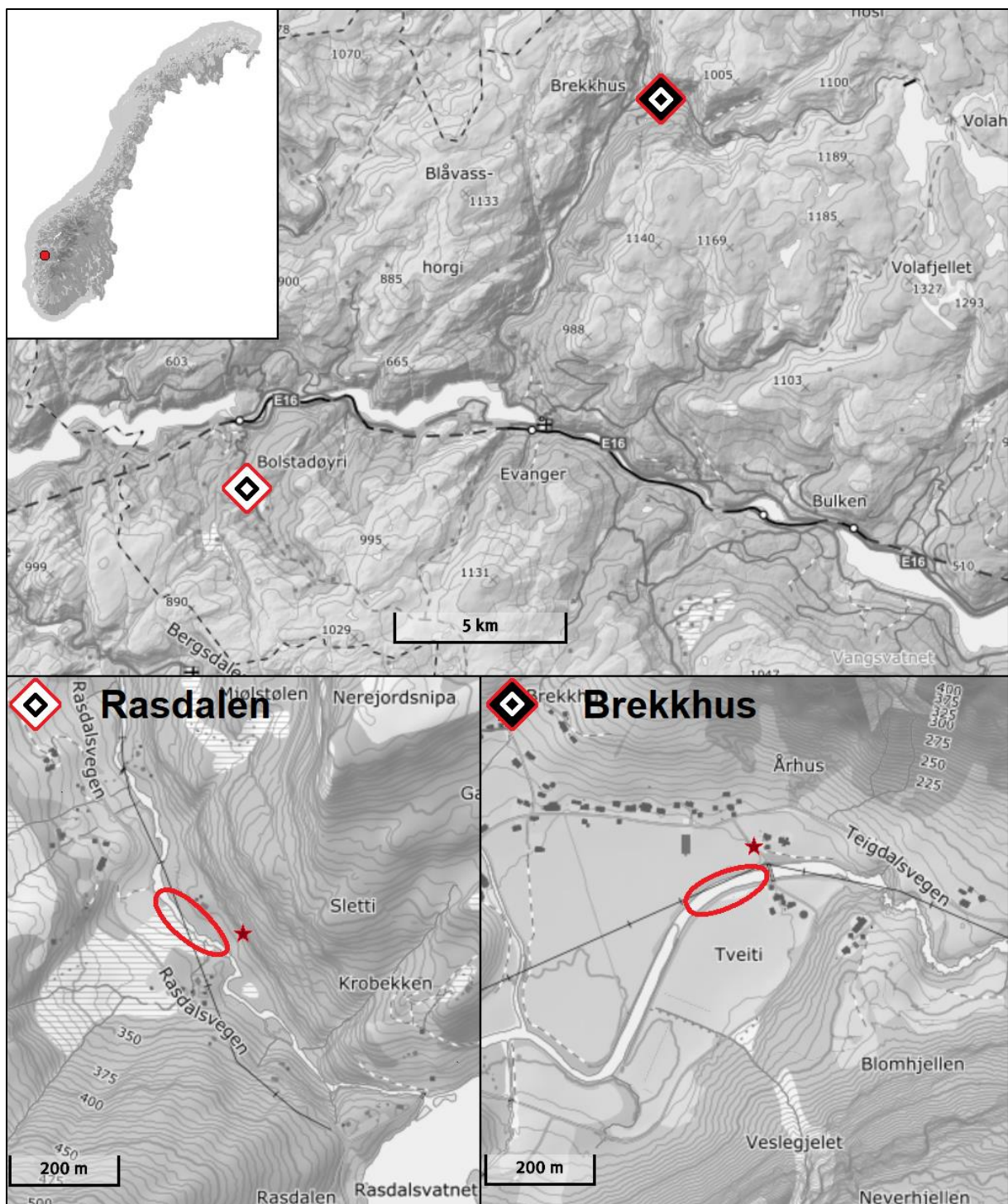
FIGURE 1. *Map showing the location of the two experimental release sites, Rasdalen and Brekkhus. The 100 m stretch is encircled in red and the star marks the start point (upstream) of the stretch. Maps are from Kartverket (https://www.kartverket.no) and modified in Microsoft Paint.*

TABLE 1. Coordinates for the start and end of the 100 m stretch used for release in Rasdalen and Brekkhus. The start coordinates are upstream of the end coordinates, meaning that the direction from start to end is <u>with</u> the current of the water.

Experimental release site	Start coordinates	End coordinates
Rasdalen	60.62102 N, 5.96606 E	60.62046 N, 5.96792 E
Brekkhus	60.73482 N, 6.15322 E	60.73507 N, 6.15317 E

The two release sites differed in stream topography. The release site in Rasdalen had in general deeper water, contained more pools, had a slightly steeper slope and a lower water velocity, compared to Brekkhus; which was mainly dominated by riffles and runs and had a higher water velocity. Both rivers had similar bottom substrate with large rocks and gravel, and both were located above a migration obstacle of the anadromous reach. Rasdalen was also a narrower stream compared to Brekkhus, which was approximately twice as wide.

2.2 Salmon egg treatment

Atlantic salmon eggs were produced through a live brood stock, originating from the original Vosso salmon population, housed at Haukvik Genebank. The eggs were transported to Voss Hatchery following standard procedures, and the batch of eggs was separated in two groups, (randomly, aiming for equal genetic variation). Both groups had prior to transportation to Voss hatchery (at the developmental stage of 70 – 90%) been group marked using Alizarin Red-S (ARS) at a concentration of 200 mgL^{-1} (Eckmann, 2003), following standard procedures and recommendations by the Norwegian Veterinary Institute (Moen et al., 2011). By binding to the calcium carbonate ($CaCO_3$) of the continuously growing otoliths, the alizarin allows marking in the shape of a ring in the otolith, and with two, time separated treatments, two rings can be created. These rings are visible under a UV-light microscope as fluorescent red.

At Voss hatchery, the group that later would be reared in an enriched tank (hereafter referred to as "enriched") was treated with a second alizarin marking, while the control group, that after hatching would be reared in a standard, impoverished tank (hereafter referred to as "plain"), did not get a second treatment, and would only have one fluorescent ring in their otoliths (Figure 2).

After marking, the eggs were returned to the hatching system, and after approximately 500 day-degrees the eggs would hatch (Table 2).
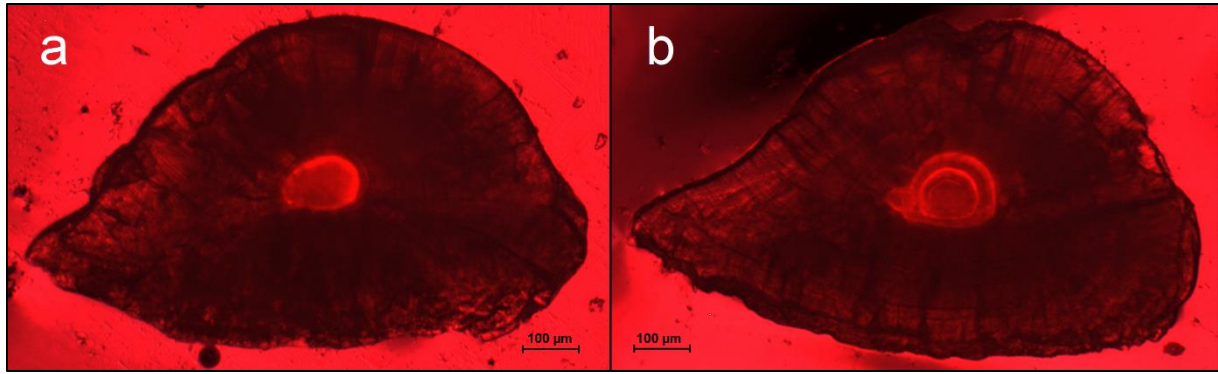
FIGURE 2. *Photographs of alizarin markings in plain (a) and enriched (b) salmon fry, under a ZEISS Axioscope 2 plus with Nikon Digital sight DS-U3 and the software NIS Elements D 4.60.00.*

2.3 Salmon fry treatment

When the two groups of alevins had absorbed their yolk and become fry, they were transferred to two separate rearing tanks (2×2 m; water volume ~ 2300 L) with approximately 8300 or 16 000 individual fish in each tank, depending on the experiment year (Appendix 1). The tanks had a flow-through system, using filtered river water at a temperature equal to what they would have experienced in the natural river. Filtration removed unwanted particles and excess nitrogen etc.

  To make the transition to the tank easier, and to avoid clumping of individuals, 3-4 biomats (38×38 cm) were initially placed at the bottom. At the onset of feeding (approximately 1-2 weeks after the biomats were introduced), the mats were removed, and enrichment was introduced in the tank housing fry marked twice using alizarin. An exception had to be done in 2016 due to an outbreak of fungi (Table 2), and enrichment was consequently two weeks later. The enrichment consisted of plastic tubing constructions and a box to provide shelter, and nylon rope and plastic sheds to simulate river flora (Figure 3; Figure 4). These structures were cleaned when required.

TABLE 2. *Overview of hatching week, date of transfer to production tank, the number of weeks the enriched group spent exposed to the enriched structure before release, age at release in weeks and the date of release. + refers to "a little more than" and – refers to "a little less than" in regards to full weeks.*

Year	Hatching week	Rearing tank	Enrichment duration (weeks)	Age at release (weeks)	Release date
2015	13.04 - 19.04	27.05	5+	12+	07.07
2016	18.04 – 24.04	26.05	8-	17+	17.08
2017	24.04 – 30.04	23.05	10-	16+	15.08

* due to an outbreak of a stronger fungi infection and the bacteria *Pseudomonas* sp., the introduction of enrichment was delayed 2-3 weeks to avoid unnecessary mortality and to ensure the re-establishment of healthy conditions.
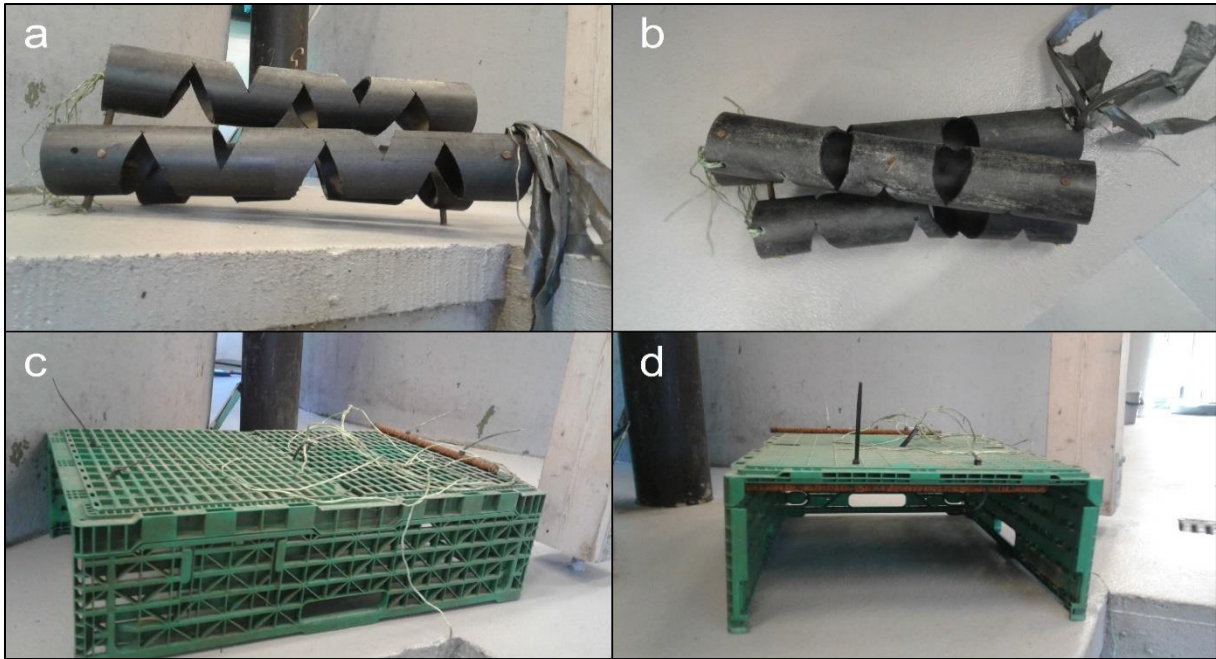
FIGURE 3. *Enrichment used in enriched rearing tanks. Tube construction (a; b): consisted of three black plastic tubes assembled by threaded rods. Individual tube: length: 43-53 cm; outer diameter: 9 cm. One bouquet of green and grey nylon threads (length: approx. 30 cm) and one bouquet of grey plastic sheds (length: approx. 30 cm) were assembled to the tube construction. Green box (c; d): length: 60 cm; width: 40 cm; height : 18 cm with assembled bouquet of green nylon rope (length: ~110 cm).*
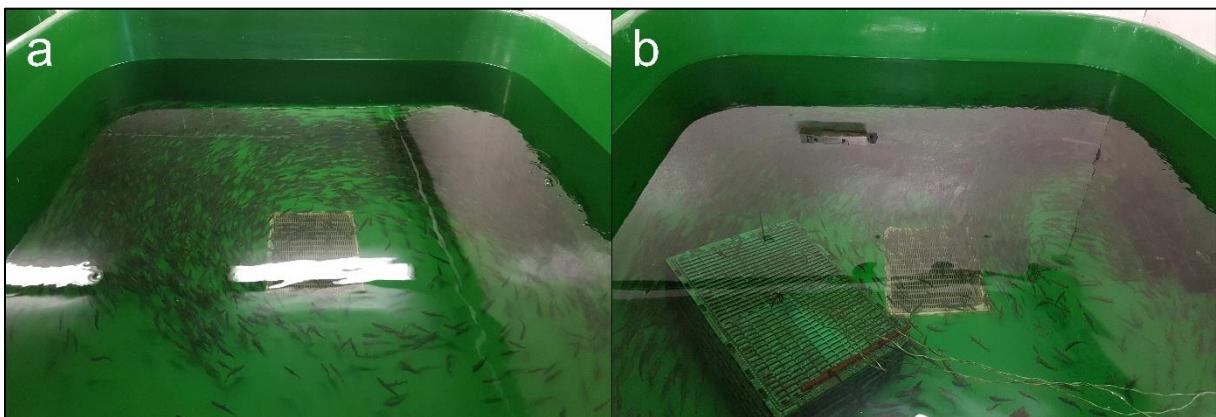
FIGURE 4. *Overview of the rearing tanks; plain treatment tank (a) and enriched treatment tank (b).*

The fry were fed under continuous light with commercial pellets (Skretting: Nutra XP) dispensed by an Aqua productions A/S automatic feeder with a few seconds intervals 5 times an hour. The fry's appetite was checked through occasional hand feeding, especially at the onset of feeding.

2.3.1 Salmon fry stocking

Prior to fry capture, the water level of the rearing tanks were lowered to about 10-20 cm to ensure easier access to the fish and random size distribution of individuals. Fish were caught

with small meshed nets (22 × 22 cm, mesh size: 1.5 mm), and a sub-sample of each rearing group of n ~ 100 was the first to be collected (Table 3).

TABLE 3. Overview of mean length (to the nearest mm) and mean weight (to the nearest 0.01 g) of sub-sampled individuals from each rearing treatment with respective standard deviation (SD).

Year	Treatment	n	Mean length (mm)	SD	Mean weight (g)	SD
2015	Enriched	93	34	3	0.73	0.15
	Plain	95	34	3	0.69	0.16
2016	Enriched	127	49	8	2.11	0.94
	Plain	123	51	6	2.21	0.65
2017	Enriched	107	55	9	3.04	1.22
	Plain	128	57	6	3.22	1.00

The fish were transported in transparent 30 L plastic bags filled with 1/3 water (10 L) and 2/3 oxygen from an oxygen tank. Every bag contained an even mix of enriched and plain fry, with a total weight of about 1 kg per bag. A total amount of 3600 individuals (1800 from each treatment) were brought to the release site each experiment year. The bags were transported by van to the site and carried by foot to the river bend.

The fry were released in high densities in the 100 m stretches previously described (Table 1). Before release, the fry were acclimated for a short period in 10 L containers with a mix of water from the bag and water from the river.

In 2017 the release in Rasdalen and Brekkhus happened the same day (Table 4). First ~1800 fish from both treatment groups were caught and transported for release in Brekkhus, and when this was completed we returned to the hatchery and caught another ~1800 of each treatment for the release in Rasdalen.

TABLE 4. Overview of release date, river temperature, time of predator sampling and the number of predator caught for each sampling in 2015, 2016 and 2017. River temperature refers to the temperature measured in the river right before release of salmon fry.

Release site	Year	Release date	River temperature (°C)	Predator sampling	Predator catch
Rasdalen	2015	07.07	6.5	09.07 (48 hours)	8
	2016	17.08	15.3	17.08 (4 hours)	13
				19.08 (48 hours)	33
	2017	15.08	11.3	15.08 (4 hours)	33
				17.08 (48 hours)	20
Brekkhus	2017	15.08	9.9	15.08 (4 hours)	10
				17.08 (48 hours)	9

2.4 Predator sampling procedure

Potential predators (fish with standard length > 100 mm) of the released salmon fry were sampled 4 hours and 48 hours after release of fry (Table 4). They were sampled by using point electrofishing with battery powered backpack generators (Terik Techonology A/S: GeOmega FA-4 and GeOmega FA-3) with a pulsed current of 1400 volts and a range of maximum 1 m from the anode (rod of the apparatus). The entire length (and some additional meters downstream) of the experimental release sites were covered by two people. They began the fishing downstream, and walked upwards, against the current, to the stretch start point (Table 1). The fishing lasted for about 0.5-1 hour until the entire stretch had been covered. The electrofishers used hand nets (diameter: 24 cm, mesh size: 5 mm) to catch the predators, and immediately housed them in containers of river water before they were transferred back to land for examination.

The predators were anaesthetized with metacain (MS222) to enable measurements of weight, length and stomach content. The stomach content was obtained by gastric lavage technique (Bromley, 1994): flushed out with water using a 60 mL syringe fitted with a thin aquarium tube (diameter: outer: 9.0 mm; inner: 0.6 mm), inserted into the mouth of the fish to the distal parts of the stomach. Stomach contents were flushed out on a sieve to remove access water. The flushing took approximately two minutes dependent on the amount of fry the predator had consumed. When flushing was complete, the predators were housed in a 30 L tank containing river water, to recover from anaesthesia, before they were released back into the river. In 2016, all predators were sacrificed since no application for the use of gastric lavage technique had been sent to the Norwegian Food Safety Authority. 23 fish were sacrificed in 2017 due time limitation and the fact that some individuals were suspected to have eaten released salmon fry based on their abdomen shape, but the diameter of the aquarium tube was evaluated to be too large to insert without hurting the fish.

The flushed stomach content and sacrificed predators were immediately put in a cooler, to reduce the digestion process.

2.5 Salmon fry recapture procedure

Approximately months after release of fry we returned to the release sites to capture a sub-sample of salmon fry to obtain the proportion of plain and enriched fry remaining in the river (Table 5). The sampling procedure was the same as for the predator samples, but included another 50 m downstream. The sampling lasted until approximately n ~ 100 salmon fry released two months earlier were caught.

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TABLE 5. *Overview of recapture dates of each year, and number (n) of recaptured salmon fry from the release the same year. Some salmon of earlier year classes were also caught (2015, n=114; 2017 Rasdalen, n=1, 2017 Brekkhus, n=6), but these are not included and will not be further analyzed in this project.*

Release site	Year	Recapture date	n fry
	2015	07.10	133
Rasdalen	2016	24.10	111
	2017	08.11	123
Brekkhus	2017	08.11	94

2.6 Predator sample analysis

All predators were identified to species, and standard length was measured to the nearest mm. Predators were weighed to the nearest g in the field and to the nearest 0.01 g if weighed in the laboratory. In 2015, the caught predators were too large for the brought scale to cover their weights, and the weight of these has therefore been calculated using a linear regression equation obtained from fish that were measured both for standard length and weight (empty stomach):

$$y = -129.6 + 1.2x$$

Only standard length was used as a parameter for predator size in the further analysis. Total weight, can be found for all predators under Appendix II, and for sacrificed predators, additional information about gutted-, gonad- and liver weight and total- and fork length are also listed.

The predators' stomach contents were weighed, and number of consumed fry counted, but no further species-identification or analysis of the content itself was done in relation to the drift-feeding diet of the fish.

2.7 Prey salmon fry sample analysis

The consumed prey fry were measured for length (to the nearest mm with measurement certainty scored from 0-3; Table 6), weight (to the nearest 0.01 g), categorized based on the fry's digestive state (Table 7) and treatment group was determined by examining the sagittae otoliths.

TABLE 6. *Scoring system used in 2016 and 2017 do determine the certainty of length measurements in consumed salmon fry. Only measurements with the score 0 and 1 were included in further analysis. VCL refers to the vertebral column length.*

Score	Explanation
0	No influence on measurement of length.
1	Possible deformations in head or body, but should not influence length measurement
2	Small part of body and/or head deformed or missing (e.g. tip of VCL), but length rather accurate.
3	Substantial part of individual missing, and standard length not certain.

2.7.1 Otolith analysis

After assigning the consumed salmon fry to a digestive state category, the sagittae otoliths were removed from the fry and fixed to individual slides with temporary mounting wax (QuickStick™ 135). The otoliths were positioned so the convex surface faced upwards, making the polishing of the otoliths easier. They were polished with grinding paper from coarse (Buehler, SiC grinding paper, grit 500 (P1000)) to fine (Hillas, PSA Disc, 3µm) until the day rings of the otoliths were visible. Furthermore, the number of fluorescent rings were evaluated by using a microscope (ZEISS Axioscope 2 plus).
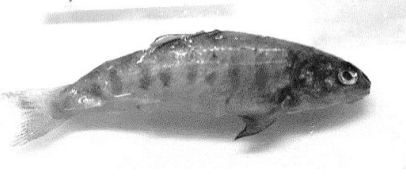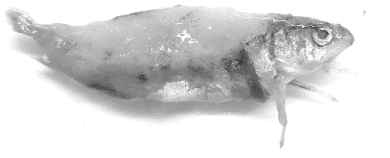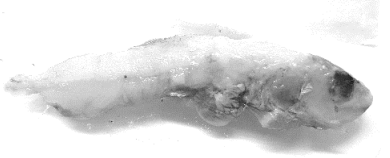
2.7.2 Mean specific growth rate

The (mean) specific growth rate (SGR), given as a percentage increase per day between day of release and the recapture two months later, was calculated as described by Ostrovsky (1995) by using the following equation.

$$\Omega = \frac{M_t^e - M_{t0}^e}{b \times t} \times 100$$

Where Ω is the SGR, M_{t0} and M_t are the body masses at time of release and recapture respectively, t is the time period, in days, between release and recapture, and b is an allometric mass exponent relating the SGR to body mass and has by Elliot and Hurley (1997) been estimated at 0.31 for Atlantic salmon (parr).

TABLE 7. Descriptive digestive state categories (from A – F) used in 2016 and 2017 salmon fry. Adapted from Berens, 2005's modification of Lindberg et al. 2002 system. The table gives approximately how much has been digested (in percentage), a description, and a figure for the approximate characteristics of the consumed fry. VCL refers to the vertebral column length.

Category	Percent of total fish digested	Description	Example pictures
A	< 5	**Skin:** all/most present **Fin rays:** most present **VCL:** complete (**Guts:** present) **General:** whole fish	
B	5 - 10	**Skin:** parts could be missing **Fin rays:** maybe present **VCL:** complete (**Guts:** present) **General:** mostly whole fish	
C	10 - 25	**Skin:** some present, or missing **Fin rays:** none **VCL:** complete **Guts:** most present **General:** some meat missing	
D	25 - 50	**Skin:** some, or missing **Fin rays:** none **VCL:** complete **Guts:** some present **General:** meat missing, partial head	
E	50 - 75	**Skin:** missing complete or incomplete **Fin rays:** none **VCL:** complete or incomplete **Guts:** some present **General:** may or may not be a recognizable fish. Meat missing, deformed head	
F	75-100	**Skin:** missing. **Fin rays:** none **VCL:** incomplete. **Guts:** absent **General:** not recognizable fish.	

2.8 Statistical analyses

All data analyses were performed using R version 3.4.4 (R Development Core Team, https://www.r-project.org/) and the additional packages: Tidyverse package set (Wickham, 2017), Rmisc (Hope, 2013) and Multcomp (Holthorn et al.2008). Analysis of- variance (ANOVA) and deviance were for used to find the order of predictor variables by stepwise model selection, in linear models (lm) and generalized linear models (glm) respectively.

2.8.1 Predator samples

Differences in the number of fry consumed by predators was tested using a generalized linear model.

$$\text{glm(N} \sim L_{pred} + \text{year} + \text{time, family} = \text{quasipoisson, data=data.df)}$$

Where N refers to the number of released fry consumed, L_{pred} is predator standard length, year is the year of release and time refers to at what time after release the predator was caught (4 or 48 hours).

To avoid overdispersion, the model was fitted using a quasipoisson error structure. Salmonids that had not consumed released fry were excluded from the analysis; it was assumed that they had not hunted for prey rather than that they were not able to capture the prey. A Post hoc Tukey HSD test was used to compare years.

A potential relationship between length of released salmon fry consumed and the size of predators was tested using a linear model.

$$\text{lm(L} \sim \text{year} + L_{pred}, \text{data=data.df)}$$

Where L refers to the standard length of consumed fry, year is the year of release and L_{pred} is predator standard length. A Post hoc Tukey HSD test was used to compare years.

To test for difference in the size distribution of predators that had eaten- and those that had empty stomachs, a Kolmogorov-Smirnov test (KS-test) was performed on cumulative density frequencies (CDF). The test was performed separately for each year, pooling the data from 4

and 48 hours after fry release, since no difference in size of predators could be detected due to low sampling sizes when tested separately.

2.8.2 Salmon fry: day of release

Differences in length at time of release for enriched- and plain fry was tested using a linear model (with and without interaction between year and treatment):

lm(L ~ year * treatment, data=data.df)
lm(L ~ year + treatment, data=data.df)

Where year refers to the year of release and treatment refers to the rearing treatment of the released fry (enriched or plain).

2.8.3 Salmon fry: consumed by predators

To test the H_0 of there being no difference in predation mortality on released plain and enriched fry, a Chi Square goodness of fit test was performed to test for significance differentiation from a 50/50 distribution. The chi-test was performed for each year separately, both pooling and separating sampling time (4 and 48 hours after release) within the respective year. Wild individuals and individuals of unknown rearing were excluded from the analysis. In 2017 the number of released fry eaten in Brekkhus was very low (n=5), and these were pooled with individuals form Rasdalen from the respective predator sampling times.

Differences in length of enriched and plain fry were tested by using the Kolmogorov-Smirnov test as described for predator samples analysis.

2.8.4 Salmon fry: recaptured from river

To test the H_0 of there being no difference in recapture proportion of released enriched- and plain fry, a Chi Square goodness of fit test was performed as described above. Wild individuals and individuals of unknown rearing were excluded from the analysis.

Comparison of weight of salmon fry the day of release compared that of individuals recaptured from the river two months later, was tested by using linear model.

lm(W ~ f + treatment, data = data.df)

Where W refers to the weight of an individual salmon fry, f is a categorical variable referring to whether the individual was from production tank or any of the recapture sites, and treatment refers to the rearing treatment of the released fry (enriched or plain).

2016 and 2017 was tested separately due to the additional release site (Brekkhus) in 2017 and the size differences between released fry the two years. A Post hoc Tukey HSD was performed to view pairwise comparisons between the two release sites and the production tank the day of release. To test differences within treatment groups, a Kolmogorov-Smirnov test was used as described above.

3.0 RESULTS

3.1 Predator samples

A total of 126 potential predators of released Atlantic salmon fry (123 brown trout and 3 Atlantic salmon) were sampled in the river system of Rasdalen and Brekkhus, Western Norway in 2015, 2016 and 2017. Of these, 78 (62 %) of the predators had consumed a total of 420 released salmon fry, but there was large variation between individual consumption (Appendix II). Brekkhus was the only site where Atlantic salmon were caught as potential predators (Appendix II), however, only brown trout had consumed released salmon fry. The remaining predators had either empty stomachs, or, in most cases, consumed different species of insects (e.g order Coloptera, Aranea and Diptera (larvae)).

The largest predator was a brown trout sampled in Brekkhus 2017 with a length of 260 mm, and this had captured and eaten two large, resident salmonids. Since this large predator had not predated on any of the released fry it is not included in further analyses in relation to the fry released in this project. The smallest predator, also brown trout, was sampled in Rasdalen 2017 and had a length of 115 mm. Average length of predating salmonids across years was 173 mm ± SD: 26 mm in Rasdalen (n=74) and 146 mm ± SD: 19 mm (n=4) in Brekkhus, while non-predating salmonids had a mean length of 141 mm ± SD: 16 mm (n=33) in Rasdalen and 160 mm ± SD: 31 mm (n=14) in Brekkhus. The frequency count of both non-predating salmonids and predating salmonids followed a normal distribution along measured potential predator standard length (Figure 5).
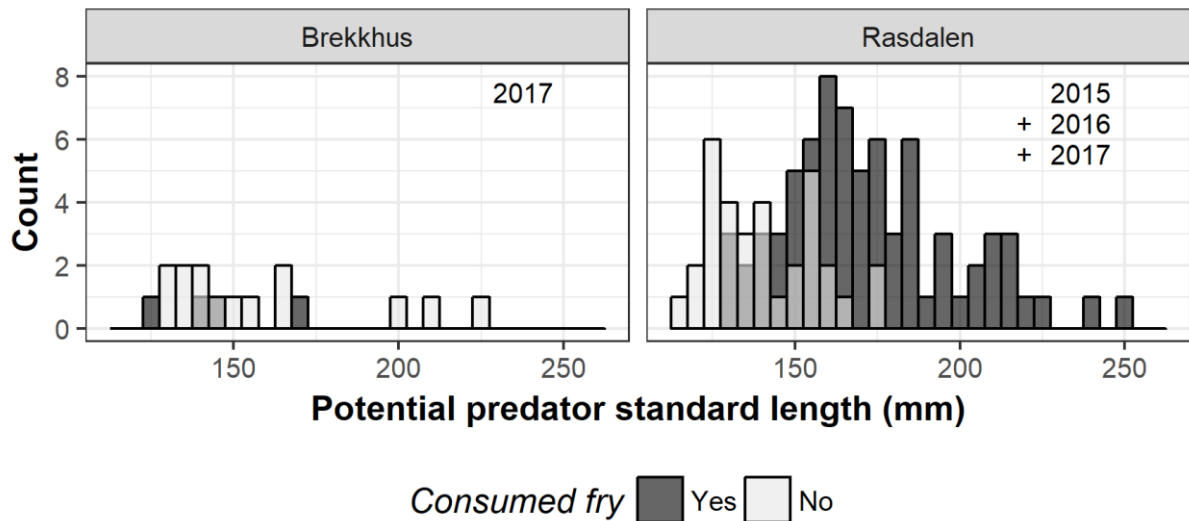
FIGURE 5. *Frequency distribution of standard length of salmonids (brown trout and Atlantic salmon) that had and had not consumed released salmon fry 4 and 48 hours after release of fry in Rasdalen in 2015, 2016, 2017 and Brekkhus in 2017.. All sampling times and years have been pooled. Overlap of counts appear as middle a grey tone. Each bar represents a 5 mm length interval.*

The salmonids that had predated on released salmon in Rasdalen 2016 and 2017 were significantly larger than the ones that had not (KS-test: 2016, D=0.608, P=0.021; 2017, D=0.634, P<0.01; Figure 6). No significant difference was found in Rasdalen 2015 or in Brekkhus 2017 (Appendix III).
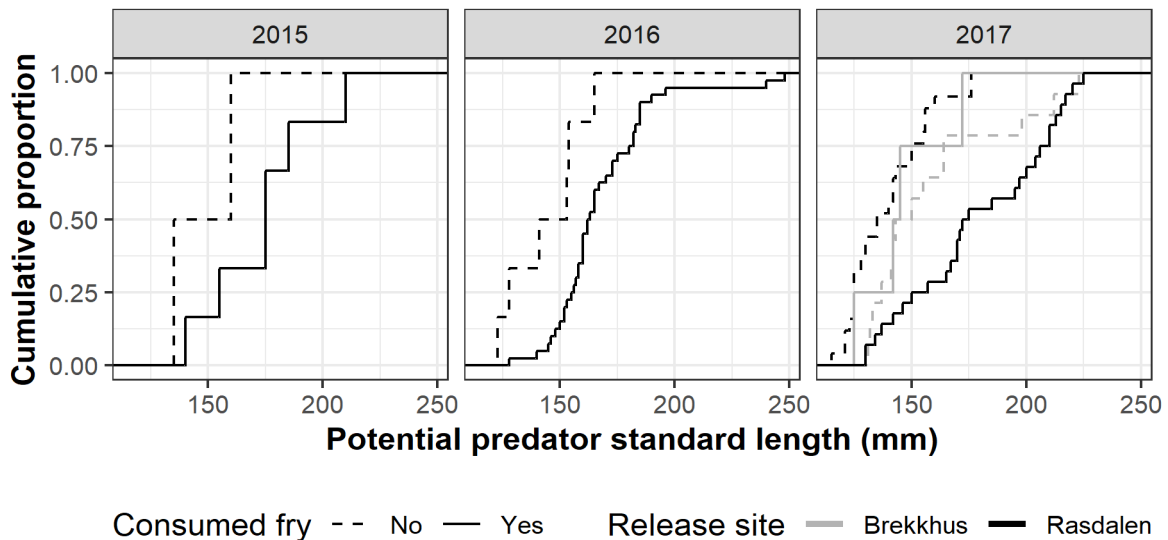
FIGURE 6. *Empirical cumulative density distributions (ECDF) of standard length of salmonids (brown trout and Atlantic salmon) that had and had not captured and eaten released salmon fry within 48 hours after release of fry in Rasdalen in 2015, 2016, 2017 and Brekkhus in 2017. Hours after release have been pooled as the Kolmogorov-Smirnov test yielded no significant difference in the CDF standard lengths of predating- and non-predating salmonids.*

The largest number of prey consumed per predator was found in Rasdalen in 2015 (Table 8), which also was the year of the largest recorded number of prey consumed by a single predator (n=33) (Appendix II). The highest number of salmon fry was obtained from predator stomachs sampled 48 hours after stocking in Rasdalen 2016, were 33 potential predators were caught, and 32 of these had consumed a total of 208 salmon fry. The samples from Brekkhus 2017 had the lowest number of predators that had captured and eaten released salmon fry, and the lowest measured average prey consumed (Table 8).

TABLE 8. *Overview of potential predators, Atlantic salmon and brown trout, sampled 4 and 48 hours after release of fry in Rasdalen in 2015, 2016, 2017 and Brekkhus in 2017. Potential predators refers to all fish > 100 mm that were caught, while predators refers to those that had consumed one or more released salmon fry.*

Year	Release site	Hours after stocking	n total potential predators	n consumed fry	n predators	Average prey per predator
2015	Rasdalen	48	8	74	6	12.3
2016	Rasdalen	4	13	31	8	3.9
		48	33	208	32	6.5
2017	Rasdalen	4	33	60	15	4.0
		48	20	42	13	3.2
	Brekkhus	4	10	2	1	2.0
		48	9	3	3	1.0

Fry found in stomachs of trout sampled 4 hours after release were mainly lightly digested (digestion state categories A-C, Figure 7), whereas fry in stomachs sampled after 48 hours were in general more heavily digested (digestive categories C-F).
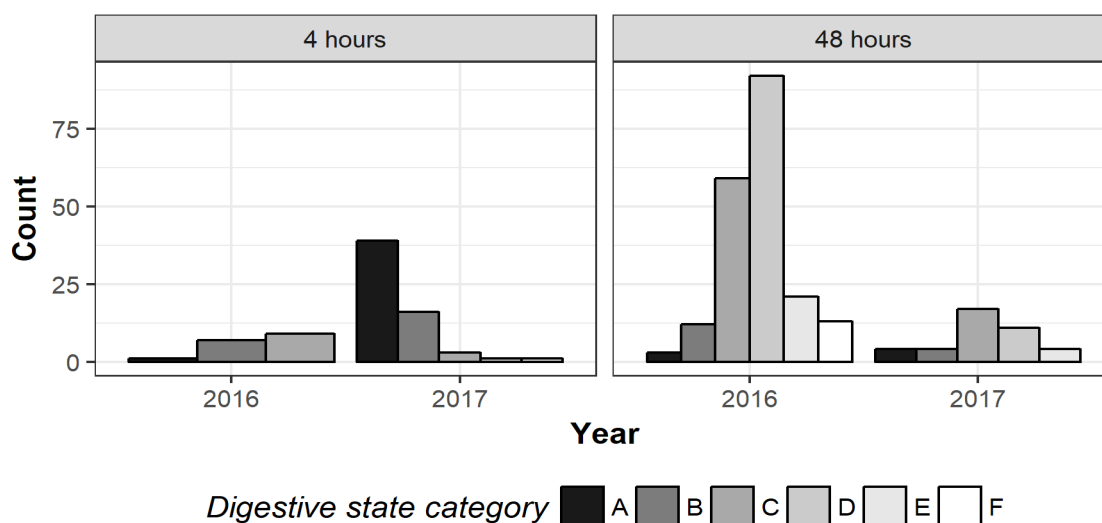
FIGURE 7. *Count of salmon fry stocked in Rasdalen in 2016 and 2017 within assigned digestion category (described in Table 7) that has consumed by brown trout within 4 and 48 hours after release.*

There was a significant relationship between predator length and the number of consumed fry, (glm, $F_{1,72}=54.682$, $P=0.012$) with larger brown trout predators consuming a larger number of prey (Figure 8). There was also found more fry in predator stomachs from the sampling 48 hours after release (glm, $F_{1,69}=6.391$, $P=0.014$), and significant differences among years (TukeyHSD: all pairwise comparisons, $P<0.001$).
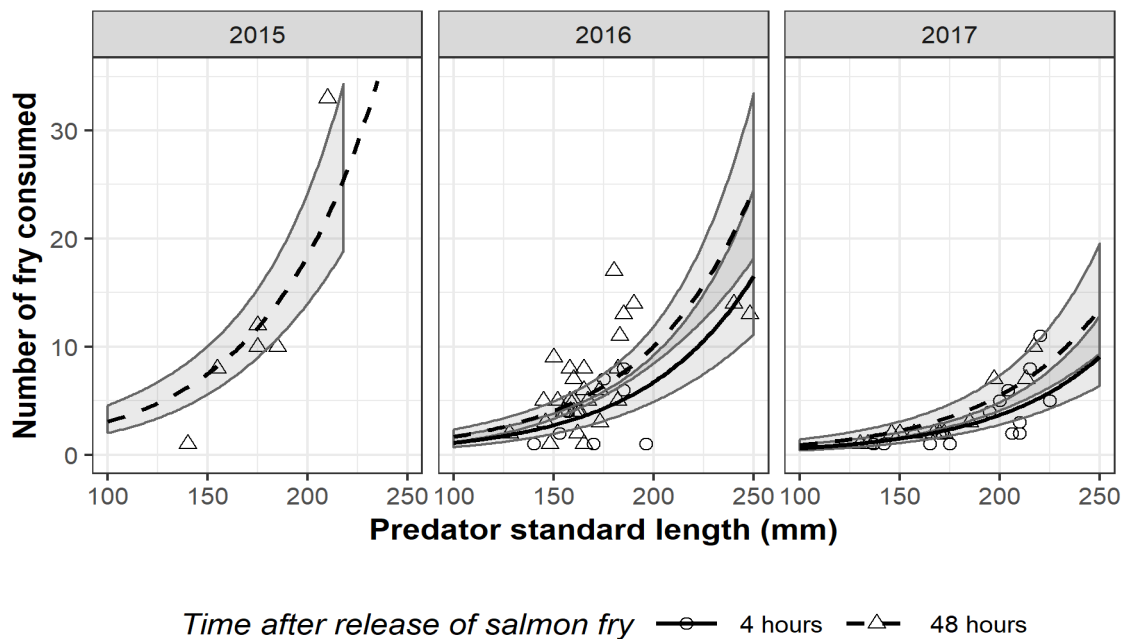
FIGURE 8. Relationship between predator standard length (brown trout) and the number of released salmon fry consumed within 4 and 48 hours after stocking of salmon fry in the river system in Rasdalen in 2015, 2016 and 2017. Predicted values from the general linearized model have been fitted to the plot (lines). The shaded area around predicted values is the 95% confidence interval of the model. In 2015 the confidence interval is not fully shown, as it is interrupted by the axis limit on the y-axis.

Analysis of variance (ANOVA) revealed a significant relationship between the standard length of the consumed salmon fry and the standard length of the predator ($F_{1,389}=6.70$, $P=0.01$), and the size increased with the size of predators (Figure 9). The size of consumed fry also differed among years (TukeyHSD: all pairwise comparisons, $P<0.001$).
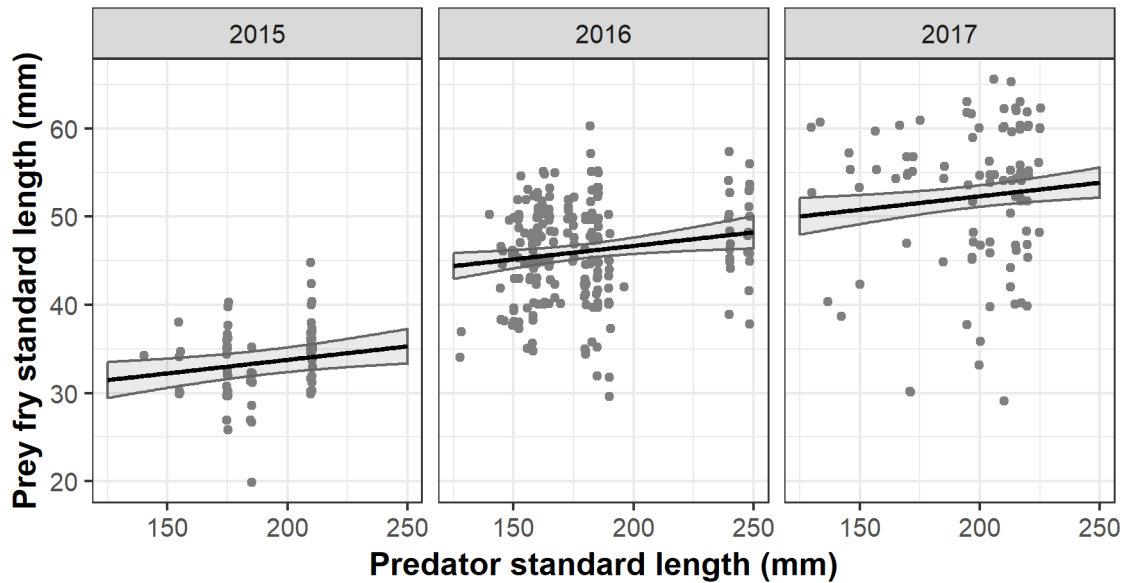
FIGURE 9. *Relationship between length of released Atlantic salmon fry eaten by brown trout predators in the river system in Rasdalen, (sampling times, 4 and 48 hours after release, have been pooled for 2016 and 2017 due to non-significant effect on standard length consumed by predators ($F_{1,388}=2.68$, $P=0.102$)) of salmon fry in 2015, 2016 and 2017. Predicted values from the linear model has have been fitted to the plot (solid line) and the shaded area around predicted values is the 95% confidence interval of the model.*

3.2 Size distribution salmon fry the day of release

Size distribution of individuals the day of release varied among years (Figure 10; Appendix V). In 2015 the distribution was very similar for enriched and plain fry treatments, whilst in 2016 and 2017 enriched fry seemed to cover a wider spectrum of sizes compared to plain fry.

The mean length of individuals varied significantly among years (TukeyHSD: all pairwise comparisons, $P<<0.001$), and there seemed to be a non-significant trend where the effect of treatment on length varied with experimental year ($F_{2,667}=2.443$, $P=0.088$) were the difference between enriched and plain fry in 2017 varied significantly from the difference found in 2015 ($T=2.164$, $P=0.031$). However, when looking at the model without the interaction term, the overall effect of rearing environment was significant ($F_{1,669}=7.83$, $P=0.005$), where plain fry was larger than enriched (Table 3; Figure 10). Kolmogorov-Smirnov test revealed that enriched fry was significantly shorter than plain fry in 2016 (KS-test: $D=0.199$, $P=0.007$), but there was no significant difference in 2015 ($D=0.030$, $P=0.920$) or 2017 ($D=0.121$, $P=0.180$).
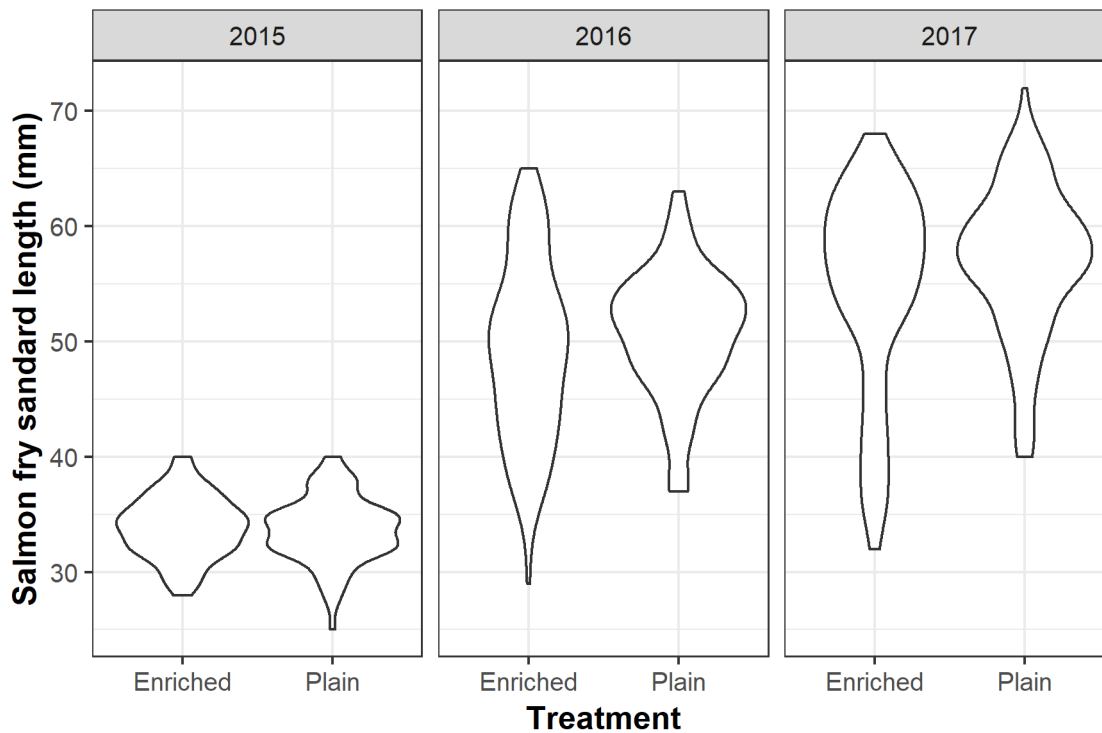
FIGURE 10. *Violin plots illustrating the frequency of individuals within different standard lengths (the wider the plot is at a certain length, the more individuals are found within this length) for salmon fry the day of release in in 2015, 2016 and 2017).*

3.3 Effects of rearing treatment on post-release predation mortality

A total of 420 released salmon fry were captured and eaten by predators in 2015, 2016 and 2017. In total, 410 fry could be identified to rearing treatment by examining their otoliths and 10 remained unknown.

2016 was the only year predators had consumed a significant higher proportion of plain- compared to enriched fry (Chi-test, 2016: X^2=9.481, P=0.002; Figure 11). In 2015 and 2017 there were no difference (Chi-test, 2015: X^2=0.127, P=0.722; 2017: X^2=0.0, P=1.0). When the analysis was done separately for the two sampling times (4 and 48 hours after release), the only significant difference in proportion was found for 2016, 48 hours after release of salmon fry (Chi-test, X^2=7.921, P=0.005; Appendix IV).
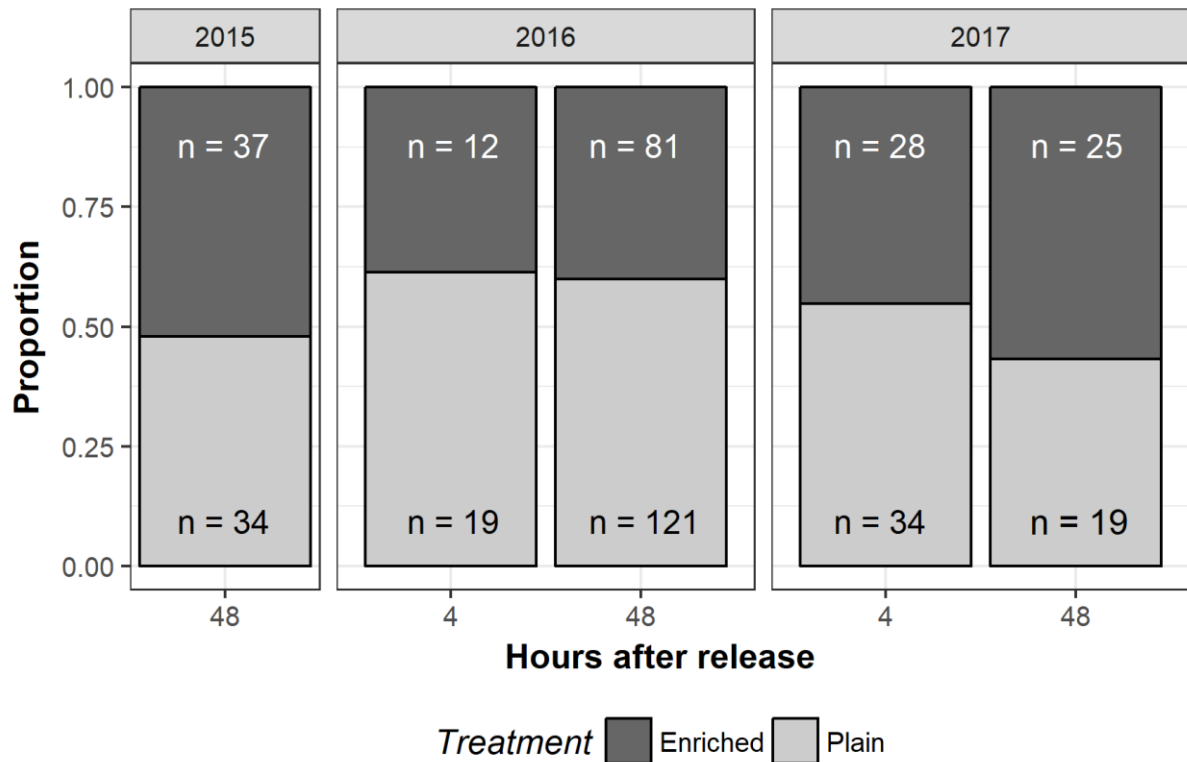
FIGURE 11. *Proportion of rearing conditions of Atlantic salmon fry obtained from stomach contents of brown trout predators sampled 4 and 48 hours after fry were released in Rasdalen and Brekkhus in 2015, 2016 and 2017.*

3.4 Effect of body size on predation mortality

Standard lengths of salmon fry in stomach contents (4 and 48 hours predator samples pooled) in 2016 and 2017 were significantly smaller compared to the size distribution of fish before release (KS-test: 2016, D=0.318, P<<0.001; 2017, D=0.231, P=0.001; Figure 12).This was also significant when the data from the respective rearing treatments were analysed separately (KS-test: 2016, plain: D=0.396, P<0.001, enriched: D=0.235, P=0.003; 2017, plain: D=0.241, P=0.015, enriched: D=0.242, P=0.019). No significant differences were found in 2015 (D=0.165, P=0.560). The released salmon consumed by predators did not differ in size in respect to rearing treatment (Appendix IV).
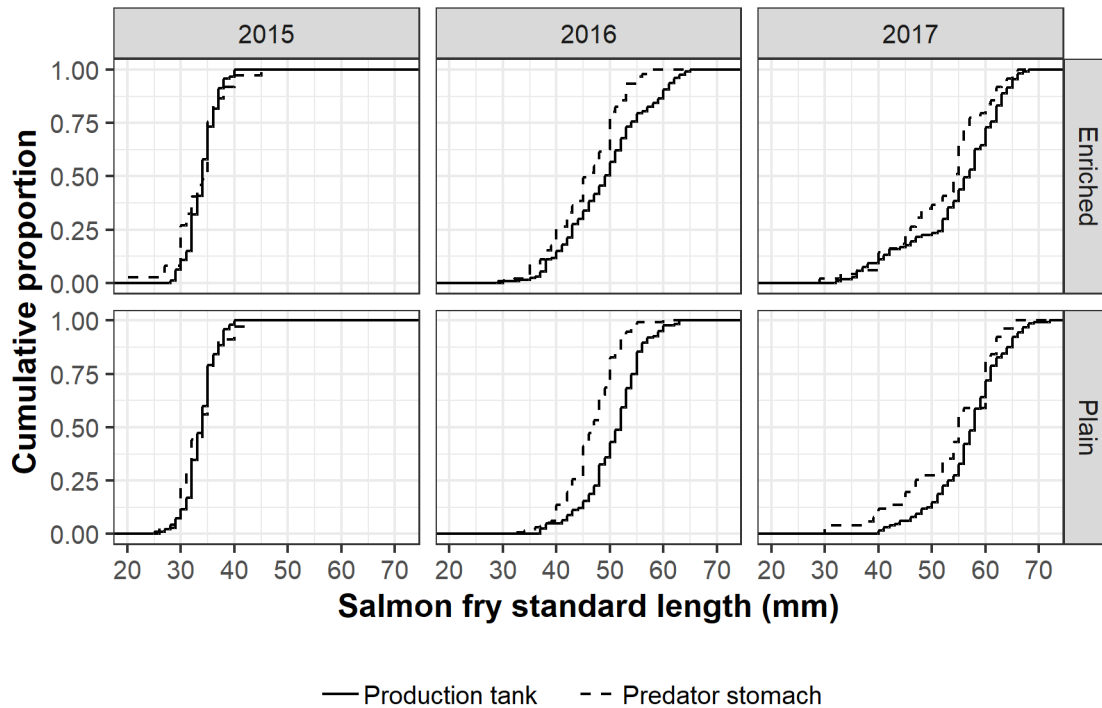
FIGURE 12. *Empirical cumulative density distributions (ECDF) of standard length of reared Atlantic salmon fry from production tanks (enriched and plain rearing pooled) and eaten by trout predators 4 and 48 hours after release in Rasdalen in 2015 (stocking: 7th of July), 2016 (stocking: 17th of August) and 2017 (stocking: 15th of August).*

3.5 Recapture of stocked fry two months after release

For all recaptures, the approximately ~ 100 individuals of salmon fry released the same year were obtained (Table 3). A total of 19 of these could not be identified to rearing treatment.

There was significant difference in proportion between the treatment groups in Rasdalen in 2017, where a significantly higher amount of plain salmon were recaptured (Chi-test: X^2=6.759, P=0.007; Figure 13). In Rasdalen 2015 and 2016, and Brekkhus 2017 there was, however, no significant difference (Chi-test: Rasdalen 2015, X=0.281, P=0.596; Rasdalen 2016, X=0.757, P=0.384; Brekkhus 2017, X-squared=0.375, P=0.540)
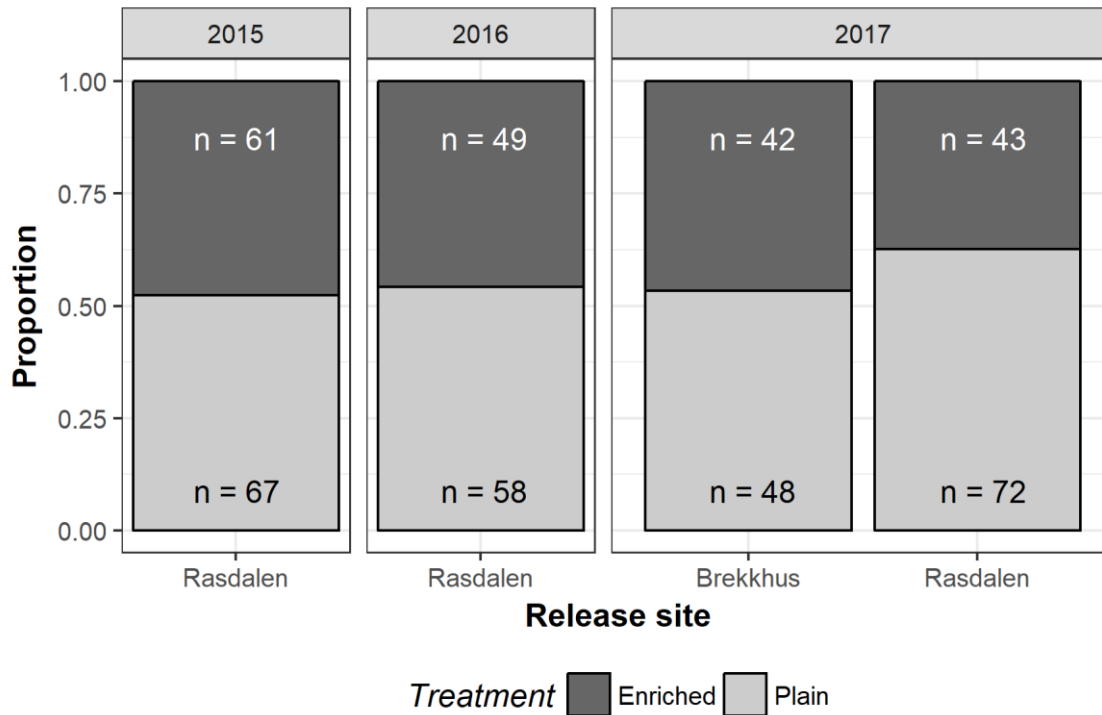
FIGURE 13. *Proportion of rearing conditions of Atlantic salmon fry recaptured from river systems in Brekkhus and Rasdalen two months after stocking of fry in 2015, 2016 and 2017. 2017. Individuals of unknown rearing group (n=14) have been removed from the proportion plot.*

Recaptured enriched salmon were significantly smaller compared to recaptured plain fry in 2017 at Rasdalen, but not at Brekkhus (KS-test: Rasdalen, D=0.239, P=0.046; Brekkhus, D=0.071, P=0.796; Figure 14.). The same trend was found in 2016, also in Rasdalen, but the difference was not significant (KS-test: D=0.226; P=0.066).
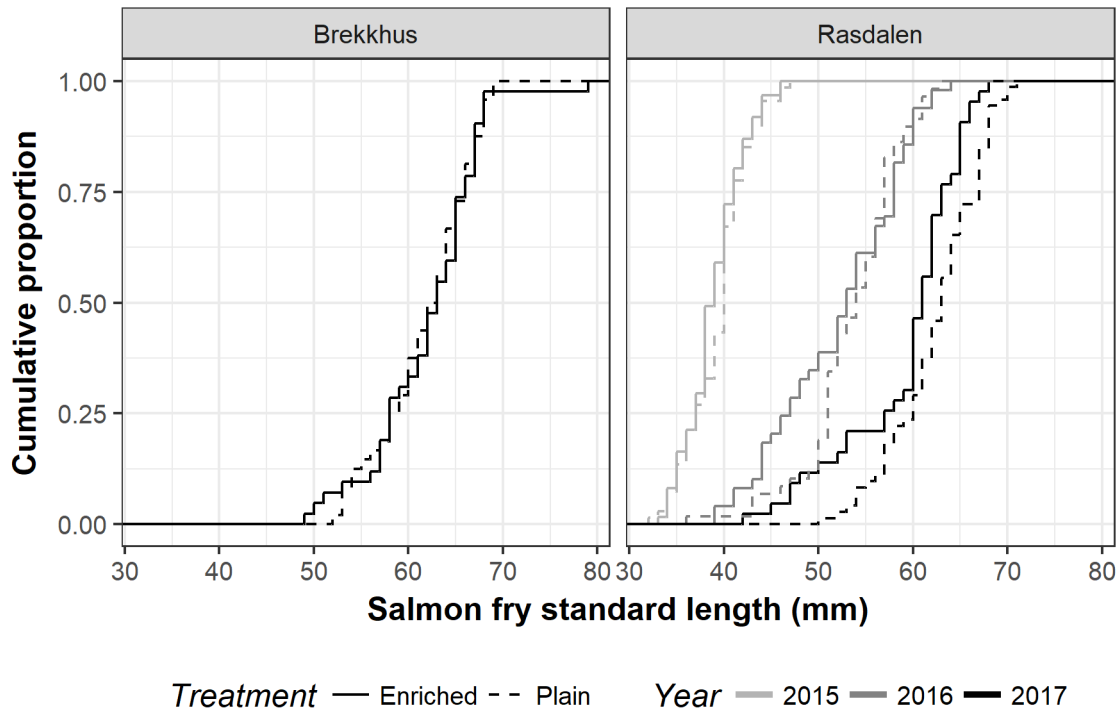
FIGURE 14. *Empirical cumulative density distributions (ECDF) of standard length of reared Atlantic salmon recaptured from river systems in Brekkhus in 2016 and Rasdalen in 2015, 2016 and 2017 two months after stocking of fry.*

The body mass of fry at both day of release and at recapture two months later varied among years (Figure 15; Table 9; Appendix V; Appendix VII). In 2015 there was a significant difference between the mean weight at release at recapture (ANOVA: $F_{1,313}=147.886$, $P\ll0.001$), where both rearing treatments had a significantly larger body mass at recapture (KS-test, enriched: $D=0.495$, $P\ll0.001$; standard: $D=0.595$, $P\ll0.001$), but no difference between rearing treatments (ANOVA: $F_{0.007,1}=0.301$, $P=0.584$). In 2016 there was no difference in mean weight at release and recapture (ANOVA: $F_{1,345}=0.013$, $P=0.910$), nor any effect of rearing treatment on weight (ANOVA: $F_{1,354}=1.774$, $P=0.184$). In 2017, within the enriched treatment, the weight at recapture compared to weight the day of release was significantly lower in Rasdalen (KS-test: enriched, $D=0.230$, $P=0.001$) and significantly higher in Brekkhus (KS-test: enriched, $D=0.230$, $P=0.041$), additionally to a significant difference between the two release sites (enriched, $D=0.432$, $P<0.001$). No significant difference was found for the plain-reared individuals (Appendix IV).
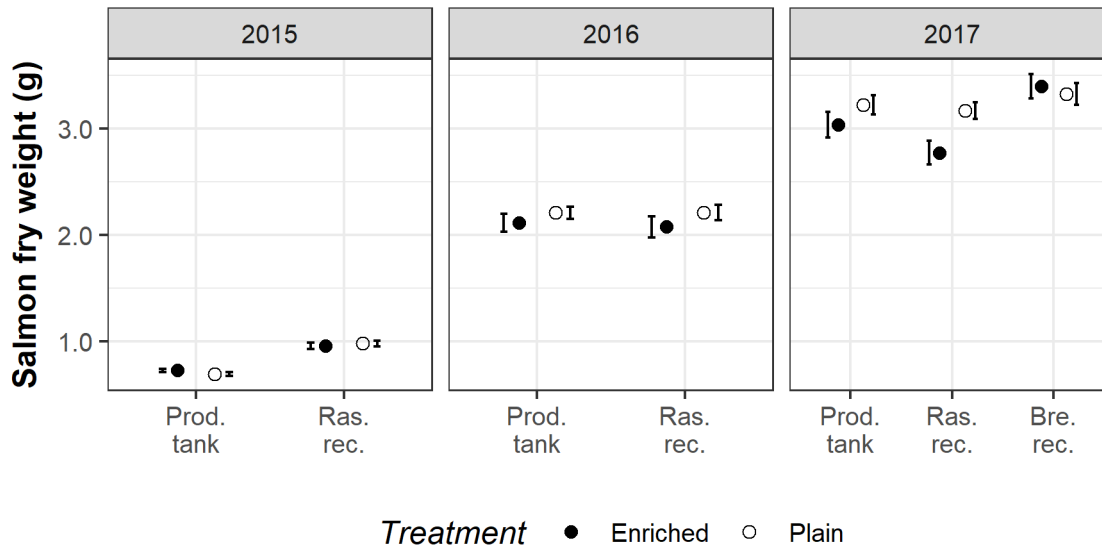
FIGURE 15. *Mean weight measured to the nearest 0.01 g of salmon fry at the time of release at Brekkhus in 2017 and at Rasdalen in 2015, 2016 and 2017 from recaptured samples ~two months later. Error bars have been fitted to their respective mean points.*

TABLE 9. *(Mean) standard growth rate (SGR) calculated from sub-sample from production tanks and sub-sample from of recaptured individuals. t refers to the time period between day of release and day of recapture, given in days.*

Year	t (days)	Release site	Treatment	Mean SGR
2015	92	Rasdalen	Enriched	0.28 %
			Plain	0.36 %
2016	68	Rasdalen	Enriched	0.0 %
			Plain	0.0 %
2017	85	Rasdalen	Enriched	- 0.11 %
			Plain	0.0 %
		Brekkhus	Enriched	0.21 %
			Plain	0.05 %

4.0 DISCUSSION

The present study provides conflicting results among experiment years in regards to the effect of rearing treatment on the immediate post-release predation mortality in newly stocked salmon fry. 2016 was the only year where fish reared in an enriched tank were found to have been consumed at a significantly lower proportion two days after release compared to fish reared in an impoverished tank. The estimated survival two months after release also varied among years, where there in 2015 and 2016 was no difference, while in 2017 fish reared in impoverished tanks were recaptured at a higher proportion in one of the two release sites. Predation pressure

seemed to differ between sites, but in general larger predators could consume larger- and more prey, and predators were overall size-selective of small salmon fry. The digestive state of consumed prey suggested that most fry were consumed shortly after release.

4.1 Effect of rearing conditions on post-release predation mortality

Both enriched- and plain-reared fry suffered from high mortality rates after stocking. The proportion of enriched and plain fry consumed by predators varied among years, and a significant difference was only found in Rasdalen 2016, where 60% of the identified fry found in the sampled predator stomachs (4- and 48-hour samples pooled) were from the plain treatment. This observation supports previous experimental works suggesting that enriched rearing can produce fish with a beneficial behaviour-repertoire for survival in the wild (e.g. Olla et al., 1998; Salvanes & Braithwaite, 2006; Salvanes et al., 2007; Strand et al., 2010). When fish are released in high densities like in the present experiment, it is likely to assume that several fish will struggle to rapidly find shelter, due to the limited shelter availability (Finstad et al., 2007). The enriched fry might have had an advantage when searching for this shelter (Roberts et al., 2011), which might be a reason for a lower number of enriched fry caught by the sampled predators in 2016. In the 2015 and 2017 the sampled predators had consumed similar amounts of fry from the two treatment groups, but in those years, sample sizes (4- and 48-hour sample pooled) were smaller (< 110 vs 233 in 2016).

It should be mentioned that is difficult to draw reliable conclusions from small-sized data sets. Preferably, all datasets should have had the size of one in 2016, however, this is not as easily achieved in field experiments compared to experiments conducted in controlled environments in a laboratory. Electrofishing could only be completed once per day per sampling site to avoid unnecessary stress exposure to the newly released salmon fry. The sample thus consists of all predators that were found within the sampling area at the time of sampling. There were a small number of fry that went unidentified due to loss or overpolishing of their otoliths, but this small number (2015, n=3; 2016, n=2) would not have affected the test results.

Nevertheless, in 2016 less enriched fry were found in predator stomach contents sampled 4 and 48 hours after release, and we may conclude that enriched rearing can have an effect on fry mortality caused by predation. However, the contradictory results from other two years could suggest that the effect is small and can only be detected at large sample sizes.

4.1.1 Size-selective mortality

Treatment was found to have a significant effect on body size of fry, and in 2016 and 2017 the length and body mass differed between the two treatments at the time of release. In both cases plain fry were larger than enriched. The observed slower growth of enriched fry is in accordance with some earlier works on salmonids in enriched environments (Fast et al., 2008; Rosengren et al., 2017) but in contrast to others (Tatara et al., 2009). The smaller size could in theory make the enriched fry more prone to negative size-selective mortality caused by predators.

The present study does provide evidence of size-selective mortality in 2016 and 2017 (but not in 2015). This was shown by the length of consumed salmon fry compared to length at release, which indicated that the predators selected smaller individuals. Negative size-selective feeding by piscivorous fish has been documented in several studies (e.g Hart & Hamrin, 1988; Furey et al., 2015). For size-selective mortality to occur, several conditions must apply; 1) there must be a variation of sizes within the population of prey fish; 2) the mortality of prey fish cannot be random; and 3) mortality rates must be high (reviewed in Sogard, 1997). In the present experiment, the two latter conditions have presumably been met. Whether the first condition was met, did however depend on the year of release, since distribution among standard lengths were wider in 2016 and 2017 compared to 2015. This might be why there was no evidence of size-selective feeding in 2015.

There might be several reasons for size-selective mortality: gape size of predators have in several cases shown to be one of the primary limiting factors of piscivorous feeding by fish (e.g. Parker, 1971; Hargreaves & Robin, 1985; Persson et al., 1996). Bluefish (*Pomatomus saltatrix*) predators attack several size groups, but only attacks on smaller individuals are successful (Juanes & Conover, 1994). Larger predators can consume larger prey and an experiment with brown trout predators found that the mean length of prey was approximately 33% of predator length (L'Abée-Lund et al., 1992). Hunting for prey is energetically costly, and optimal foraging theory indicate that the costs of prey handling should not extend the profitability in terms of for example energy gain from that individual (Emlen, 1966). Larger prey are bigger sources of energy, but the predator might select smaller individuals as the larger-sized prey often require more energy to catch (Gill, 2003).

It should also be mentioned that some bird species like white-throated dipper (*Cinclus cinclus*) and goosander (*Mergus merganser)* (both found in Norway) can prey upon salmon fry as they emerge from the gravel and, for the latter, also during smolt migration. The direction of size-selectivity in piscivorous birds seem to change with life stage of the fish, but can under several circumstances be selective of larger individuals (reviewed in Sogard, 1997). However,

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predation by birds is not covered in the present experiment and based on local knowledge of the two release sites it is expected that brown trout is the most important predator of salmon fry.

Nevertheless, it is difficult to say whether the distribution of the two treatment groups found in predator stomach contents would have been different if the fish released in 2016 and 2017 were of the same size. In 2015, when sizes were similar, equal numbers of fry from both treatments were found in predator stomach contents. Perhaps could the estimated lower predation-mortality of enriched fry in 2016, suggest that possible benefits of enriched rearing become more evident at larger sizes.

4.1.2 Variation in duration of enriched treatment among years

The constructions used as enrichment were the same for all years, but the duration of the treatment differed (2015 < 2016 < 2017). A longer time in enriched environments have shown to have positive effects on behavioural flexibility and learning ability (Bergendahl et al., 2016). This could potentially have contributed to the fact that there was no observed difference in predation mortality between the two treatment groups in 2015, while there in 2016 was a significantly larger amount of plain fry found in predator stomachs.

However, in 2017 the exposure to enrichment was even longer than in 2016, but there was found no difference in the proportion of plain and enriched fry consumed by predators. Perhaps are there more factors to be taken into account for the enriched rearing to have an effect on survival. Bergendahl et al. (2016) found no effect of the duration (5 weeks vs 12 weeks) of enriched rearing on anxiety trials, which were tested by releasing the fish into a novel tank and assessing the anxious behaviour like avoidance of open water, motionlessness and limited movement from the edges of the experimental tank. It could be that the duration of enriched rearing does not have an effect on stress recovery when fish are released into the wild. It is, however, difficult to extrapolate what effects observed in controlled environments in a laboratory would also affect the release in the wild, and no firm conclusion can be reached without further research.

4.2 Release-related stress factors

It is important to mention that hatchery-reared fish are exposed to several potential stressors during the time elapsed between capture from production tank until they are released into the river. Handling, which occurs when the fish are moved from rearing tank to water filled containers before transport, is a known stressor for the fish (e.g. Wedemeyer, 1972; Barcellos

et al., 2011). The following transportation is another stressful experience (Barton & Peter, 1982), and the release into the wild habitat, a large change from the rearing tank, is also considered to cause major stress in the fish.

One minute of handling-stress has been shown to negatively affect the predator avoidance of Coho-salmon *(Oncorhynchus kisutch)* (Olla & Davis, 1989). However, when the stressed fish in the mentioned study was given 90 minutes to recover from the stress, they seemed to be able to avoid predators at the same level as a non-stressed control group. If fish are exposed to stress for longer periods of time and of more intense types, the regaining of normal behaviour might take longer. The transport in this study took approximately two hours. Gilthead seabream *(Sporatus aurata)* exposed to two hours of crowding-stress density did not regain normal cortisol levels (a commonly used indicator of stress in fish) until two days after stress exposure (Ortuño et al., 2001). However, anti-predator behaviour in an unstressed state can be regained faster than what the level of cortisol indicates (Olla et al., 1992) and it is suspected that enriched individuals can return to an unstressed state faster than plain-reared counterparts (Salvanes & Braithwaite, 2005).

Since differences in proportions consumed by predators only were observed for one year, it could by hypothesized that release-related stress overshadow the potentially positive effects of enriched rearing that has been proposed by earlier experimental works (e.g. Berejikian et al., 2000; Armstrong et al., 2003; Salvanes et al., 2013). In the present experiment, fry were acclimatized for a short period of time in containers with mixed water from the river and the plastic bag they had been transported in. This acclimatization might not have been sufficient for the fish to adjust to the river temperature, and seemingly not to the other environmental factors like river flow, bottom substrate etc. Perhaps would it have been beneficial for the fish to be acclimatized at a larger scale before release, to more factors than just water temperature.

4.3 General predation mortality

The predation pressure on newly released salmon fry was high within the first 48 hours after release. This is in accordance with previous works which also report high predation mortality of released fish shortly after stocking (Henderson & Letcher, 2003). Larger predators were more likely to consume more and larger prey, which is supported by earlier works on predator-prey-size relationships (Juanes, 2016; Gaeta et al., 2018), and stomach capacity in relation to body mass (Brett, 1971; Gosch et al., 2009). The largest average number of fry consumed by predators were found in 2015, presumably due to the small size of released salmon fry this year. Smaller fish are often susceptible to a wider range of predators, since less predators are gape-

limited and/or unable to catch them (reviewed in Sogard, 1997). The low body mass of small-sized fish occupies less volume in the stomachs, and predators must furthermore consume a larger number of individuals to achieve satiation.

4.3.1 Time of ingestion by predators

It is likely to assume that most of the released fish in this experiment was captured and eaten by predators very soon after release, since relatively few salmon fry were freshly eaten (i.e., digestive state categories A and B; cf. Table 7) in the predator stomachs sampled 48 hours after stocking. Nothing can be said about the predation after this point since no predators were sampled at a later time. For both treatment groups, most of the prey salmon in the stomachs of predators sampled 48 hours after stocking, were medium digested (i.e., digestive state categories C and D; cf. Table 7). Naturally, salmon fry consumed by predators sampled 4 hours after release, were less digested than fry found in predator stomachs sampled 48 hours after release.

One should be aware of that the use of the categories for digestive state as indices for time elapsed since the salmon fry was eaten by a predator has its limitations. Digestion is highly dependent on various factors; such as water temperature (e.g. Yamamoto et al. 2007; Legler et al., 2010) and bolus size, and digestion time is proportional to the size of the bolus (Salvanes et al., 1995). A prey's location within the bolus is also likely to play a role, as the centre of the bolus will be less exposed to digestive enzymes than the outer parts (Knutsen & Salvanes, 1999). However, with these limitations taken into account, there should theoretically not be any severe bias regarding the limited use of digestive state categories in this experiment, since most predators had consumed relatively few salmon fry.

4.3.2 Predator experience

The lack of freshly eaten fry in predator stomachs sampled 48 hours after release could be due to lack of hunger or motivation to feed by predators shortly before the sampling. It could also be that the salmon fry quickly adapted to the presence of predators after surviving the first predator encounters.

The possible adaptation to predator presence is supported by earlier experiments where fish previously exposed to predator cues are quicker to initiate risk-averse behaviour when exposed to new predator encounters (Lonnstedt et al., 2012). This behaviour is thought to improve rapidly with experience (Olla & Davis, 1989; Hossain et al., 2002), and juvenile rainbow trout (*Oncorhynchus mykiss*) have shown to be able to remember predator cues even

21 hours after conditioning (Brown & Smith, 1998). Perhaps has the released salmon that survived the first predator encounters achieved enhanced anti-predator behavioural responses and furthermore better chances of surviving new ones (Vilhunen, 2006).

It is also likely to assume that the high densities of fish released makes it easy for the trout to catch fry, as not all fry will be able to find shelter in the vicinity of the release site (Griffiths & Armstrong, 2002). As the predation is thinning the group of released fry, it becomes harder for predators to pinpoint the remaining individuals – especially if they also have gained experience and fled from their recent predator encounters.

4.3.3 Mortality differences between biotopes

There were differences in predation between the two release sites. Few of the potential predators sampled in Brekkhus 2017 had consumed released salmon fry (26%) compared to Rasdalen the same year (53%). An explanation to this could be that there were less hunting predators in Brekkhus. Perhaps were the potential predators found here predominantly drift-feeders, as the high water velocity of the river possibly produce a larger amount of aquatic-derived drift (Naman et al., 2017).

Riffles and runs, which are dominating in Brekkhus, are also the preferred habitat of wild, juvenile salmon parr and fry (Gibson, 1993). This is likely due to the suitable substrate and less competition with brown trout, which predominantly is found in deeper areas with slower waterflow (especially older trout) (Kennedy & Strange, 1982; Crisp, 1993). The larger number of pools with slower flowing water found in Rasdalen therefore suggest a presumably larger abundance of large brown trout (Kennedy & Strange, 1982; Heggenes, 1996), which most likely are more active predators of released salmon. It is likely to assume that these differences between the two release sites could explain the lower predation pressure observed in Brekkhus.

4.4 Treatment proportions in the river two months after release

In the present experiment, the relative recapture rate between enriched and plain fry two months after release was used to evaluate the effect of rearing treatment on fry survival. Results varied among years, and the proportion distribution was only found to be different in Rasdalen, 2017, where a significantly higher proportion (0.63) of plain fry was found in the recaptured sample from the river. This observation, and the otherwise similar proportion distributions among the other recaptures, are opposing results to the hypothesis of enrichment providing enhanced survival.

It should be mentioned that the use of recaptures as an estimate of survival in the present study has its limitations. When limited by a sub-sample size, one is not guaranteed to achieve a good representation of the actual distribution in the river, since the released fry have become dispersed after release. However, by covering 50 m downstream of the release site in additionl to the whole initial stretch, the electrofishers took the potential downstream dispersal of released fry into account, and one can assume that the recapture provides a reasonable estimate.

The finding of no difference in both 2015, 2016 and Brekkhus, 2017 is in correspondence with a few earlier field experiments, that also found no difference in survival estimated by recapture rates of enriched- compared to conventionally reared salmonids (Brockmark et al., 2007; Tatara et al., 2009). These findings are, however, challenged by another study that estimated survival based on recapture, that showed significantly improved survival after release, as a result of enrichment (Hyvärinen & Rodewald, 2013).

However, none of these experiments can explain the larger proportion of plain fry being recaptured in Rasdalen 2017. One possible explanation could be that the larger size of plain-reared salmon fry becomes a more predominant factor for survival with time, when both rearing treatments obtain experience in the wild. In Hyvärinen & Rodewald's (2013) experiment, the studied salmon were smolts, and both treatment groups might have been less prone to potential predation mortality due to their large size compared to e.g. salmon fry, and the young-of-the-year salmonids in the other two experiments (Brockmark et al., 2007; Tatara et al., 2009). This theory is supported by the fact that in Rasdalen, 2016 (mean difference, length: 2 mm, weight: 0.10 g) the same trend of higher survival of plain fry was found (however, not significant). Additional support for this theory is found in 2015, when released salmon from both rearing treatments were of approximately the same length, and there was no difference in survival estimated by the recapture proportion. Since the survival of salmon is highly linked to their size, these survival rates could suggest that the size-selective feeding by predators possibly could have masked a possible effect of enriched rearing compared to standard, plain rearing.

It might also be that the type of enrichment used in this experiment do not necessarily provide the fish with improved survival in relation to competition and further predation risk when foraging. It could also be that the effect of enrichment can vary with the life stage of the salmon and perhaps could different types of enrichment have a larger, positive effects on fry survival. (Brockmark et al., 2007) found no effect of structural complexity as enrichment on estimated survival by recaptures. They, and others, have. However, found positive effect of reduced rearing density on post-release survival in salmonids (e.g .Jonsson et al., 2010). Perhaps

could a combination of the two, where the enrichment is chosen accordingly to the species in question, be a way to improve survival at a larger scale.

4.4.1 Mean weight comparisons

The mean body mass at the day of release compared to the mean at recapture varied among years and release sites. This is not surprising, taking into account the differences in duration of treatment, release month and release site topography.

The fish released in 2015 were relatively small compared to the fish released in 2016 and 2017. By potentially being more prone to predation due to their small size, it could be that predators quickly thinned out the group and that the growth of the remaining fry were not as density-dependent compared the larger fry released in 2016 and 2017, which either had a lower mean body mass at recapture, or no difference between the two. It is also a possibility that the earlier release in 2015 could have benefitted salmon fry growth.

The largest difference in mean weight was found within the enriched treatment, where there was a significant lower body mass at recapture at Rasdalen compared to the recapture at Brekkhus (mean difference: 0.63 g). The same trend was found for the plain treatment, but the difference was not significant (mean difference: 0.15 g). This could suggest that there were differences between the release site. However, a firm conclusion cannot be made, since the mean weight of the recaptured sample is supposedly dependent on several factors like size-selective predation mortality, density-dependent growth and other conditions in the river.

Nevertheless, the differences found between years suggest that the growth of fish can vary with rearing treatment and might depend on the size of the fish at time of stocking, and the release site biotype.

4.5 Implications for the future

The results from the present study indicate that there might be a potential effect of enriched rearing on immediate post-release predation mortality in newly stocked salmon fry. However, the contradictory findings in this study of proportions of enriched and plain fry in stomach contents of predators just after release, and in recaptured samples two months later, could be taken as supporting evidence for that the effect on survival must be small or limited.

The present study raises the question of whether enrichment used in this experiment has been sufficient for improving post-release survival. There are several types of enrichment that can be used in rearing; for example substrate, underwater feeding, changes in waterflow, food dispersal etc. Perhaps could a different, or an additional type of enrichment, have improved the

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survival of the fry. Since wild salmon fry are highly dependent on the substrate of the river to survive, it might be that a better enrichment type for hatchery-reared salmon fry is to provide them with a substrate in the tank resembling that of the river.

The structures in this experiment were meant to simulate potential shelter and river flora, but this might not have been sufficient. The type of enrichment chosen in captive rearing should aim to benefit the species and life stage in question, and further research should be done to see what type of enrichment might provide the best effects in terms of survival.

As already discussed, it might be that the potential effect of enrichment on survival can have been limited by the stress related to release procedures. Stress has shown to reduce predator-avoidance in a stressed state in Coho-salmon (Olla & Davis, 1989), and even though enrichment have shown improve the ability of fish to recover from mild stressors in the laboratory (Salvanes & Braithwaite, 2005; Pounder et al., 2016), the stress at release lasts longer and is more intense. The present study raises the question of whether fish are properly acclimatized before release when they are only acclimatized in a container with mixed water from the river and the transportation bag.

Perhaps would the benefits from enrichment have become more evident if the acclimatization was done at a larger scale. This could for example be done by creating predator-free enclosures in the river, where the hatchery-reared fish could acclimatize for a while before the actual release. An acclimatization within such predator-free enclosures have shown potential to improve post-release survival of brown trout (Jonssonn et al., 1999) common snook (*Centropomus undecimalis*) (Brennan et al., 2006). However, based on these two experiments, the acclimatization alone could perhaps be the main contributor to increased survival. Enriched rearing could still contribute to a development of the brain more similar to that of wild counterparts (Kihslinger, 2006; DePasquale et al., 2016) and, if done correctly, be beneficial in a fish welfare aspect.

In the present experiment fish were released in high densities to create competition between individuals. They were also reared in relatively high densities in their respective production tanks, which is the common procedure in hatcheries. However, high rearing densities seem to reduce growth, and studies suggest that a reduced rearing density has a larger effect on survival than the exposure to structural enrichment (Brockmark et al., 2007; Rosengren et al., 2017). By rearing a lower numbers of fish, the individual survival is perhaps higher, but it might be that numbers are too low to be able to enhance wild population abundance.

To further investigate the aforementioned factors, one need larger scaled experiments both in the hatchery and at release, with several replicate rivers to compare. Such a large-scale experiment would also need detailed planning, but could potentially provide future hatcheries and scientists with knowledge of how to best improve survival of released hatchery-reared fish.

5.0 CONCLUSION

The present study provides evidence for high predation mortality of newly released Atlantic salmon fry, and that this mortality can be negatively size-selective and more extensive in certain biotopes. The results from the two main experiments: immediate predation mortality, and two-month survival, could be interpreted as revealing conflicting findings with respect to the testing of whether enriched rearing produce fish with a behaviour repertoire more beneficial for survival than that of plain-reared counterparts. The data on immediate post-release predation mortality show that there either was an equal proportion distribution of the two treatment groups consumed, or the predators stomach contents consisted of larger proportion of plain-reared fish. In contrast, the recapture samples from electrofishing two months later, showed equal proportions of enriched and plain-reared fry in the sample, or a higher proportion of plain-reared fish.

The overall results from these data could suggest that enriched rearing can provide salmon with an enhanced ability to hide from predators immediately after release, but that effect is small and that the enrichment might not be sufficient for promoting improved survival beyond this. Since the survival of juvenile Atlantic salmon is highly linked to their size, and fish from the enriched treatment were smaller when released, the question remains whether the documented size-selective feeding by predators possibly could have masked the effect of enriched rearing. A second important aspect is that stress related to the release procedure could possibly have been too extensive, and that the fish would have needed a longer time to acclimatize for the enrichment to have noticeable effect on survival. Further research on the practice of hatchery-rearing and release should be done in order to find the most optimal strategy for obtaining higher survival in released hatchery-reared fish.

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7.0 APPENDICES

APPENDIX I. *Number (n) of fry in each rearing tank at the beginning of rearing, and the approximate number of fish in each rearing tank the day of release. The number of fish was reduced by hatchery technicians in 2016 and 2017, but not in 2015.*

Year	Start of rearing: n fish	Day of release: n fish
2015	~ 8 300	~ 8 300
2016	16 000	~ 3 000
2017	16 000	~ 4 000

APPENDIX II. Overview of measurements completed on sampled predators in 2015, 2016 and 2017. ID of predator gives information about year, experimental site and how long after release it was captured. Example: P15R48.01 is a predator caught in 2015 (P15), in Rasdalen (R), 48 hours after release of salmon fry (48), and it was the first predator examined (.01). Sp. refers to the species of predator, where "trutta" is brown trout and "salar" is Atlantic salmon. Tot.L., Std.L and Fork.L refers to total- standard- and fork length respectively. Tot.W, Gutted.W, Liver.W and Gonad.W refers to total-, gutted-, liver- and gonad- weight respectively. Emp.Stom.W refers to the weight without stomach content and Scw refers to the weight of the stomach content. Fry refers to the number of fry consumed by the predator. The empty stomach weight was in 2015 calculated by using the mentioned equation under 2.6 Predator sample analysis (marked with *) and by adding the weight of the stomach content, the total weight was obtained (marked with **).

ID	Sp.	Tot.L.mm	Std.L.mm	Fork.L.mm	Tot.W.g	Gutted.W.g	Liver.W.g	Gonad.W.g	Sex	Emp.stom.W.g	Scw	Fry
P15R48.01	trutta	NA	175	NA	88.75**	NA	NA	NA	NA	86.37*	2.38	12
P15R48.02	trutta	NA	135	NA	37.01**	NA	NA	NA	NA	37.01*	0	0
P15R48.03	trutta	NA	210	NA	134.24**	NA	NA	NA	NA	129.55*	4.69	33
P15R48.04	trutta	NA	185	NA	101.04**	NA	NA	NA	NA	98.71*	2.33	10
P15R48.05	trutta	NA	175	NA	88.41**	NA	NA	NA	NA	86.37*	2.04	10
P15R48.06	trutta	NA	155	NA	63.75**	NA	NA	NA	NA	61.69*	2.06	8
P15R48.07	trutta	NA	140	NA	43.47**	NA	NA	NA	NA	43.18*	0.29	1
P15R48.08	trutta	NA	160	NA	67.86**	NA	NA	NA	NA	67.86*	0	0
P16R4.01	trutta	195	170	190	71.05	58.65	1.03	2.25	Female	69.97	1.08	1
P16R4.02	trutta	180	154	169	52.57	48.11	0.17	0.17	NA	45.06	7.51	0
P16R4.03	trutta	200	175	189	92.47	69.88	0.83	3.07	Female	80.8	11.67	7
P16R4.04	trutta	212	185	205	108.02	82.15	0.62	1.88	Male	95.49	12.53	6
P16R4.05	trutta	210	185	205	131.08	102.5	1.09	3.37	Male	116.49	14.59	8
P16R4.06	trutta	162	140	155	52.94	45.17	0.54	0.34	Female	50.78	2.16	1
P16R4.07	trutta	145	123	140	32.43	29.08	0.25	0.24	Female	32.28	0.15	0
P16R4.08	trutta	181	157	172	71.98	57.17	0.43	1.29	Male	65.55	6.43	4

P16R4.09	trutta	172	153	169	62.71	47.41	0.48	2.66	Female	57.4	5.31	2
P16R4.10	trutta	175	153	172	61.62	50.68	0.95	2.88	Female	61.62	0	0
P16R4.11	trutta	226	196	218	136.24	117.32	1.02	4.05	Male	134.47	1.77	1
P16R4.12	trutta	161	141	155	43.63	39.48	0.14	0.33	Female	43.56	0.07	0
P16R4.13	trutta	184	165	180	65.84	55.84	0.81	3.38	Female	65.55	0.29	0
P16R48.01	trutta	180	156	174	72.21	57	0.46	2.18	Male	67.62	4.59	4
P16R48.02	trutta	205	182	198	100.08	77.35	0.51	1.31	Male	90.15	9.93	5
P16R48.03	trutta	206	182	200	116.83	84.43	1.29	6.73	Female	106.11	10.72	8
P16R48.04	trutta	189	163	183	79.51	59.47	0.93	3.85	Female	73.59	5.92	4
P16R48.05	trutta	195	167	185	80.81	62.1	0.52	1.37	Male	72.8	8.01	5
P16R48.06	trutta	170	148	163	52.54	43.85	0.3	0.64	Male	50.44	2.1	1
P16R48.07	trutta	190	165	180	71.36	59.24	0.91	3.7	Female	69.94	1.42	1
P16R48.08	trutta	200	173	192	111.91	85.23	0.92	2.97	Male	100.44	11.47	6
P16R48.09	trutta	275	240	265	218.03	170.11	1.71	0.24	Male	191.47	26.56	14
P16R48.10	trutta	218	190	208	126.56	92.23	1	2.75	Male	107.06	19.5	14
P16R48.11	trutta	185	162	177	82.61	67.37	1.51	4.87	Female	80.51	2.1	2
P16R48.12	trutta	211	185	204	132	87.32	1.57	4.44	Female	109.46	22.54	13
P16R48.13	trutta	195	173	189	86.53	68.22	0.84	3.22	Female	81.02	5.51	3
P16R48.14	trutta	290	248	279	207.82	163.84	1.24	0.17	Male	182.41	25.41	13
P16R48.15	trutta	170	150	163	65.06	44.96	0.52	1.05	Male	54.09	10.97	9
P16R48.16	trutta	182	158	176	72.17	55.71	0.51	0.93	Male	62.64	9.53	8
P16R48.17	trutta	210	180	200	114.47	75.7	0.76	2.32	Male	92.27	22.2	17

P16R48.18	trutta	185	160	175	75.59	55.62	0.63	1.44	Male	65.65	9.94	7
P16R48.19	trutta	180	160	175	74.39	59.52	0.55	2.05	Male	69.11	5.28	4
P16R48.20	trutta	150	128	140	33.7	30.36	0.27	0.13	Female	33.52	0.18	0
P16R48.21	trutta	176	152	167	62.37	50.6	0.5	1.11	Male	58.34	4.03	5
P16R48.22	trutta	165	145	158	55.15	42.82	0.42	0.3	NA	49.19	5.96	5
P16R48.23	trutta	188	165	180	87.11	61.23	0.6	2.03	Male	73.15	13.96	8
P16R48.24	trutta	185	165	180	75.45	58.29	0.52	2.17	Male	67.67	7.78	6
P16R48.25	trutta	183	162	178	69.66	53.73	1.05	2.38	Female	65.25	4.41	4
P16R48.26	trutta	170	146	160	51.3	44.79	0.5	1.2	Male	49.28	2.02	3
P16R48.27	trutta	177	155	171	62.35	48.18	0.42	1.86	Male	56.68	5.67	4
P16R48.28	trutta	148	128	140	38.44	32.17	0.43	0.79	Female	36.54	1.9	2
P16R48.29	trutta	180	158	175	67.9	51.12	0.95	2.17	Female	61.11	6.79	5
P16R48.30	trutta	184	160	178	83.14	64.58	0.53	1.87	Male	73.66	9.48	5
P16R48.31	trutta	211	183	201	114.93	80.2	0.85	2.49	Male	94.78	20.15	11
P16R48.32	trutta	176	160	170	60.56	47.43	0.36	1.36	Male	54.47	6.09	5
P16R48.33	trutta	172	152	162	68.51	51.59	0.81	2.33	Female	60.18	8.33	5
P17B4.01	trutta	150	141	NA	30.4	NA	NA	NA	NA	30.4	0	0
P17B4.02	salar	151	142	NA	36.8	NA	NA	NA	NA	36.8	0	0
P17B4.03	trutta	220	212	NA	109.6	NA	NA	NA	NA	109.6	0	0
P17B4.04	trutta	202	198	NA	93.4	NA	NA	NA	NA	93.4	0	0
P17B4.05	trutta	171	164	NA	51.2	NA	NA	NA	NA	51.2	0	0
P17B4.06	salar	140	131	NA	27.4	NA	NA	NA	NA	27.4	0	0

P17B4.08	trutta	179	172	NA	62	NA	NA	NA	NA	62	0	1
P17B4.09	trutta	170	164	NA	46	NA	NA	NA	NA	46	0	0
P17B4.10	salar	142	137	NA	36.6	NA	NA	NA	NA	36.6	0	0
P17B4.11	trutta	142	133	NA	30.4	NA	NA	NA	NA	30.4	0	0
P17B48.01	trutta	144	125	NA	34.6	NA	NA	NA	NA	33.2	1.4	1
P17B48.02	trutta	251	223	NA	156	NA	NA	NA	NA	151.28	4.72	0
P17B48.03	trutta	290	260	NA	275	NA	NA	NA	NA	263.16	11.84	2
P17B48.04	trutta	164	145	NA	53	NA	NA	NA	NA	50.32	2.68	1
P17B48.05	trutta	162	143	NA	49.2	NA	NA	NA	NA	49.2	0	0
P17B48.06	trutta	179	155	NA	55.5	NA	NA	NA	NA	55.5	0	0
P17B48.07	trutta	162	150	NA	48	NA	NA	NA	NA	48	0	0
P17B48.08	trutta	160	142	NA	42.8	NA	NA	NA	NA	42.01	0.79	1
P17B48.09	trutta	155	132	NA	45	NA	NA	NA	NA	45	0	0
P17R4.01	trutta	235	210	NA	144	NA	NA	NA	NA	139.8	4.2	2
P17R4.02	trutta	233	204	225	145.6	115.37	1.22	0.16	Male	129.32	16.28	6
P17R4.03	trutta	245	215	NA	164.6	NA	NA	NA	NA	141.73	22.87	8
P17R4.04	trutta	223	200	NA	110.6	NA	NA	NA	NA	100.3	10.3	5
P17R4.05	trutta	235	210	NA	126.6	NA	NA	NA	NA	115.93	10.67	3
P17R4.06	trutta	245	220	NA	181.4	NA	NA	NA	NA	147.8	33.6	11
P17R4.07	trutta	230	206	NA	132.4	NA	NA	NA	NA	125.75	6.65	2
P17R4.08	trutta	251	225	NA	176.2	NA	NA	NA	NA	159.14	17.06	5
P17R4.09	trutta	220	195	NA	113.6	NA	NA	NA	NA	101.61	11.99	4

P17R4.10	trutta	191	170	NA	74	NA	NA	NA	NA	68.95	5.05	2
P17R4.11	trutta	201	175	NA	82.8	NA	NA	NA	NA	78.88	3.92	1
P17R4.12	trutta	202	176	193	73.92	64.03	0.76	3.52	Female	73.56	0.36	0
P17R4.13	trutta	161	140	152	43.65	38.3	0.5	1.16	Female	43.57	0.08	0
P17R4.14	trutta	181	156	172	61.91	55.37	0.41	1.28	Male	61.66	0.25	0
P17R4.15	trutta	201	176	197	83.32	73.47	0.85	2.11	Female	83.01	0.31	0
P17R4.16	trutta	183	160	175	61.38	53.11	0.64	2.49	Female	61.1	0.28	0
P17R4.17	trutta	165	142	160	51.51	42.84	0.56	2.16	Female	49.92	1.59	1
P17R4.18	trutta	175	150	161	53.31	45.61	0.75	2.37	Female	52.99	0.32	0
P17R4.19	trutta	190	165	184	71.12	61.28	0.42	1.07	Male	67.84	3.28	1
P17R4.20	trutta	162	142	157	43.9	39.41	0.33	0.05	NA	43.72	0.18	0
P17R4.21	trutta	198	171	190	74.76	64.24	1.06	2.19	Female	73.61	1.15	2
P17R4.22	trutta	145	125	139	29.82	27.05	0.26	0.1	Female	29.61	0.21	0
P17R4.23	trutta	152	130	145	34.57	31.03	0.39	0.1	Female	34.35	0.22	0
P17R4.24	trutta	140	121	133	29.15	26.49	0.24	0.12	Female	28.97	0.18	0
P17R4.25	trutta	145	125	140	33.68	29.76	0.21	0.75	Male	33.54	0.14	0
P17R4.26	trutta	140	121	133	27.57	24.84	0.21	0.12	Female	27.24	0.33	0
P17R4.27	trutta	182	156	176	63.62	58.28	1.33	0.42	Male	63.25	0.37	0
P17R4.28	trutta	165	143	156	45.95	42.22	0.36	0.1	Female	45.74	0.21	0
P17R4.29	trutta	148	128	140	34	30.87	0.28	0.09	Female	33.79	0.21	0
P17R4.30	trutta	145	125	138	28.71	26.01	0.21	0.1	Female	28.56	0.15	0
P17R4.31	trutta	158	137	151	37.95	32.67	0.24	0.88	Male	36.87	1.08	1

P17R4.32	trutta	156	135	147	38.24	34.96	0.3	0.06	Female	38.14	0.1	0
P17R4.33	trutta	145	125	138	28.05	25.48	0.2	0	NA	27.86	0.19	0
P17R48.01	trutta	169	146	NA	55.2	NA	NA	NA	NA	50.7	4.5	2
P17R48.02	trutta	232	213	NA	137	NA	NA	NA	NA	120.28	16.72	7
P17R48.03	trutta	190	167	NA	65.5	NA	NA	NA	NA	61.61	3.89	2
P17R48.04	trutta	141	123	NA	27.5	NA	NA	NA	NA	27.5	0	0
P17R48.05	trutta	162	142	NA	43.4	NA	NA	NA	NA	43.4	0	0
P17R48.06	trutta	172	155	NA	48.4	NA	NA	NA	NA	48.4	0	0
P17R48.07	trutta	145	130	NA	37	NA	NA	NA	NA	34.78	2.22	1
P17R48.08	trutta	151	134	NA	43	NA	NA	NA	NA	38.84	4.16	1
P17R48.09	trutta	142	130	NA	35.4	NA	NA	NA	NA	34.12	1.28	1
P17R48.10	trutta	249	217	NA	176	NA	NA	NA	NA	149.8	26.2	10
P17R48.11	trutta	190	170	NA	76.2	NA	NA	NA	NA	72.29	3.91	2
P17R48.12	trutta	220	197	NA	126.2	NA	NA	NA	NA	112.58	13.62	7
P17R48.13	trutta	196	172	NA	84.6	NA	NA	NA	NA	78.58	6.02	2
P17R48.14	trutta	210	185	NA	86.4	NA	NA	NA	NA	81.41	4.99	3
P17R48.15	trutta	169	150	NA	52	NA	NA	NA	NA	49.55	2.45	2
P17R48.16	trutta	176	157	NA	63.6	NA	NA	NA	NA	59.47	4.13	2
P17R48.17	trutta	131	115	NA	25	NA	NA	NA	NA	25	0	0
P17R48.18	trutta	168	150	NA	49.8	NA	NA	NA	NA	49.8	0	0
P17R48.19	trutta	150	130	NA	32.6	NA	NA	NA	NA	32.6	0	0
P17R48.20	trutta	155	135	NA	34.4	NA	NA	NA	NA	34.4	0	0

APPENDIX III. *Overview of all Kolmogorov-Smirnov tests and their respective D- and P-values for standard length of predators that had and had not consumed released salmon fry. CDF1 and CDF2 refers to the groups that have been compared. The IDs of each CDF can be interpreted like this:15 = 2015; 16 = 2016; 17 = 2017. Ras = Rasdalen; Bre = Brekkhus. 4h = 4 hours after release; 48h = 48 hours after release; yes = has consumed ≥1 salmon fry; no = has not consumed any salmon fry.*

CDF 1	n CDF 1	CDF 2	n CDF 2	D	P-value
Sampling times pooled					
Predator.15.Ras.yes	6	Predator.15.Ras.no	2	0.667	0.264
Predator.16.Ras.yes	40	Predator.16.Ras.no	6	0.608	0.021
Predator.17.Ras.yes	28	Predator.17.Ras.no	25	0.634	<0.001
Predator.17.Bre.yes	4	Predator.17.Bre.no	14	0.107	0.931
Sampling times separate					
Predator.15.Ras.48h.yes	6	Predator.15.Ras.48h.no	2	0.667	0.264
Predator.16.Ras.4h.yes	8	Predator.16.Ras.4h.no	5	0.625	0.090
Predator.16.Ras.48h.yes	32	Predator.16.Ras.48h.no	1	0.969	0.162
Predator.17.Ras.4h.yes	15	Predator.17.Ras.4h.no	18	0.756	<0.001
Predator.17.Ras.48h.yes	13	Predator.17.Ras.48h.no	7	0.615	0.032
Predator.17.Bre.4h.yes	1	Predator.17.Bre.4h.no	9	0.778	0.337
Predator.17.Bre.48h.yes	3	Predator.17.Bre.48h.no	5	<<0.001	1

APPENDIX IV. Overview of all Kolmogorov-Smirnov tests and their respective D- and P-values for standard length salmon fry.. CDF1 and CDF2 refers to the two groups that have been compared. The IDs of each CDF can be interpreted like this: Tank = fry from production tank; Consumed = fry captured and eaten by predators; Recapture = fry recaptured from river two months after release. 15 = 2015; 16 = 2016; 17 = 2017. Ras = Rasdalen; Bre = Brekkhus. 4h = 4 hours after release; 48h = 48 hours after release. P = plain fry; E = enriched fry.

CDF 1	n CDF 1	CDF 2	n CDF 2	D	P-value
Production tank					
Tank.15.E	93	Tank.15.P	95	0.030	0.9201
Tank.16.E	127	Tank.16.P	123	0.2	**0.00715**
Tank.17.E	107	Tank.17.P	128	0.121	0.1804
Predator stomachs					
Consumed.15.Ras.48h.E	37	Consumed.15.Ras.48.P	34	0.05	0.9097
Consumed.16.Ras.4h.E	12	Consumed.16.Ras.4h.P	19	0.281	0.3138
Consumed.16.Ras.48h.E	79	Consumed.16.Ras.48h.P	114	0.1151	0.286
Consumed.17.Ras.4h.E	26	Consumed.17.Ras.4h.P	34	0.167	0.4378
Consumed.17.Ras.48h.E	23	Consumed.17.Ras.48h.P	17	0.384	**0.05629**
Predator stomachs (sampling times pooled)					
Consumed.16.Ras.E	91	Consumed.16.Ras.P	133	0.134	0.1429
Consumed.17.Ras.E	49	Consumed.17.Ras.P	51	0.208	0.1158
Production tank compared with predator stomachs					
Tank.15.P	95	Consumed.15.Ras.48h.P	34	0.126	0.4533
Tank.15.E	93	Consumed.15.Ras.48h.E	37	0.174	0.2021
Tank.16.P	123	Consumed.16.Ras.4h.P	19	0.411	0.004
Tank.16.P	123	Consumed.16.Ras.48h.P	114	0.394	<< 0.001
Tank.16.P	123	Consumed.16.Ras.P	133	0.396	<< 0.001
Tank.16.E	127	Consumed.16.Ras.4h.E	12	0.293	0.1516
Tank.16.E	127	Consumed.16.Ras.48h.E	79	0.230	0.005645
Tank.16.E	127	Consumed.16.Ras.E	91	0.235	0.002826
Tank.17.P	128	Consumed.17.Ras.4h.P	34	0.260	0.02638
Tank.17.P	128	Consumed.17.Ras.48h.P	17	0.201	0.2964
Tank.17.P	128	Consumed.17.Ras.P	51	0.241	0.01472
Tank.17.E	107	Consumed.17.Ras.4h.E	26	0.237	0.09494
Tank.17.E	107	Consumed.17.Ras.48h.E	23	0.337	0.01362
Tank.17.E	107	Consumed.17.Ras.E	49	0.243	0.01901
Production tank compared with predator stomachs (sampling times pooled)					
Tank.17	235	Consumed.17	100	0.2313	0.0005507
Tank.16	250	Consumed.16	225	0.318	<<0.001
Tank.15	188	Consumed.15	74	0.165	0.5599
River recapture					
Recapture.15.Ras.E	61	Recapture.15.Ras.P	67	0.163	0.182
Recapture.16.Ras.E	49	Recapture.16.Ras.P	58	0.226	0.06593
Recapture.17.Bre.E	42	Recapture.17.Bre.P	48	0.071	0.7957
Recapture.17.Ras.E	43	Recapture.17.Ras.P	72	0.239	0.04576
River recapture (release sites pooled)					
Recapture.17.E	85	Recapture.17.P	120	0.113	0.2792

APPENDIX V. Overview of mean standard length of fry consumed by predators 4 and 48 hours after release in Rasdalen and Brekkhus 2015, 2016 and 2017 and the respective standard deviation (SD), standard error (SE), 95% confidence interval (CI) and number (n) of consumed fry.

Year	Release site	Hours after release	Treatment	n	Mean length (mm)	SD (mm)	SE (mm)	CI (mm)
2015	Rasdalen	48	Enriched	37	34	4	1	2
			Plain	34	34	4	1	1
2016	Rasdalen	4	Enriched	12	44	7	2	4
			Plain	19	47	5	1	2
		48	Enriched	79	46	6	1	1
			Plain	114	47	5	1	1
2017	Rasdalen	4	Enriched	26	51.1	11	2	4
			Plain	34	52.9	9	2	3
		48	Enriched	23	53.0	6	1	3
			Plain	17	55.1	7	2	4
	Brekkhus	4	Enriched	2	57.0	3	2	25
			Plain	0	NA	NA	NA	NaN
		48	Enriched	1	54.0	NA	NA	NaN
			Plain	1	50.0	NA	NA	NaN

APPENDIX VI. Overview of mean standard length of fry from production tanks in 2015, 2016 and 2017 and the respective standard deviation (SD), standard error (SE), 95% confidence interval (CI) and number (n) of fry.

Year	Treatment	n	Mean length (mm)	SD (mm)	SE (mm)	CI (mm)	Mean weight (g)	SD (g)	SE (g)	CI (g)
2015	Enriched	93	34	3	<0.5	1	0.73	0.15	0.02	0.03
	Plain	95	34	3	<0.5	1	0.69	0.16	0.02	0.03
2016	Enriched	127	49	8	1	1	2.11	0.94	0.08	0.16
	Plain	123	51	6	1	1	2.21	0.65	0.06	0.12
2017	Enriched	107	55	9	1	2	3.04	1.22	0.12	0.23
	Plain	128	57	7	1	1	3.22	1.00	0.09	0.17

APPENDIX VII. Overview of mean standard length of fry from recaptured samples in 2015, 2016 and 2017 and the respective standard deviation (SD), standard error (SE), 95% confidence interval (CI) and number (n) of fry.

Year	Release site	Treatment	n	Mean length (mm)	SD (mm)	SE (mm)	CI (mm)	Mean weight (g)	SD (g)	SE (g)	CI (g)
2015	Rasdalen	Enriched	61	39	3	<0.5	1	0.96	0.23	0.03	0.06
		Plain	67	39	3	<0.5	1	0.98	0.22	0.03	0.05
2016	Rasdalen	Enriched	49	52	7	1	2	2.08	0.70	0.10	0.20
		Plain	58	54	5	1	1	2.21	0.55	0.07	0.15
2017	Rasdalen	Enriched	43	54	6	1	2	2.77	0.73	0.11	0.22
		Plain	72	63	5	1	1	3.17	0.68	0.08	0.16
	Brekkhus	Enriched	42	62	6	1	2	3.40	0.74	0.11	0.23
		Plain	48	62	5	1	1	3.32	0.73	0.10	0.21