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SUMMARY

Many Atlantic salmon populations have been lost or experienced severe declines across their natural distribution due to anthropogenic factors, such as damming of rivers, habitat destruction, overfishing, and pollution. To compensate for these declines, large numbers of hatchery-reared salmon are annually released into nature in several nations. However, stocked salmon usually have lower survival in nature compared to their wild counterparts. Previous research suggests that erosion to the fins and other injuries directly or indirectly caused by the hatchery environment are partly responsible for this pattern. Damages to the opercula are of particularly concern for the post-release survival as they play important functional roles in protection of the gills and maintaining an effective respiration. Therefore, it is desirable to develop and optimize rearing techniques that mitigate the incidence and degree of damages to the fins and opercula.

Here, we conduct two separate experiments to investigate whether feeding frequency and feed dispersal strategy affect growth as well as fin (dorsal and pectoral) and opercula condition of hatchery-reared Atlantic salmon during the first half year of their life. The reasoning behind these experiments is that hatchery feeding strategies can affect the level of aggressive confrontations among individuals, and since bites and aggressive attacks have been recognized as a primary cause of fin erosion, it becomes imperative to implement an appropriate feeding management. The cause of operculum erosion has not yet been established, but aggressive interactions among individuals represent a likely factor.

In the feed dispersal experiment, salmon either received feed from a timer controlled automatic feeder placed in the corner of the rearing tank or a modified feeder deployed in the center of the tank allowing feed pellets to be spread over the entire surface. Feed dispersal strategy did not affect the degree of erosion to the opercula or growth rate of the fish. However, fish receiving pellets spread over the surface of the rearing tank had slightly more eroded dorsal and right pectoral fins compared to individuals fed by the feeder deployed in the tank corner, suggesting a higher level of aggressive behaviour in the former feeding regime. In the feeding frequency experiment, fish were fed 12 or 48 times per day with feed pellets. We found no effects of feeding frequency on the degree of erosion to the fins or opercula. Growth and the size distribution of the salmon were also statistically similar between the two feeding regimes.

In conclusion, feed dispersal strategy only had minor influence on fin condition and it is questionable whether the observed differences in dorsal and pectoral fin erosion between the two feeding regimes will translate into differences in post-release survival. Although the feeding frequency and feed dispersal strategy had no significant effect on opercula condition in the present experiments, it is possible that other feeding methods, such as altered feed type and daily feed ratio, can help to reduce the incidence and degree of erosion to the opercula. We encourage researchers to continue to develop rearing methods that mitigate physical injuries to the fish and improve their survival following release into nature.

1. INTRODUCTION

Supportive breeding is a common management practice to maintain and enhance natural populations of salmonids. This process implies that hatchery-reared offspring of wild-caught fish are released into nature at various life-stages, including fry, parr, and smolts. However, the efficiency of many stocking programs has been questioned because fish raised in captivity often adapt poorly to natural conditions, showing impaired performance and diminishing return rates when compared to their wild counterparts (Brannon et al. 2004, Fraser 2008, Jonsson and Jonsson 2009, Johnsson et al. 2014). It is therefore important that fish are raised in a way that increases their post-release survival. Unfortunately, however, despite recent technological improvements in the area of fish farming, hatchery fish often develop morphological anomalies (e.g., in skull, skeleton, jaw, and fins) that may reduce the likelihood of survival in natural environments (Latremouille 2003; Petersson et al. 2013). For instance, a resent meta-analysis based on more than 40 years of tagging and recapture data showed that fin erosion and other injuries reduced the probability of survival of hatchery-reared Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) after release into nature (Petersson et al. 2013).

Aggressive interactions between individuals, such as bites and attacks, have repeatedly been recognized as a primary cause of fin damage in hatchery-reared salmonids (Abbott and Dill 1985; Turnbull et al. 1998; Latremouille 2003). Several previous studies have shown a direct relationship of aggression and territoriality to feeding (Symons 1968), and development of an appropriate feeding management is essential to mitigate the incidence and severity of fin damage (Latremouille 2003). While some researchers have found that the level of aggressive interactions increase after feeding (Newman 1956; kalleberg 1958), others have shown an overall decrease in agonistic behaviour following feeding (Symons 1968). Regardless of the outcome, feeding frequency and feed ratio have been acknowledged as important factors for the welfare of hatchery-reared salmonids (e.g., Moutou et al. 1998; Latremouille 2003; Rasmussen et al. 2007; Cvetkovikj et al. 2015). Likewise, feed dispersal strategy has the potential to shape social hierarchies and alter aggression levels in hatchery-reared salmonids (Reinersten et al. 1993; Pennell and Barton 1996; Jones et al. 2012).

Besides damaged fins, opercular deformities have regularly been noticed in hatchery-reared Atlantic salmon (Kazlauskienė et al. 2006; Larsen et al. 2016; see Fig.1). The prevalence of operculum erosion often reaches 60% and sometimes exceeds 90% (unpublished data, Martin H. Larsen). The opercula are essential for respiration by maintaining a constant water flow over the gills (Fernandes et al. 2007). They also protect the gills from pathogens and mechanical damage, and are involved in ion regulation (McCormick 1994). Thus, there are many potential reasons to minimize the frequency of operculum erosion in hatchery environments.

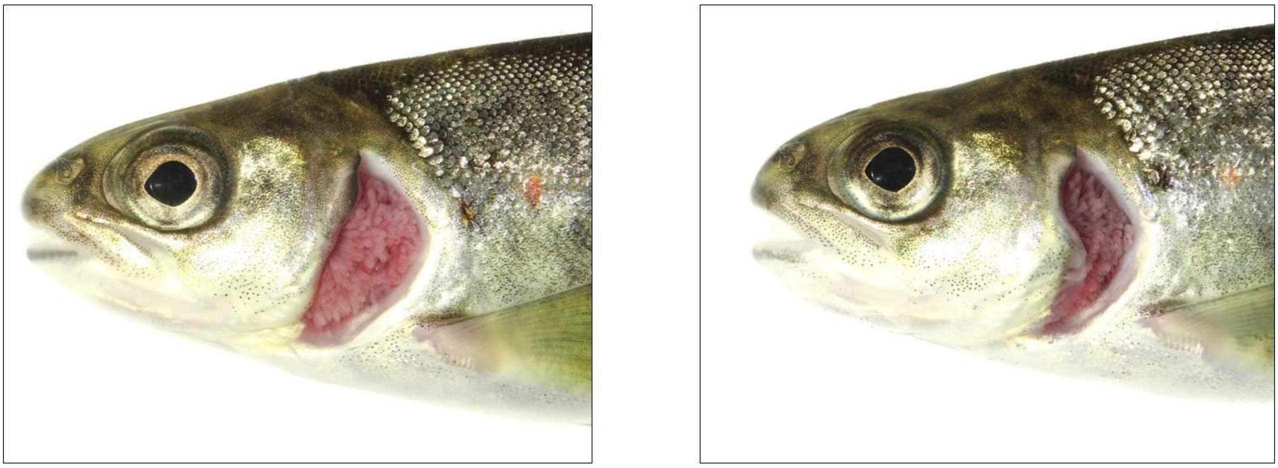

Figure 1. Hatchery-reared Atlantic salmon smolts with erosion to the opercula.

The definitive cause of operculum erosion in salmonids remains largely unknown, but agonistic interactions between the fish represent a likely factor. This hypothesis is supported by recent studies showing that the first visible signs of damage to the opercula appeared at the beginning of active feeding (Kazlauskienė et al. 2006, unpublished data). Assuming that erosion to the opercula is caused by bites and aggressive attacks from conspecifics, it becomes important to develop feeding practices that mitigate aggressive interactions between individuals to improve the condition of the opercula.

The aim of this study was to investigate whether feeding frequency (i.e., number of feeding sessions per day) and dispersal of feed in the rearing tanks affect fin and operculum condition as well as growth of Atlantic salmon during the first half-year of their life. This report focuses on the potential effects of feeding strategy on the condition of the opercula as no research has been done in this topic previously. We hypothesize that delivery of feed pellets over a wide surface area in the rearing tanks, rather than being released in the corner, should reduce fin and opercula erosion by lowering territorial defense and aggressiveness of the salmon. We also expect there will be growth differences among fish receiving these different food distributions. Specifically, we predict that point feeding from the tank corner creates favorable conditions for dominant individuals, resulting in large size variation among fish in the rearing unit compared to conspecifics receiving feed distributed across the tank surface. Because previous research has generated conflicting results regarding the effects of feed delivery rate on aggression levels in salmonids, it is difficult to envisage the potential effects of feeding frequency on the degree of erosion to the fins and opercula a priori. Nevertheless, we predict that lowered feeding frequency will reduce the number of aggressive interactions between fish as long as they are feed to satiation. We conducted two separate experiments to test these hypotheses. The first experiment was performed at the Wildlachszentrum located in Germany, and tested the potential influence of feed dispersal strategy in the rearing tanks on fin and opercula condition (herein referred to as “feed dispersal strategy”). The second experiment was performed at the Danish Centre for Wild Salmon, Denmark, and tested the potential effects of the number of feeding sessions per day on fin and opercula condition (herein referred to as “feeding frequency”).

2. MATERIALS AND METHOD

2.1 Feed dispersal strategy

The experimental fish were first-generation (F1) offspring of Atlantic salmon originating from the River Sieg, Germany. The parental fish were caught in the autumn of 2015 in a fish-trap located at the monitoring station for diadromous fish species at weir and fish passage Buisdorf, Sieg. The fish were transported to the Wildlachszentrum in Siegburg, Germany, and kept in indoor rearing tanks until eggs were stripped and fertilized. The rearing tanks were supplied with water from a recirculation system (RAS) with a daily water system volume exchange rate of 5%. The fertilized eggs were incubated in egg trays and hatched in the beginning March 2016. After hatching, the alevins were maintained in the hatching trays until the yolk sac was absorbed. Next, fish were transferred to indoor flow-through rearing tanks (2×2 m) for exogenous feeding on commercial feed pellets (Aller performa, Aller Aqua, Denmark). Fish were randomly assigned into two feeding regimes. In the first feeding regime a timer-controlled automatic feeder (LINN Profi 5 kg, Germany) was installed on the tank wall close to the corner and water inlet (hereafter referred to as "standard"). Thus, feed pellets were released in the corner of the tank and merely distributed by the circular water flow. In the other feeding regime, a slightly modified automatic feeder of the same model was deployed in the center of the tank. This feeder had a plate with scrubber attached underneath the feeding chamber that rotated when feed was released from the dispenser, allowing pellets to be spread across the entire surface area of the rearing tank (hereafter referred to as "spread"). Each feeding regime was replicated in 2 rearing tanks. The number of fish in each rearing tank was approximately 22,000 individuals. The feeding frequency was similar for the two feeding regimes and fish were fed 2% of body mass per day in all rearing tanks. The pellet size was adjusted according to the manufacturer's recommendations as the fish increased in size.

On 4th and 5th of April 2016, at start feeding, 50 fish were randomly netted from each of the 4 rearing tanks to investigate whether fish size and fin as well as operculum condition was similar between the two feeding regimes. The fish were anesthetized (benzocaine) until the opercular rate became slow and irregular. Once unresponsive, fish were individually placed in a Petri dish filled with water and photographed on both sides using a digital single lens reflex (DSLR) camera (Canon EOS 600D; Canon Inc., Tokyo) equipped with a macro lens (Canon EF 100 mm f/2.8 USM Macro 1:1). The camera was vertically mounted on a copy-stand above the Petri dish which was fitted with a scale bar for reference. Total length of the fish was determined to the nearest ± 0.1 mm from the photographs using ImageJ 1.46r. Body mass was measured to the nearest ± 0.01 g. Erosion to the fins (dorsal and pectoral) and opercula were visually quantified using an ordinal scale of 0, 1, 2, 3, and 4 (after Hoyle et al. 2007). Level 0 corresponded to intact opercula or fins with no erosion. A score of 1 was given for fins with splits (separation of fin rays greater than 3 mm) and opercula with erosion to the outer edge, that is, the gill cavity was fully covered by the operculum. Level 2, 3, and 4 corresponded to mild erosion (1-24% eroded), moderate erosion (25-49% eroded), and severe erosion (≥50% eroded), respectively. In these instances the gill cavity was not completely covered by the operculum (see Fig. 2). The degree of erosion was scored by the same person to avoid bias.

At experimental termination, on 22 and 23 June 2016, 50 were salmon were sampled from each of the 4 rearing tanks by netting to examine fin and operculum condition. The fish were collected from the corners and center of each tank in roughly equal numbers ensuring a representative sample of fish. The final length and mass of the salmon were noted. Fin and opercula condition were inspected as above. After these measurement fish were killed with an overdose of anaesthetic.

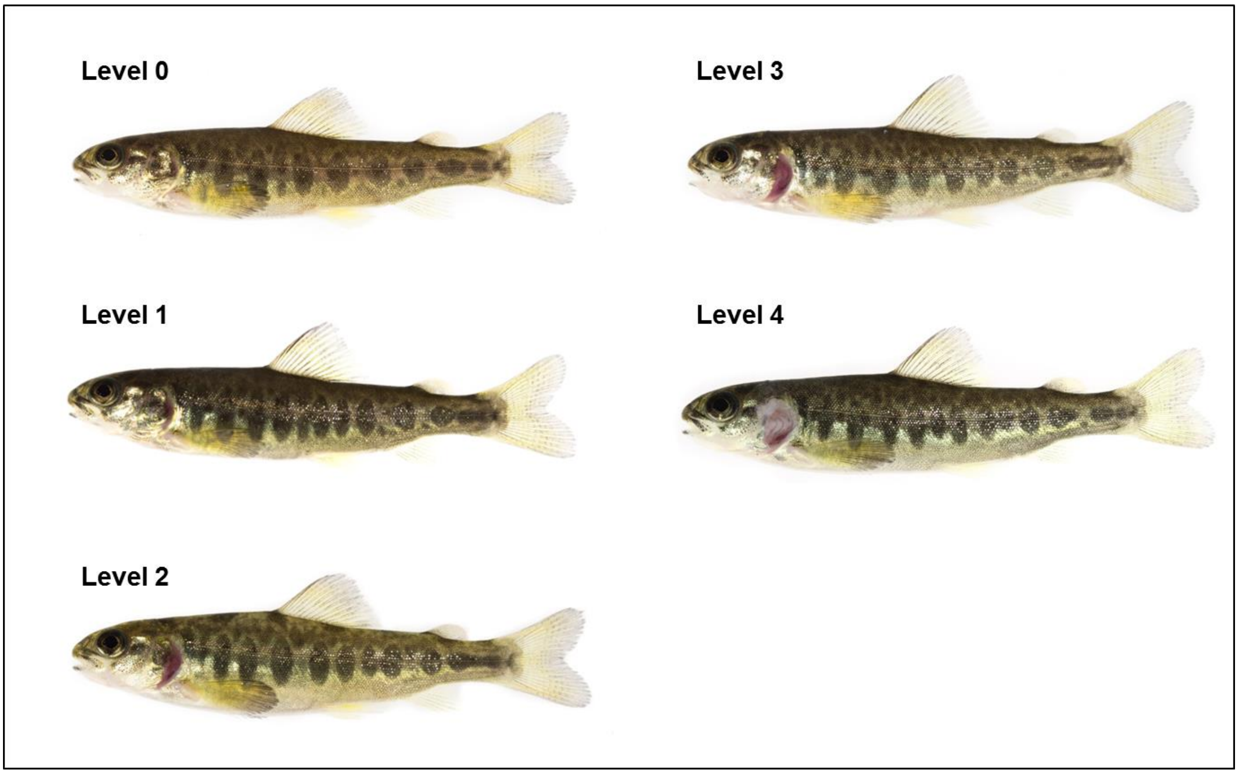

Figure 2. Representative erosion levels of the operculum of Atlantic salmon *Salmo salar*. Level 0: no erosion (0% eroded); Level 1: erosion to the outer edge of the operculum; Level 2: mild erosion (1-24% eroded); Level 3: moderate erosion (25-49% eroded); Level 4: severe erosion (≥50% eroded).

2.2 Feeding frequency

The experimental fish in this study was first-generation (F1) offspring of wild Atlantic salmon. The parental fish were caught by electrofishing in River Storå during autumn 2015 and transported to the Danish Centre for Wild Salmon in Randers, Denmark. In December 2015, eggs from 31 females were stripped and fertilized with the milt from 33 males, approaching sperm:egg ratios of 1:1. The fertilized eggs were placed in hatching trays. Fry were transferred to 4 flow-through rearing tanks (2×2 m) for exogenous feeding in the beginning of May 2016. A subsample (n = 120) of fish were measured for length and body mass immediately before fish were moved to the rearing tanks. The fins (dorsal and pectoral) and opercula of these fish were also visually inspected for damages.

An automated feeder (LINN Profi 5 kg, Germany) was placed in the corner of each tank, near the inflow of water. In two of the tanks, fish received feed pellets (Aller performa, Aller Aqua, Denmark) 12 times per day (hereafter referred to as “LOW”), while fish in the remaining two tanks were fed 48 times per day (hereafter referred to as “HIGH”). A subsample of salmon (n = 300) was randomly collected form each tank every 14 day and subsequently weighed, ensuring that fish received the same amount of feed in relation to body mass (2 to 4 % of body mass per day) across the two feeding regimes. Feeding took place during the hours of daylight. The number of fish in each rearing tank was approximatively 22,000 individuals.

Between 13-16 August 2016, 50 fish from each rearing tank were randomly netted. These fish were measured for length and mass and erosion to the fins (pectoral and dorsal) and opercula were evaluated using the protocol described above. This was done to assess whether fin and opercula condition as well as growth differed between the two feeding regimes at the end of the experiment.

2.3 Statistical analyses

2.3.1 Feed dispersal strategy

Generalized linear models (GLMs) with Gaussian distribution and identity link function were used to test whether mass and length differed between the two feeding regimes at start feeding and experimental termination. Additionally, a two-sample Kolmogorov-Smirnov (K-S) test was applied to assess if the length-frequency distribution of the salmon was affected by feeding regime. Lastly, we used Chi-squared tests to determine if the degree of erosion to the fins (dorsal and pectoral) and opercula differed between the two feeding regimes at experimental termination.

2.3.2 Feeding frequency

We used a GLM with Gaussian distribution and identity link function to assess if length and mass differed between the LOW and HIGH feeding regime at the end of the experiment. The potential effect of feeding frequency on the length-frequency distribution of the salmon was investigated using a K-S test. At the end of the experiment, potential differences in the degree of erosion to the fins (dorsal and pectoral) and opercula were assessed using Chi-square tests.

2.3.3 General statistical notes

The statistical analyses were performed in R 3.0.1 (R Development Core Team 2013). Prior to the analyses, data explorations were applied following a protocol described by Zuur et al. (2010). Assumptions of homogeneity of variance and normality were assessed by graphical inspection of the residuals. Variation in association with recorded mean values is given as standard deviation throughout. Statistical significance for all analyses was set at $p < 0.05$.

3. RESULTS

3.1 Feed dispersal strategy

The average length and body mass of the Atlantic salmon did not differ between the two feeding regimes at start feeding (GLM, length: $F = 0.081$, $df = 1$, $p = 0.776$; body mass: $F = 0.132$, $df = 1$, $p = 0.717$) or experimental termination (GLM, length: $F = 0.119$, $df = 1$, $p = 0.730$; body mass: $F = 1.491$, $df = 1$, $p = 0.224$; Fig. 3). In addition, the length-frequency distribution of the salmon at the end of the experiment was not influenced by feeding regime (K-S test, $D = 0.15$, $p = 0.211$; Fig. 4).

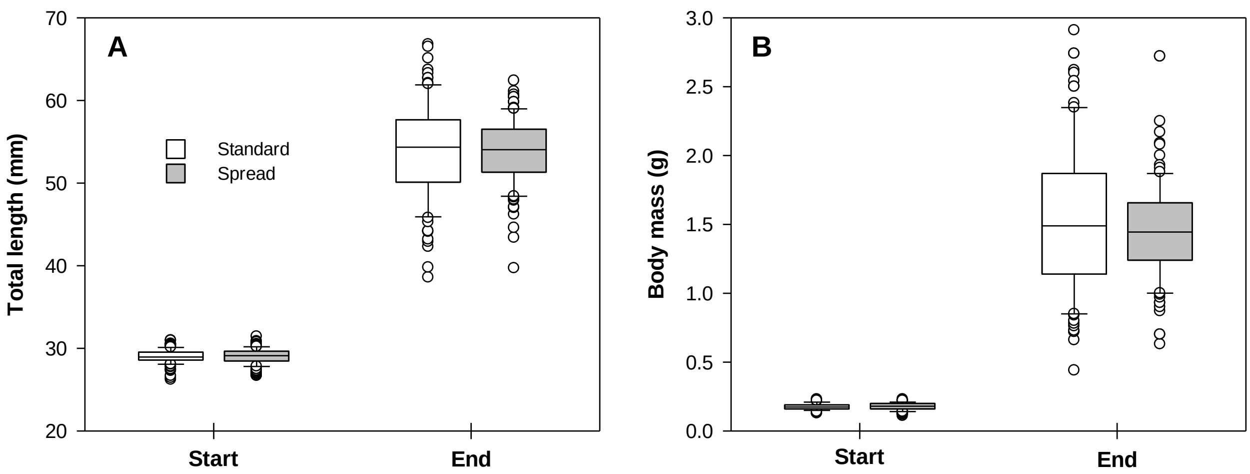

Figure 3. (A) Total length (mm) and (B) body mass (g) of Atlantic salmon at start feeding (April 2016) and end of the experiment (June 2016). The fish received feed pellets from a standard automatic feeder placed in the corner of the tank (standard) or a slightly modified feeder placed in the center of the tank allowing pellets to spread across the entire surface of the tank (spread). See text for more details. Horizontal lines within each box represent median values, ends of boxes represent the 25^{th} and 75^{th} percentiles, and whiskers represent the 10^{th} and 90^{th} percentiles. Open circles indicate outliers outside the 10^{th} and 90^{th} percentiles.

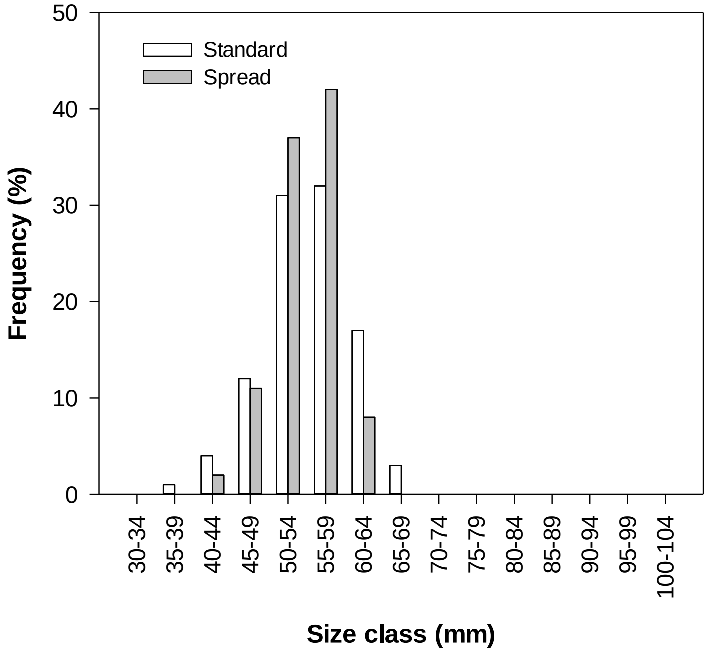

Figure 4. Length-frequency distribution at experimental termination of Atlantic salmon receiving pellets from a standard automatic feeder placed in the corner of the tank (standard) or a slightly modified feeder placed in the center of the tank that allowed pellets to spread across the entire surface of the tank (spread).

No erosion to the fins (dorsal and pectoral) and opercula was observed at the first inspection that occurred at start feeding. The degree of erosion to the fins and opercula at the end of the experiment are shown in Table 1 and Figure 5. The severity of erosion to the left and right operculum was statistically similar among fish reared at the two feeding regimes (Table 1). However, fish receiving feed from the modified feeder (i.e., the spread feeding regime) had a higher degree of erosion to the dorsal and right pectoral fin than fish fed by the automatic feeder placed in the corner of the tank (Table 1). There was no significant difference in the degree of erosion to the left pectoral fin between feeding regimes. In addition, the degree erosion to the right and left operculum was statistical similar across feeding regimes (Chi square test: $\chi^2 = 9.511$, df = 4, p = 0.05).

Table 1. Percentage of Atlantic salmon (*Salmo salar*) with erosion to the opercula and fins (pectoral and dorsal) receiving pellets from a standard automatic feeder placed in the corner of the tank (standard) or a slightly modified feeder placed in the center of the tank allowing pellets to spread across the entire surface of the tank (spread). Summary statistics of Chi-square tests are also shown. Stars indicate significant differences ($p < 0.05$) between the two feeding regimes.

	Degree of erosion					Chi-squared test		
	0	1	2	3	4	χ^2	df	p
Left operculum								
Standard	46	8	33	10	3	6.207	4	0.185
Spread	47	10	20	18	5			
Right operculum								
Standard	54	4	16	17	9	2.648	4	0.618
Spread	54	9	16	15	6			
Left pectoral								
Standard	71	6	18	5	0	8.791	4	0.067
Spread	82	0	14	3	1			
Right pectoral								
Standard	87	3	4	5	1	4.618	4	0.047*
Spread	83	0	10	2	5			
Dorsal								
Standard	57	2	34	6	1	11.072	4	0.026*
Spread	54	0	28	7	11			

The intensity of erosion was quantified using an ordinal scale of 0 (no erosion to fin or operculum), 1 (fin split or erosion to the edge of the operculum), 2 (1-24% of fin or operculum eroded), 3 (25-49% of fin or operculum eroded), and 4 (≥50% of fin or operculum eroded). See text for further details.

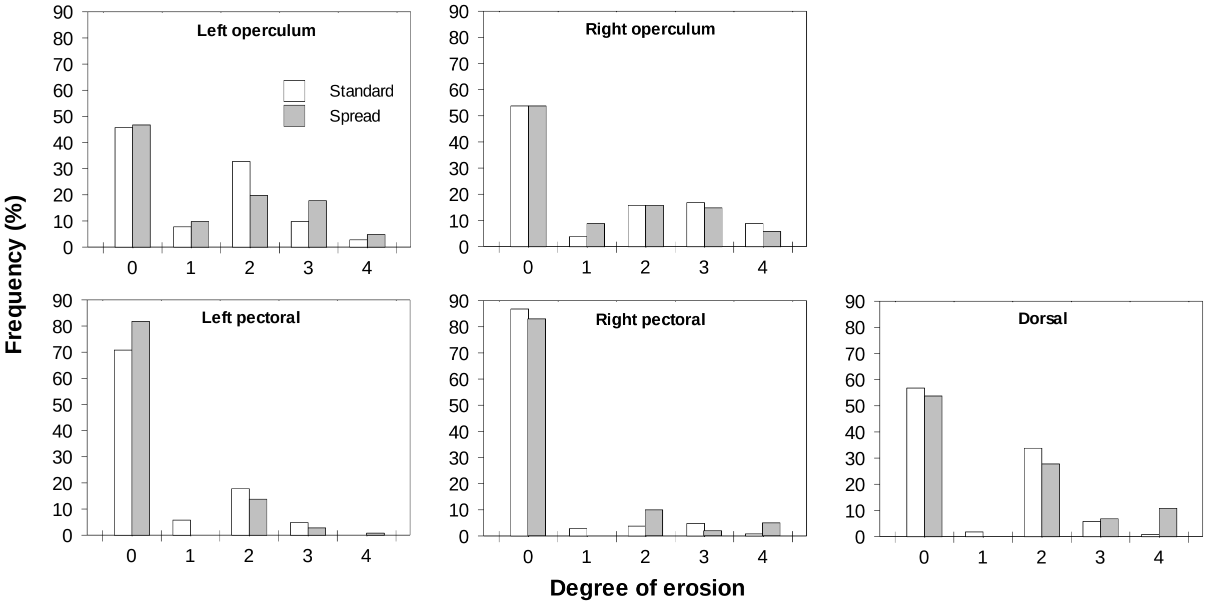

Figure 5. Frequency (%) of opercula and fin (pectoral and dorsal) erosion of Atlantic salmon receiving pellets from a standard automatic feeder placed in the corner of the tank (standard) or a slightly modified feeder placed in the center of the tank allowing pellets to spread across the entire surface of the tank (spread). The intensity of erosion was quantified using an ordinal scale of 0 (no erosion to fin or operculum), 1 (fin split or erosion to the edge of the operculum), 2 (1-24% of fin or operculum eroded), 3 (25-49% of fin or operculum eroded), and 4 (≥50% of fin or operculum eroded).

3.2 Feeding frequency

The average length and mass of the Atlantic salmon at start feeding were 30.0 ± 1.16 mm and 0.17 ± 0.02 g, respectively. At experimental termination, there were no significant difference in average length and body mass between the feeding regimes (GLM, length: $F = 2.535$, $df = 1$, $p = 0.113$; body mass: $F = 2.590$, $df = 1$, $p = 0.109$; Fig. 6). Furthermore, the feeding frequency did not influence the length distribution of the samlon (K-S test, $D = 0.19$, $p = 0.054$; Fig. 7).

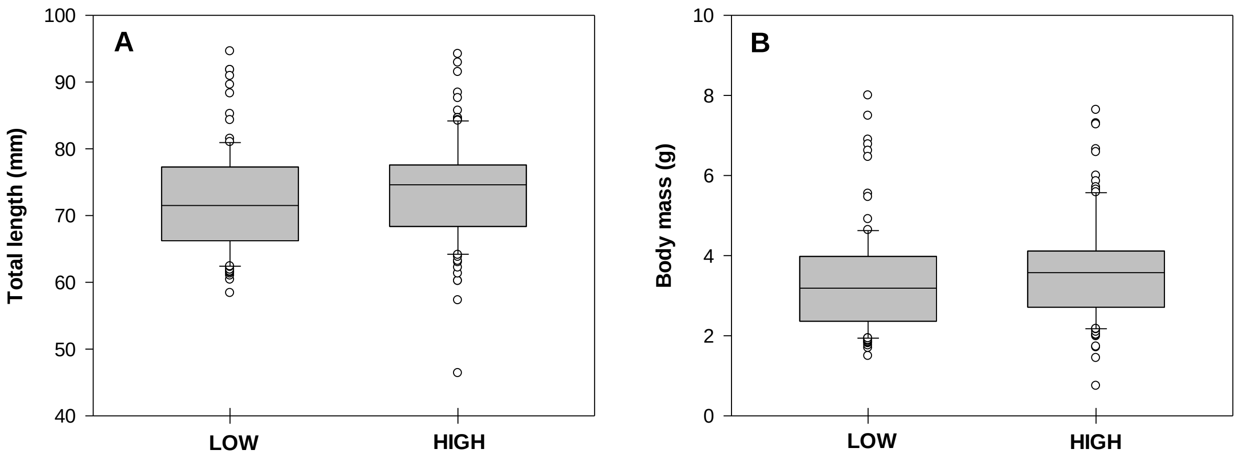

Figure 6. (A) Total length (mm) and (B) body mass (g) at experimental termination (August 2016) of the Atlantic salmon fed 12 (LOW) or 48 (HIGH) times per day during rearing. Horizontal lines within each box represent median values, ends of boxes represent the 25th and 75th percentiles, and whiskers represent the 10th and 90th percentiles. Open circles indicate outliers outside the 10th and 90th percentiles.

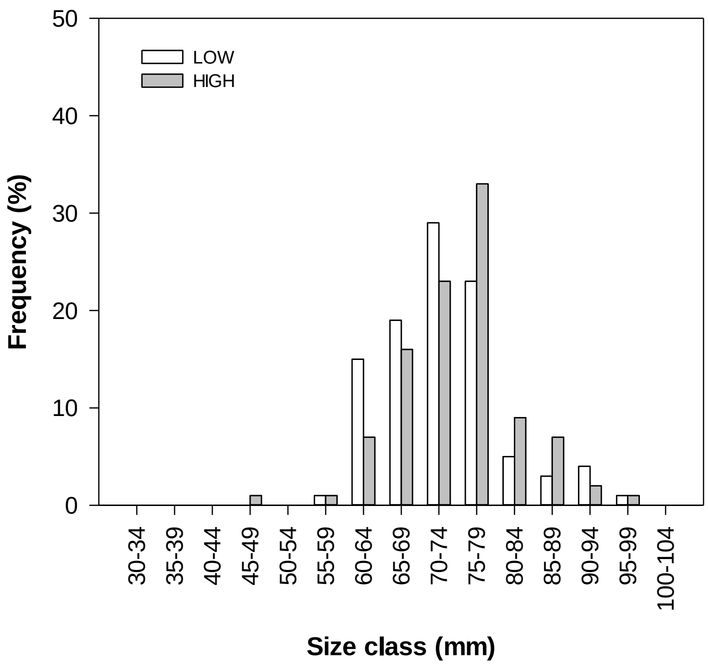

Figure 7. Length-frequency distribution at experimental termination of Atlantic salmon fed12 (LOW) or 48 (HIGH) times per day from automatic feeder.

We observed no erosion to the opercula or fins (dorsal and pectoral) at start feeding in either of two feeding regimes. Table 2 and Figure 8 show the degree of erosion to the fins and opercula at the end of the experiment for fish fed 12 and 48 times per day. Chi-square tests revealed no significant difference in the degree of erosion to the fins or opercula between the LOW and HIGH feeding regime. Regardless of feeding regime, the erosion to the right operculum was more severe than that of the left operculum (Chi square test: $\chi^2 = 46.108$, df = 4, $p < 0.0001$). Overall, 88.5% of the fish had erosion to the right operculum, while 65.5% individuals had erosion to the left operculum. Lastly, it is notably that the damages to the dorsal and pectoral fins were mainly fin splits (i.e., level 1; see Table 2 and Fig. 8).

Table 2. Percentage of Atlantic salmon (*Salmo salar*) with erosion to the opercula and fins receiving feed 12 (LOW) or 48 (HIGH) times per day. Summary statistics of Chi-square tests are also shown.

	Degree of erosion					**Chi-square test**		
	0	1	2	3	4	χ^2	df	p
Left operculum								
LOW	35	17	19	20	9	1.705	4	0.790
HIGH	34	18	25	17	6			
Right operculum								
LOW	14	9	21	26	30	1.876	4	0.759
HIGH	13	13	22	29	33			
Left pectoral								
LOW	42	56	2	0	0	3.306	2	0.192
HIGH	35	65	0	0	0			
Right pectoral								
LOW	39	61	0	0	0	0.021	1	0.884
HIGH	37	63	0	0	0			
Dorsal								
LOW	40	49	4	0	7	6.808	4	0.146
HIGH	44	51	1	2	2			

The intensity of erosion was quantified using an ordinal scale of 0 (no erosion to fin or operculum), 1 (fin split or erosion to the edge of the operculum), 2 (1-24% of fin or operculum eroded), 3 (25-49% of fin or operculum eroded), and 4 (≥50% of fin or operculum eroded). See text for further details.

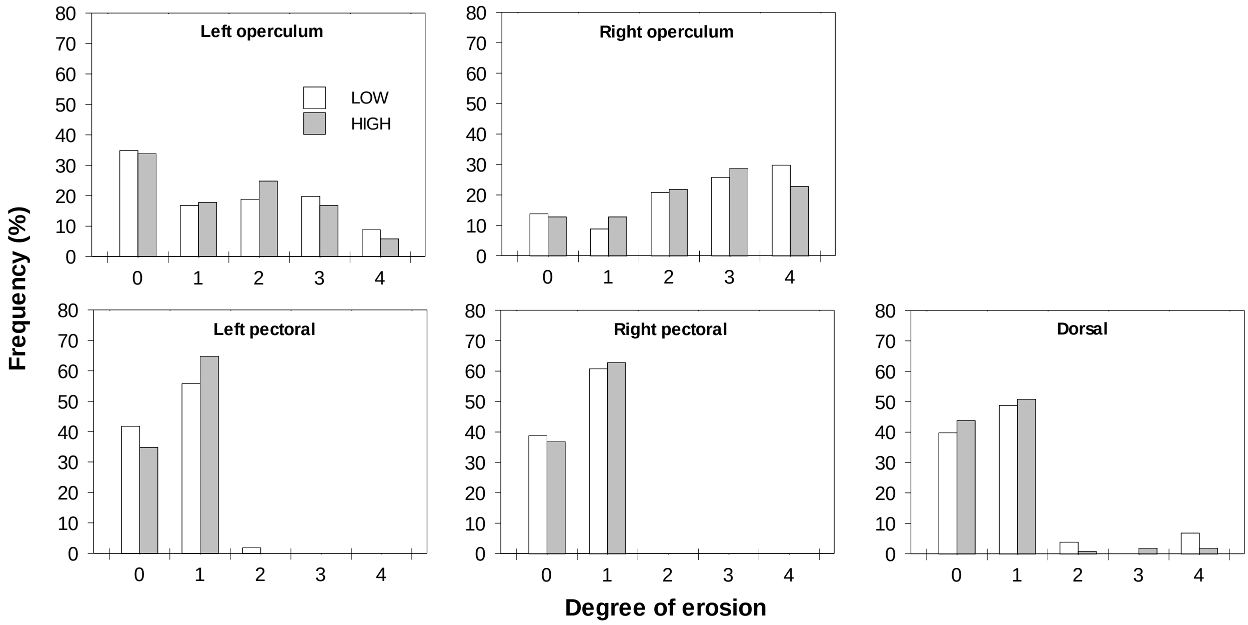

Figure 8. Frequency (%) of opercula and fin erosion among the Atlantic salmon fed12 (LOW) or 48 (HIGH) times per day. The intensity of erosion was quantified using an ordinal scale of 0 (no erosion to fin or operculum), 1 (fin split or erosion to the edge of the operculum), 2 (1-24% of fin or operculum eroded), 3 (25-49% of fin or operculum eroded), and 4 (≥50% of fin or operculum eroded).

4. DISCUSSION

4.1 Feed dispersal strategy

Feed dispersal strategy did not affect erosion to the opercula and growth of the Atlantic salmon. However, fish receiving feed pellets spread over the surface of the rearing tank generally had a higher degree of erosion to the dorsal and right pectoral fin compared to conspecifics fed by the feeder placed in the tank corner. These results are in contrast to our initial prediction that delivery of feed across the entire surface of the rearing unit should reduce erosion to the fins. This hypothesis is based on the assumption that unpredictable dispersal of feed prevents formation of feeding territories and ensures that all fish, regardless of their social status, can obtain adequate amount of food. Consequently, this feeding protocol may decrease competition over feed in the rearing units and reduce aggressive interactions among the fish, potentially lowering fin erosion (Ryer and Olla 1995). On the other hand, delivery of feed from a point source allows this source to be defended and hierarchies to be formed (Eaton 2010). As such, the point feed method may create advantageous conditions for dominant individuals to monopolize feed, typically resulting in large size variation among fish in the rearing unit (Ryer and Olla 1995). It should be emphasized that destabilization or breakdown of dominance hierarchies can also increase aggressive interactions until social ranks have been reestablished (Eaton 2010). In effect, stable dominance hierarchies usually avoid excessive competition over feed and aggressive encounters may be reduced.

Visual observations during the experiment revealed that the distribution of the salmon in the rearing tanks varied considerably between the two feeding regimes. In the standard feeding regime, fish were particularly crowed in the areas close to the automated feeder. Fish mainly positioned themselves near the tank walls in the highest water velocities and a low uniformity of fish distribution was obtained in the whole tank. It was also observed that the distribution of fish in the tank was size-dependent such that the largest fish occupied the areas close to the feeder. The smallest fish were concentrated in the center of the tank. Salmon in the spread feeding regime, on the other hand, were more uniformly distributed in the rearing tank and no size-dependent distribution was noted, suggesting a better use of the entire rearing volume. It is possible that these differences in tank occupation among fish in the two feeding regimes reflect distinct shapes of social dominance hierarchies. In particular, since dorsal fin damage is primarily caused by bites and nipping, the present results suggest a higher level of aggression in the spread feeding regimen. However, in spite of these indications of differences in dominance hierarchies and aggression levels, the size distribution of fish was not affected by feed dispersal strategy, as would be expected had the social order differed markedly between the feeding regimes (Ryer and Olla 1995). Hence, additional studies including social network analysis are required to confirm our assumptions. Lastly, albeit significant, it should be stressed that the differences in erosion levels of the dorsal and right pectoral fin between the feeding regimes were rather minor (Table 1 and Fig. 5). It remains questionable whether these differences in fin erosion will translate into differences in post-release survival of the salmon.

4.2 Feeding frequency

The results of this experiment showed no effects of the applied feeding frequencies (fish were fed 12 or 48 times per day) on the incidence and degree of erosion to the fins and opercula. It is worth noting that the damages to the fins were mostly fin splits and erosion was rarely noted, while erosion to the opercula was frequently observed in both feeding regimes. Assuming that opercula erosion is caused by aggressive interactions, these findings may suggest that the operculum is a preferred site of attack in Atlantic salmon. Yet, video recordings of agonistic behaviour amongst individuals are required to confirm this assumption.

Regardless of feeding frequency, the severity of erosion to the right operculum was greater than that of the left operculum. The direction of water flow in the rearing tanks was counterclockwise such that the right side of the fish's body was usually directed towards the center of the tank. Hence, it is possible that the tank walls offered some protection to the left operculum against aggressive attacks, at least for fish staying close to the tank walls. Although this assumption awaits further proof, this possibility could offer an explanation for the lower degree of erosion to the left operculum.

Feeding frequency has previously been acknowledged as an important factor for the welfare of many fish species during rearing (Brännäs and Johnsson 2008). Frequent feeding may satiate the fish and reduce competition over feed as well as aggressive behaviour (Wagner et al.1996). Conversely, an increase in feeding frequency may increase the number of aggressive interactions between individuals by stimulating foraging and territorial behaviour (Rasmussen et al. 2017). Based on the fin condition, we found no evidence that feeding frequency altered aggressive behaviour of the salmon in the present experiment. In addition, as noted in the feed dispersal experiment, the size distribution and growth of the Atlantic salmon was not influenced by the present feeding frequencies. Taken together, these results suggest that salmon are able to adapt to a wide range of feeding strategies. Our results also highlight that fin and opercula erosion is a widespread problem in hatchery environments.

5. CONCLUSIONS

In summary, the severity of erosion to the opercula and growth rate of the Atlantic salmon was not influenced by feeding frequency or feed dispersal strategy in the present experiments. Erosion to the dorsal and pectoral fins was also unaffected by the feeding frequency and the dispersal strategy of feed pellets only had minor effects on the condition of the dorsal and pectoral fins. The dorsal and right pectoral fins were generally more eroded among fish receiving feed spread over the entire surface of the rearing tanks compared to individuals fed by the point source feeder installed on the tank wall.

Although our results showed no effect of the tested hatchery feeding practices on the condition of the opercula, it cannot be ruled out that other feeding methods, including altered feed type and amount of feed delivered on a daily basis, might influence the degree of erosion to the opercula of hatchery-reared Atlantic salmon. It is also important to keep in mind that other variables, such as rearing density, addition of structure (e.g., plastic vegetation and pipes for shelter) in the rearing tanks, water velocities, light conditions, water quality might affect fin and opercula condition. We submit that additional studies are required to identify the cause of opercula erosion and highly recommend researchers to investigate whether and to what extend damages to the opercula influence the post-release performance of hatchery-reared Atlantic salmon.

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