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# Aquaculture

journal homepage: www.elsevier.com/locate/aquaculture

# Context-dependent impact of an ectoparasite on early marine growth in Atlantic salmon

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#### ARTICLE INFO

Keywords: Lepeophtheirus salmonis Marine survival Salmon Salmo salar Sea lice Scale analysis

# ABSTRACT

The impact of sea lice on post-smolt growth (PSG) was studied by comparing growth patterns in the scales of recaptured adult salmon originating from hatchery-reared smolts that were untreated or were previously treated for sea lice infestation during the years 2003–2014. Growth in the returning hatchery-reared fish was also compared to the growth of wild fish from the same smolt year class. PSG was greater in treated versus untreated fish in the early part of the time series, which was a period of low marine survival. However, the differentiation in PSG disappeared in the later portion of the time series, which coincided with a shift from low to higher marine survival. This transition was demarcated by the year 2009. During this later period, PSG correlated with the marine survival of salmon, whereas in the early period, this correlation was not evident. Wild fish had faster PSG than untreated hatchery fish throughout the study period, but had slower PSG than treated hatchery fish during the early part of the time series. The effects of sea lice alone cannot explain the observed shift in marine survival occurring in 2009. However, it seems evident that the effect of antiparasitic treatment was contingent on poor marine survival, showing that the impacts of parasites on the PSG of Atlantic salmon are context dependent.

#### 1. Introduction

Marine survival and growth dynamics are perhaps the least understood aspects of the life history of Atlantic salmon (Thorstad et al. 2011). The problem of quantifying recruitment dynamics of fish in the marine environment is not unique for salmon, but exists for a wide range of marine species (Anderson 1988; Cushing 1975; Hjort 1914). The particular challenges facing salmon biologists are the extensive marine migrations made by Atlantic salmon, whereby salmon effectively evades directed survey gear and only sporadically appear in incidental catches. Inference about the marine phase has been facilitated through the use of scale analysis, which has been an important source of information on the growth and survival dynamics of salmon (McCarthy et al. 2008; Peyronnet et al. 2007). In salmon, these patterns have been used to characterize growth during the early marine migration through the first winter at sea, which is marked by the formation of the winter annuli; this growth period is termed post-smolt growth (PSG). PSG is considered an important determinant for the marine year-class strength in salmon (Friedland et al. 2009; Peyronnet et al. 2007). This hypothesis has been tested by correlating PSG with marine survival indices in Atlantic salmon (Peyronnet et al. 2007) as well as in other salmonid species (Friedland et al. 2014a), showing that high early marine growth

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https://doi.org/10.1016/j.aquaculture.2019.04.038 Received 3 August 2018; Accepted 11 April 2019 Available online 13 April 2019 0044-8486/ © 2019 Elsevier B.V. All rights reserved. corresponds with strong year classes on a regional basis.

One of the most controversial topics related to the marine survival of salmon in recent years, has been the impact of ectoparasite sea lice (Lepeophtheirus salmonis Krøyer 1837 and Caligus spp.) on salmon populations and the role of fish farming in increasing infection rates in migratory routes used by young salmon smolts on their way to the sea. Sea louse is a natural parasite on salmonids (Caligus spp. also have other host species) and have posed a challenge for the production of salmonids in net-pen installations located in marine waters (Torrissen et al. 2013). In recent decades, concerns have emerged both scientifically, and in the public sector, that sea lice could be impacting populations of wild salmon (Krkosek et al. 2007), which are already under threat from various man-made factors (Forseth et al. 2017). In Norway, this has led to the establishment of a management system that regulates the allowable biomass production in fish farms, in different regions of Norway, based on the estimated impact of sea lice originating from fish farms on wild populations (Vollset et al. 2017).

The effect of sea lice on the physiology and survival of salmon, has been well documented in laboratory settings (Wagner et al. 2008). However, the population-level effects of sea lice on wild populations are not as well known and are still under active debate (Jackson et al. 2014; Krkošek et al. 2014). An important source of information on the effects







of sea lice on wild fish is the use of randomized control trials (RCTs) based on releases of hatchery-reared groups of salmon smolts, half of which are treated against sea lice using an antiparasitic agent. The fish are recaptured as adults, generally after 1 to 4 years at liberty, to evaluate how the experimental group was affected by the treatment. These studies have shown that sea lice have an effect on survival and on the age of maturity in salmon (Krkosek et al. 2013; Skilbrei et al. 2013; Vollset et al. 2016a), although the impact is highly variable and relatively small compared to the overall variation in these parameters in adult recaptures. One of the main conclusions from a meta-analysis of all such RCTs in Norway, was that  $\sim$ 70% of the heterogeneity in the effect of the treatment could be explained by the release location, time period and baseline survival as measured by the recapture rate of the adults in the control group (Vollset et al. 2016a). Hence, it was concluded that the effect of parasites was likely context dependent and higher when marine survival was poor.

The early marine growth of salmon provides a useful indicator of the year-class strength of populations in the Northwest Atlantic (Friedland et al. 2000; Friedland et al. 2009; Peyronnet et al. 2007); thus, we sought to investigate how sea lice might be influencing growth patterns. We collected PSG data from recaptured adult salmon from RCT experiments in the Vosso River, Norway, during the period 2003–2014. In addition, because the growth, physiology, and behaviour of wild fish vary from those of hatchery fish, we collected similar data from wild fish for comparative purposes. Finally, we evaluated whether PSG was linked to variation in the recruitment of salmon in this region, by comparing scale growth data to independently collected data for returning adult salmon.

# 2. Materials and methods

# 2.1. Ethics statement

All tagging and handling of animals in these experiments was conducted with the appropriate animal welfare approval. Legislation and regulations changed throughout the time period of the study. In the last several years of the experiments, approval from the animal welfare committee in Norway was required, and approval was obtained accordingly (FDU ID5192 & ID6217). Salmon smolts were raised and tagged in an approved salmon hatchery with a high standard of animal welfare. Only trained personnel handled adults during capture in trap net installations. In general, efforts were made to minimize animal handling and stress.

# 2.2. Description of release group studies and scale collection

Scale samples were collected during the period 2003-2014 from fish originating in the Vosso River in Norway. In this river, groups of hatchery-reared salmon tagged with coded wire tags (23 mm), have been released since 2000, and half of these fish were treated with an antiparasitic agent. At the outset of the experiment, the fish were released in the river; however, due to poor returns in the early years, the design was changed, and fish were towed in a container through the inner fjords and released at various locations (indicated by I = inner and O = outer release locations in Fig. 1). This design change increased the return rates dramatically and provided sufficient samples for analysis of the different release groups. We mention this change since towing creates differences in how wild and hatchery fish encounter sea lice. Towing the fish shields the salmon, to a certain degree, from parasitic infection during the first 50-70 km of seaward migration, as the towing is done in a tank. However, the infestation rate during this early migration is already low, because salinity in the surface layers in the inner fjord is almost always below 20 ppt during the smolt run (Vollset et al. 2016b). In addition, fish that have been towed reach the outer part of the fjord system earlier in the season than wild fish (Vollset et al. 2016b), when infestation pressure is known to be lower

(Kristoffersen et al. 2018). Consequently, we expect wild salmon to experience somewhat higher infestation pressure than hatchery fish, which should be considered when interpreting the results.

Return information was assembled from fishery and survey data at various locations in the fjord system. The return rates of hatchery salmon are based on the capture of tagged fish in two trap net locations in the inner fjord (T1 and T2, Fig. 1). Fish were also sampled in the Vosso River using rod gear, and through sport fishing in nearby rivers. Adult wild salmon were collected from rod fishing in the river or from the trap nets in the Vosso estuary, 12 and 14 km from the river outlet (T1, Fig. 1). Tagging experiments have shown that fish caught at this location are very likely to be returns to the Vosso River (Barlaup B.T., unpublished data); thus, we assumed that these fish had originated from the Vosso River.

We assembled hatchery scale samples for the growth analysis from the returning salmon from various release locations, but primarily from the outer release location O1 (Fig. 1). This location had the most complete data series from attempts to collect 30 individuals per year per treatment combination, where half of the individuals were 1 seawinter (SW, i.e. fish staying one winter at sea) fish and half were 2SW fish. However, when survival was poor, fish from a nearby outer release location (O2) were used, and if those were not sufficient, samples from the inner release locations was chosen successively (I1-I3). Finally, fish from other age-at-maturation groups were also used if 30 individuals had not been reached (3-4SW). Although this may have biased our results to a degree because of the linkage between early growth and age at maturation, we argue that the between-year variation and treatment effects are likely much greater than any bias on an annual basis. The same sample selection process was used for wild fish, with the limitation that wild fish only originated from one collection location (i.e., T2, Fig. 1) to ensure that these were wild fish originating from the Vosso River. In appendix Tables 1 and 2, we have listed the origins and ages of the fish used in the analysis according to release year. The release year for wild fish is the back-calculated year the fish emigrated from the river based on the scale analysis.

# 2.3. Scale analysis

Scale analysis was conducted by the Natural Resources Institute Finland, following the methods for scale pressing and image processing in McCarthy et al. (2008). These methods involve making an impression of the scales on a cellulose acetate slide, and selecting scales that have regeneration in - > 1/3 of the freshwater zone. Images of the impressions, were taken using a Wild M420 photomacroscope with a QImaging Retiga 4000R (Leica) camera using calibrated magnifications. Scale measurements were made using Image-Pro Plus (version 7.01). First, a line from the centre of the scale to the edge of the scale was drawn along the 360° axis of the scale. Second, the end of the freshwater zone was identified by the increased circuli spacing representing sea entry. Third, the intervals between the circuli (circuli spacings) from the end of the freshwater zone to the outer edge were automatically detected and manually checked for accuracy.

# 2.4. Calculating freshwater growth and post-smolt growth

Scale measurements were used to develop a freshwater growth index and multiple measures of PSG. Freshwater growth was defined as the distance from the centre of the scale to the end of the freshwater zone. The PSG increment was taken as the 8-month growth period from sea entry to midwinter, assuming the winter annulus is most likely formed as a consequence of day length. The increment was measured as the distance between the end of the freshwater zone and the first minimum in circuli spacing or the first winter annulus. The location of the first winter annulus was found by calculating 5-point moving averages of the circuli spacings and finding the lowest value. Once the winter annulus was identified, we extracted the increment length as the



Fig. 1. Map of region, indicating outer (O) and inner release sites (I), the trap net locations, and locations of fish farms (indicated with a fish symbol). The location of the two trap net locations T1 and T2 is indicated in the map by a filled triangle, while the rivers Vosso, Ekso and Dale is drawn in black.

total sum of the circuli spacings (CS) in the increment and the total number of circuli (CN) in the increment. Further indices were developed based on the putative month associated with the increment.

# 2.5. Putative monthly growth indices

CS can be further attributed to monthly growth by assuming that approximately the same number of circuli are deposited every month and dividing the circuli spacing data into eight monthly groupings. McCarthy et al. (2008) suggested dividing the spacing based on rounding, thus resulting in an uneven distribution of spacing data between fish with varying numbers of circuli in the increment. We improved on this method by using the decimal number to divide the effect of a circuli spacing that straddles two months. For example, if there were an average of 3.6 circuli spacings for each month, the first 3 circuli spacings plus a weight of 0.6  $\times$  the 4th circuli spacing would be used to compute the mean of the first month. The mean of the second month would be computed with a weight of  $0.4 \times$  the 4th circuli spacing; circuli spacings 5, 6, 7; and a weight of  $0.2 \times$  circuli spacing 8 to represent the influence of 3.6 circuli spacings. This process would be followed for the eight putative months. The method is described in more detail and is compared to the previous approach in appendix 1.

#### 2.6. Return rates of salmon

To assess whether marine survival was linked to post-smolt growth, we used the return rates of the tagged hatchery fish as an index of marine survival. We also calculate the relative difference in survival between the treated and untreated groups as described earlier in Vollset et al. (2017). In this study, we use the average attributable fraction of treatment (i.e., the reduction in control group survival compared to that of the treated group, as %), pooled by year, to be able to compare the treatment effect to that of the other MSIs. The recapture rate of tagged salmon is, however, not a good estimate of marine survival, because effort has inevitably changed during the time series (the number of traps being deployed and the time period during which they have been deployed have changed). We therefore collected spawning count data from the nearby Dale and Ekso rivers (Fig. 1) with a time series of spawning count data from 2004 to present. These spawning count data were collected through visual observations by divers, and the method is described in more detail in Vollset et al. (2014b). During the spawning counts, wild salmon were distinguished from hatchery salmon by adipose fin clips. Wild salmon were not harvested/killed during sport fishing, and the number of wild salmon observed in these rivers is therefore an independent, unbiased estimate of marine survival during the time series. The Vosso River is not suitable for snorkelling, due to its low visibility and the size of the river. The total number of wild fish caught in the trap nets operated in the estuary of the Vosso River was also collected (T1, Fig. 1). The data on the return rates of adult salmon from the spawning count were divided into three size groups, assumed to reflect 1-, 2- and 3- (and older) seawinter returning salmon. The number caught in each size group was assigned to the assumed smolt year to create a marine survival index (MSI) for each year of emigration. The index was refined to only include 1- and 2- seawinter fish due to the concern that the largest group may contain repeat spawners.

#### 2.7. Data analysis

To analyse the effect of treatment against the effects of parasites and origin (fish originating from hatcheries or from the wild), linear mixed effect models were used in which the year was defined as a random variable. Since we did not have a full factorial design of treatment and origin (i.e., we had no treated wild fish), we opted to analyse the effects of treatment and origin as one variable (group) with three levels (treated hatchery, untreated hatchery and wild). In addition, seawinter was included as a fixed effect with four levels (1-, 2-, 3- and 4SW fish). Treated hatchery and 1SW fish were set as the intercept in the model. A clear shift in marine survival index has been observed from 2008 to 2009 (Skoglund et al. 2013; Vollset et al. 2014b), and we therefore included a period variable that divided the data into two separate time periods to evaluate whether a shift was also observed in PSG. An interaction between these time periods and the difference between the groups was also included. The response variables were freshwater growth (FG), circuli spacings until winter annuli (CS), circuli number to the first annulus (CN) and month of maximum growth. FG and CS were modelled using a Gaussian distribution, while CN (count data) was analysed using a Poisson distribution Figs. 4 and 5

MSI was correlated to PSG (CS or CN) using a simple linear model including group and period and the interaction PSG:period. Model assumptions were evaluated using standard diagnostic plots. All model combinations were compared using the corrected Akaike information criterion (AICc). Models with a delta AICc of < 2 were considered similar. All analyses were done in R (R Core Team 2017) using the package lme4 (Bates et al. 2014).

#### 3. Results

#### 3.1. Marine survival indices (MSIs)

As seen in other monitoring data (Skoglund et al. 2013), there appears to have been a regime change in the return rate of salmon, where return rates were generally poor before 2009 and higher thereafter, with a peak survival in 2009 (Fig. 2a). This pattern in marine survival was most noticeable in the marine survival index (MSI) based on the snorkelling count data from the rivers, with mean returns of 57.8 versus 293.1 and 60.7 versus 252 between the early and late time periods in the Dale and Ekso rivers, respectively (Fig. 2b). The number of wild fish caught in the trap nets close to the Vosso River (T1, Fig. 1) exhibited a similar, albeit weaker, signal, with mean returns of 19.6 and 54 in the early and late time periods, respectively (Fig. 2b). This signal was also observed in the return rates of hatchery fish both in the treated and untreated groups (Fig. 2a). The effect of treatment on survival, calculated as the attributable fraction (%), had an opposite trend, with generally higher values (mean 21%) before 2009 and lower values (mean 4.9%) after 2009 (Fig. 2a).

#### 3.2. Freshwater growth

Since traits attained during the freshwater phase can, in theory, impact growth and survival during the marine phase, it was important to assess group differences in freshwater growth. Models comparing the freshwater effects are presented in Table 1. The top model shows that the FG for wild fish was significantly lower than that of the hatchery fish (Table 2). The average FG values for hatchery fish were 1.005 mm and 0.979 mm for the treated and untreated fish, respectively. The FG for wild fish was 0.813 mm. The interaction term indicates that while the FG of the two hatchery fish groups was similar between the first and second period, for wild fish, the FG decreased from an average of 0.871 mm during the first period to an average of 0.797 mm in the second period (Fig. 3, Table 2).

# 3.3. Post-smolt growth - circuli spacing (CS)

Models comparing the circuli spacing (CS) effects are presented in Table 3. The top model demonstrates that the CS was significantly lower for wild fish than that for treated hatchery fish during the first period but was slightly higher for wild fish than for treated hatchery fish during the second period. Furthermore, the CS of untreated



**Fig. 2.** Upper figure depicts recapture rates (%) of hatchery smolt treated (dashed line) and untreated (solid line) against salmon lice and released in the fjord. Grey filled squares indicate the attributable fraction of treatment, i.e. the relative reduction in fish comparing treated and untreated fish within year. Lower figure indicates total number of wild salmon observed during snorkelling surveys in Dale (dashed line) and Ekso (dotted line) backcalculated for the given year class. Solid line is based on captures of wild fish on the trap net in the Vosso estuary (T2, Fig. 1.).

hatchery fish was smaller than the CS of both treated hatchery fish and wild fish, but there was no difference between the CS of the treated and untreated hatchery fish during the second period (Table 4). During the first period, the CS was 16.7% larger for the treated than for the untreated hatchery fish. The second-best model did not include seawinter (with a  $\Delta$ AICc of 2.08), and sea winter did not have any substantial effect on the parameter values of the other coefficients. Even so, sea winter was included in the final model, and CS decreased with sea winter (Table 4).

# 3.4. Post-smolt growth - circuli number (CN)

Models comparing the effects of circuli number (CN) are presented in Table 5. The top model demonstrated that the CN was significantly lower for wild fish than that for treated hatchery fish during the first period, with an estimated difference in circuli number of 7.6 (Table 6). Furthermore, the CN of untreated hatchery fish was smaller than the CN of both treated hatchery fish and wild fish (Fig. 6, Table 6). There was no difference in CN between the groups during the second period. During the first period, treated fish had 19.6% percent greater CN values than those of untreated fish.

#### 3.5. Dividing post-smolt growth into months

When the CS was divided into putative months, the effect of treatment during the first period (2003–2008), measured as the difference between the CS of treated and untreated fish, was largest during the first two months and decreased thereafter (Fig. 6a), while no difference

#### Table 1

Top five models from model selection of freshwater growth (FG). Top model is presented on top. Group and Period is as described in the text, df is degrees of freedom, AICc is corrected Aikake Information Criterion, delta is the relative difference in AICc. between model and top model, weight is the support in favor of the given model calculated as described in Burnham and Anderson (2002). Year is set as a random effect in all models. Models are fitted using Maximum likleyhood.

Formulas	df	logLik	AICc	delta	weight
FG~Group + Period + Period:Group	8	381.22	-746.2	0	0.67
FG~Group + Period + Period:Group + SW	11	383.595	-744.8	1.41	0.33
FG~Group	5	369.789	-729.5	16.75	0
FG~Group + SW	8	371.948	-727.7	18.54	0
FG~Group + Period	6	369.789	-727.5	18.78	0

#### Table 2

Summary of final linear mixed effect models describing the effect of origin, period and treatment against salmon lice on fresh water growth. Year is defined as a random effect given as the standard deviation of the intercept. ":" indicates interaction.

	Estimate	Lower (95% c.i.)	Upper (95% c.i.)
Fixed effects			
(Intercept)	0.922	0.859	0.979
Untreated cultivated	0.066	0.006	0.126
Wild	-0.059	-0.113	-0.005
Period First	0.077	0.005	0.156
Untreated Cultivated: Period first	-0.059	-0.127	0.008
Wild: Period first	-0.149	-0.210	-0.088
Random effects s.d. (intercept)	0.045	0.026	0.084



**Fig. 3.** Freshwater growth in mm calculated as the distance from the center till the freshwaterzone in salmon scales. Solid lines indicated fish treated against salmon lice, while dotted line indicate untreated fish. Triangles indicate wild fish wild dots indicate hatchery fish.

in growth was observed for any months during the second period (2009–2014, Fig. 6b). The difference in CS between hatchery and wild fish was highest during putative month 6 in the first period (2003–2008, Fig. 6c) and during putative month 3 in the second period (2009–2014, Fig. 6d).

#### 3.6. Correlation between growth indices and marine survival indices (MSIs)

The return rate and the spawning count data did not correlate with the post-smolt growth estimates throughout the time series. However, when the time series was separated into two time periods before and after 2009, there was a significant correlation between PSG and return



**Fig. 4.** Post smolt growth measured as the total circuli spacing between the freshwater zone and the first winter at sea (see text for details). Solid lines indicated fish treated against salmon lice, while dotted line indicate untreated fish. Triangles indicate wild fish wild dots indicate hatchery fish.



**Fig. 5.** Post smolt growth measured as the number of circuli spacing between the freshwater zone and the first winter at sea (see text for details). Solid lines indicated fish treated against salmon lice, while dotted line indicate untreated fish. Triangles indicate wild fish wild dots indicate hatchery fish.

rates for marine survival indices from 2009 onwards, but no correlation before 2009. This correlation was indicated by a significant interaction term between PSG and period (ANOVA,  $F_{22,1} = 7.91$ , p < .05, Fig. 7). The correlation was apparent when using the spawning count from both the Dale and Ekso rivers to define marine survival (Fig. 7a and b, respectively). However, it is important to note that these correlations are based on few data points (5 years before 2009 and 6 years after 2009)



**Fig. 6.** Difference in CS between cultivated treated and untreated salmon (upper panels, a & b) and difference in CS between untreated wild and cultivated salmon (lower panels, c & d), measured as the total circuli spacing for the 8 putative months between leaving freshwater and the first winter at sea. To illustrate the difference between the first and second part of the dataset the separate plots has been made for the period 2003–2008 (left panels, a &c) and 2009–2014 (right panels, b & d).

and are therefore sensitive to outliers. No correlations were found between MSI and freshwater growth.

# 4. Discussion

During the initial segment of our study's time series, we found that the post-smolt growth of Atlantic salmon was greater in salmon treated with an antiparasitic agent than that of untreated fish. We have confidence in this finding since other studies have reported similar results concerning the effects of sea lice on the growth of salmonids. Perhaps most relevant are the analogous results for other Norwegian salmon populations that have shown that untreated returning salmon have lower masses than treated returning salmon (Skilbrei et al. 2013). The effect of treatment has also been seen in maturation rate data from Norwegian salmon populations, indicating that untreated salmon tend to mature later than treated fish, an effect that has been attributed to slower growth due to parasite load by Vollset et al. (2014a). The effect also appears to be impacting other species. For instance, Shephard et al. (2016) found a correlation between the condition of sea trout and their distance from fish farms, suggesting that sea lice from fish farms were the main factor in the growth differentiation. The results presented here are consistent with these findings, suggesting that sea lice can reduce the post-smolt growth of Atlantic salmon.

In contrast to the growth response that was observed during the first period, there was no difference in PSG between the treated and untreated salmon in the second segment of the time series. The study period of our experiment bracketed a dramatic change in the marine survival of salmon along the coast of Norway. During the time series, survival went from extremely low levels during the early segment of the time series (prior to 2009), to relatively much higher levels during the later, or second, period. This shift created a fortuitous test of the influence of marine survival conditions on the effect of sea lice on PSG. It seems clear that the shift in survival was associated with a decrease in the effect of treatment on post-smolt growth. Although this is a post hoc analysis, we believe this change in the effect of treatment on growth associated with survival is important, because it supports the contention that the effect of parasites on growth is context dependent. Our current results further support the findings of Vollset et al. (2016a), who found a strong negative relationship between the survival in the control group and the risk ratio between the survival of the treated, and untreated groups in a meta-analysis of RCTs in Norway. They concluded that the impact of sea lice was strongest during periods of low marine survival. The implication of this result is that it will be difficult to link the infestation pressure of sea lice from fish farms to population-level effects, without taking into consideration marine conditions. It is important to note that the effect of parasites does not seem to be the sole cause of this dramatic shift in survival, because the increase in marine survival was several times higher than the effect of treatment against sea lice. Additionally, the shift in marine survival observed after 2009, has been observed across > 40 rivers surveyed during autumn spawning count surveys on the western coast of Norway (Skoglund et al. 2016). Consequently, it is evident that the dramatic shift in survival occurs at a larger spatial scale than in the local fjord system.

Though we did not observe growth differentiation between the treated and untreated groups during the period of improved marine survival, we did observe a correlation between post-smolt growth and marine survival during this period. This was not apparent during the first period with low survival. Growth-mediated survival is a wellsupported hypothesis for Northeast Atlantic salmon stocks, with similar correlations observed in other Northeast Atlantic populations (McCarthy et al. 2008; Peyronnet et al. 2007). However, there are alternate hypotheses regarding salmon survival, that range from survival being mediated by PSG (Friedland et al. 1993; Friedland et al. 2000), to survival being mediated by changes in predation pressure (Friedland et al. 2014b; Friedland et al. 2017). The study period may therefore have bracketed a regime shift in marine survival on the western coast of Norway, or, more importantly, a shift in the survival mechanism of the stocks in this region. The key component supporting a survival mechanism that is independent of growth is a survival bottleneck driven by varying predation pressure, which is often dependent on the nature of the post-smolt migration habitats and environment. Shifts in salmonid marine survival due to shifts in the marine ecosystem have previously been observed in the North Atlantic. For example, Beaugrand and Reid (2012) argued that increased temperature (due to climate change) in the North Atlantic, has led to a cascading effect reducing prey availability for salmon. However, these trends could only



**Fig. 7.** Correlation plot between adult returns and post smolt growth (in circuli numbers) using return data from the river Dale (a) and the river Ekso (b). Wild fish are indicated in dark grey, untreated hatchery fish are indicated in red, while treated hatchery fish are indicated in blue. The time period before 2009 are indicated with dots, while the time period from 2009 to 2014 are indicated with crosses. Lines are correlations between post smolt growth and adult returns for the three groups for the period 2009–2014. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

be seen on large time scales. Climate can also shift predator distributions. For example, increased anoxic conditions in the central basin of the Baltic Sea, due to warming waters, has shifted the distribution of cod northwards – which has subsequently increased predation on postsmolts from northern rivers during their southward feeding migrations (Friedland et al. 2017). This exemplifies the potential complex physicalbiological coupling that can lead to shifts in the growth and survival of Atlantic salmon. Until now, no single factor has been identified that can explain the apparent regime shift observed in 2009.

In this study, wild salmon had lower PSG than treated hatchery fish during the first period of low marine survival, but had higher PSG than untreated hatchery fish. During the later period, wild salmon had slightly higher PSG than both treated and untreated hatchery fish. This

#### Table 4

Summary of final linear mixed effect models describing the effect of origin, period and treatment against salmon lice on circuli spacing. Year is defined as a random effect given as the standard deviation of the intercept. ":" indicates interaction.

	Estimate	Lower (95% c.i.)	Upper (95% c.i.)
Fixed effects			
(Intercept)	2.162	1.966	2.353
Untreated cultivated	-0.443	-0.660	-0.226
Wild	-0.152	-0.342	0.039
Period First	-0.343	-0.568	-0.110
SW 2	-0.110	-0.195	-0.025
SW 3	-0.132	-0.256	-0.007
SW 4	-0.321	-0.837	0.195
Untreated Cultivated: Period first	0.428	0.186	0.669
Wild: Period first	0.255	0.038	0.472
Random effects s.d. (intercept)	0.128	0.078	0.223

suggests that wild salmon were impacted by sea lice during the first period; however, PSG of wild fish was generally higher than that of hatchery fish. The survival and behaviour of hatchery reared salmon smolts are known to deviate from those of wild fish. For example, hatchery fish have generally lower marine return rates (Jonsson et al. 1991) and show different migration timing than wild fish (Kallio-Nyberg et al. 2011). Jonsson et al. (2003) found no difference in growth between 1-year-old smolts of hatchery origins and wild fish during first year at sea, but did find that 2-year-old smolts grew slower - indicating a genetic or phenotypic effect of the length of stay in the hatchery. In our study, we have demonstrated that surviving hatchery fish also have a different post-smolt growth pattern compared to their wild counterparts. Several non-mutually exclusive hypotheses can be invoked to explain this difference: (1) Behaviour; hatchery fish may have suboptimal foraging skills compared to wild fish. Hatchery-reared fish are usually fed with pellets in tanks with a high fish density; optimal behaviour in these conditions is clearly very different than in the wild, which may impact the early marine growth of the fish. (2) Morphology; the morphology of hatchery fish may deviate from that of the wild fish, giving hatchery fish a disadvantage. For example, hatchery fish usually have a higher weight-to-length ratio than wild fish, and fin erosion is common for fish held in tanks with high fish densities (Kallio-Nyberg et al. 2011). (3) Scale deposition rate; in theory, differences in physiology can affect the scale deposition rate, thus impacting our interpretation of scale growth history and the comparisons with wild fish. (4) Development; somatic growth is not directly correlated to development. Fast growing conditions in the hatchery may induce a "largebaby" effect, i.e., an effect in which a fish is seemingly large and physiologically ready to smoltify, but the individual is not as developed as its slower-growing wild counterpart.

Monthly growth indices indicated that the difference in PSG between treated and untreated fish was highest during the first months at sea, but was also relatively high throughout the entire 8-month post-

# Table 3

Top five models from model selection of circuli spacing (CS). Top model is presented on top. Group and Period is as described in the text, df is degrees of freedom, AICc is corrected Aikake Information Criterion, delta is the relative difference in AICc. between model and top model, weight is the support in favor of the given model calculated as described in Burnham and Anderson (2002). Year is set as a random effect in all models. Models are fitted using Maximum likelyhood.

Formulas	df	logLik	AICc	delta	weight
CS~Group + Period + Period:Group + SW CS~Group + Period + Period:Group	11 8	- 576.52 - 580.644	1175.4 1177.5	0 2.08	0.719 0.254
CS~Group+SW	8	- 583.868	1183.9	8.53	0.01
CS~Group + Period + SW	9	-582.86	1184	8.56	0.01
CS~Group	5	- 587.969	1186	10.62	0.004

#### Table 5

Top five models from model selection of circuli number (CN). Top model is presented on top. Group and Period is as described in the text, df is degrees of freedom, AICc is corrected Aikake Information Criterion, delta is the relative difference in AICc between model and top model, weight is the support in favor of the given model calculated as described in Burnham and Anderson (2002). Year is set as a random effect in all models. Models are fitted using Maximum likleyhood.

Formulas	df	logLik	AICc	delta	weight
CN~Group + Period + Period:Group	8	-2762.27	5540.7	0	0.833
CN~Group + Period + Period:Group + SW	11	-2761.25	5544.9	4.13	0.106
CN~Group	5	-2768.8	5547.7	6.94	0.026
CN~Group+Period	6	-2768.38	5548.9	8.14	0.014
CN~1	3	-2771.95	5549.9	9.18	0.008

#### Table 6

Summary of final linear mixed effect models describing the effect of origin, period and treatment against salmon lice on circuli number. Year is defined as a random effect given as the standard deviation of the intercept. ":" indicates interaction.

	Estimate	Lower (95% c.i.)	Upper (95% c.i.)
Fixed effects			
(Intercept)	3.617	3.545	3.686
Untreated cultivated	-0.231	-0.305	-0.158
Wild	-0.073	-0.135	-0.010
Period First	-0.134	-0.222	-0.042
Untreated Cultivated: Period first	0.229	0.147	0.311
Wild: Period first	0.117	0.045	0.188
Random effects s.d. (intercept)	0.056	0.036	0.096

smolt period. In contrast to salmon, sea lice exhibit deterministic growth, meaning that they stop growing after reaching adult size. Given that infestation occurs mainly during nearshore migration, the cost of sea lice infestation to the salmon smolt is in all likelihood highest during the first few months at sea, which could explain the pattern showing the largest difference in growth between the treated and untreated salmon during these months. In contrast, the difference between hatchery and wild salmon did not manifest itself to a large degree during the first month, but was larger during the later period of postsmolt growth. McCarthy et al. (2008) found that PSG is most important for the recruitment of salmon during the 4th and 5th month, and the effects of sea lice and hatchery origin may impact this pattern by decreasing PSG during these months. To calculate the monthly growth indices, we extended the method reported in McCarthy et al. (2008) by more accurately assigning growth data to putative monthly divisions. The biggest impact of this methodological change, can be seen in the data for the first two months, during which circuli spacing increased relatively quickly. Consequently, the method does not seem to have a large impact on the results of the previous work, but could be relevant when trying to understand the impacts of salmon lice during the first months of marine growth.

# 5. Conclusions

PSG was greater in treated versus untreated fish during a period of low marine survival before 2009, supporting the hypothesis that sea lice can affect the marine growth of wild Atlantic salmon. However, this difference in PSG disappeared from 2009 onward, which coincided with a shift from low to higher marine survival. The effects of sea lice alone cannot explain the observed shift in marine survival occurring in 2009, because the marine survival shift appears to have happened over a large geographical area. However, it seems evident that the effect of antiparasitic treatment was contingent on poor marine survival. Our data thus support the hypothesis that the impact of parasites on Atlantic salmon is context dependent. Consequently, any management advice regarding the long-term management of Atlantic salmon should aim to mitigate the effects of salmon lice according to a precautionary principle, since it is, as of now, not possible to accurately predict marine survival conditions for salmon.

#### Acknowledgements

We thank all the people involved in producing, releasing and recapturing salmon during the study period, for supporting the Vosso project. We express appreciation to the Voss hatchery staff for their professional and dedicated work. We acknowledge the significant contributions of Eirik Straume Normann, for his tagging and recapture work in the field, and Ina Birkeland and Tore Wiers, who also helped in field activities. Appreciation is expressed to the staff at the Laboratory for Freshwater Ecology and Inland Fisheries at NORCE. Helge Skoglund provided comments on an early draft of the manuscript and general discussion about salmon ecology and the history of the Vosso project. This study was jointly funded by the Norwegian Research Council through the projects BaseLice (project no. 243912/E50) and SeaSalar (project no. 280308), the Hordaland County Governor, the Norwegian Environmental Directorate and the strategic institute effort "Aquaculture-Environment Interactions" of Uni Research Environment. Cultivated fish were produced with financial support from the power company BKK and from regional fish farms (Vossolauget).

# Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2019.04.038.

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