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Atlantic salmon (*Salmo salar*) – Current status of selective breeding in Europe

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Summary

This report describes the current status of selective breeding of Atlantic salmon (Salmo salar) in European aquaculture. A survey among the seven major breeding companies provided insight into the main characteristics of breeding companies and their egg production. Data on national egg production were collected in order to estimate the market share of eggs produced by breeding companies in the total European egg production. All breeding companies perform family selection and commonly selected traits include growth performance, processing yield, product quality and disease resistance. Most of the salmon has been selected for about 10 generations in 2012. Illustrative for the achieved genetic gain is a substantial increase in harvest weight while the growing period has been reduced. After an equal growing period currently produced salmon reaches a three times higher bodyweight than that wild salmon would in the same conditions. The egg production in Europe in 2012 was estimated at 473 million of which 26-31 million did not originate from active breeding programs. Therefore it was concluded that in 2012 the market share of breeding companies was 93-95%. This proportion has increased to 96-97% in 2013.

1. Introduction

With an annual production of 1.5 billion tonnes, Atlantic salmon (*Salmo salar*) production accounts for >65% of European aquaculture production (table 1). More than 80% of the European production is produced in Norway (FEAP, 2014).

Table 1. Atlantic salmon production volume and value in Europe in 2012

Country	Production volume [a] (tonnes)	Production volume [b] (tonnes)	Production value [b] (1000 €)
Faroe Islands	76 800	76 564	377 979
France	300	300	1 351
Iceland	3 104	2 923	10 920
Ireland	12 000	12 440	75 681
Norway	1 240 000	1 232 095	3 742 495
Spain	0	4	15
UK	162 223	162 605	746 368
Total	1 494 427	1 486 931	4 954 810

[a] (FEAP, 2014)
[b] (FAO, 2014)

The history of salmon breeding is relevant for aquaculture today, as the strains used by modern breeding companies originate to a large extent from four original strains. These are the Jakta, Bolaks, Mowi and Aquagen strain. At several breeding organisations some mixing with other strains has occurred in the past, but a major contribution can often be traced back to these strains.

Bolaks and Jakta strain:
Very limited information on the history of these strains is available. The Bolaks strain has been collected around 1974-1975 and Jakta has probably been collected somewhere in the 1980's. Both strains were collected from the Vosso watercourse and the Årøy river in Norway. Before 1999 breeding was done by phenotypic selection on own performance, which was followed up by family selection as of 2000. Selected traits were growth performance, condition factor, late maturation and appearance (Bakke, 2014). Assuming an average four year generation interval, six generations of

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selection have been performed on the Bolaks strain until 1999 and three or four generations on the Jakta strain.

Mowi strain:
The Mowi strain was established from fish of the Norwegian fish farm Mowi AS (Gjedrem et al., 1991) in the 1960's. The genetic basis originates primarily from fish from the Bolstad and Årøy rivers, with contributions of salmon captured in the sea near the Oster fjord and Sotra in Western Norway. Phenotypic selection on growth performance and late maturation was employed until 1999. This selection regime involved crossing five year old males and four year old females, resulting in approximately 6–7 full generations at the time. As of 1999, a family selection programme was initiated based on 250 females and 80 males characterised by DNA fingerprints with a generation interval of four years (Glover et al., 2009).

AquaGen strain:
Because of the four year generation interval, four generations of wild salmon were collected between 1972 and 1975 from 40 rivers in Norway and one Swedish river by AKVAFORSK. A total of 442 full-sib families, the offspring of 188 sires and 428 dams, were tagged and performance tested at different private marine farms. The selection regime applied was combined between families and within family selection to increase growth rate and to reduce early sexual maturity. Family selection has been applied to improve specific disease resistance since 1989 and product quality since 1990 (Gjedrem, 2012). Even though there was a relatively even distribution of river strains amongst the populations initially, in the third generation of selection (1984-1987) three of the populations were dominated by a strain collected from the Namsen river and one population originated from the fish farm Mowi AS (Gjedrem et al., 1991), hence the genetic basis of this strain consisted for one quarter of the Mowi strain. The current genetic composition of the AquaGen strain is unclear. In 1992, when four generations of selection were performed and 16 year classes were established, the breeding operations were transferred to AquaGen AS.

Over the course of the years these four original strains have been copied and transported to all major salmon producing countries in Europe. They have been incorporated in local breeding programs and been subjected to different selection intensities and breeding goals. Mixing with other strains has occurred in several cases, but to what extent is unclear.

Various estimates on genetic gain achieved over the first generations are available. Gjerde and Korsvoll (1999, Cited in: (Gjedrem & Baranski, 2009)) reported an average realized selection differential of 14% per generation in growth performance for the first six generations, corresponding well to other values in literature (O'Flynn et al., 1999 ; Thodesen et al., 1999). The selection response in feed conversion ratio during the first five generations is estimated to be somewhere in between 1.3% to 4.6% per generation (Thodesen et al., 1999) and estimates for sexual maturation vary between 3% (Gjedrem et al., 2012) and 8% per generation (Gjedrem, 2005).

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In 2009, Gjedrem and Baranski (2009) estimated that 97% of the global salmon production originated from genetically 'improved stocks'. However no coherent overview of the current status of selective breeding in European salmon aquaculture exists. Therefore this report aims to:

1. Describe the main characteristics of breeding companies.
2. Estimate the market share of breeding companies in Europe.

2. Materials and Methods

2.1. Characterisation of breeding companies

In a survey conducted in collaboration with AQUATRACE[1], questionnaires were distributed among the seven major breeding companies. This questionnaire included questions related to the type of selection, the number of selected generations, selected traits, the application of genetic markers and genomic selection, the monitoring of inbreeding, protection strategies and the quantity of eggs produced. The term 'eggs' was defined as ova laid down to hatch, corresponding to the eyed egg stage. The market was dominated by the sales of eggs, hence smolt production was ignored. In order to assess the relative use of original strains by breeding companies, the egg production of breeding companies was pooled according to the strain used. When a mixture of strains was used, the reported egg production was assigned to these strains in a 1:1 ratio.

2.2. Egg production

For the estimation of the market share of egg production by breeding companies, an estimate of the total European egg production was required. As these data are not routinely collected on a European level, national egg and trade statistics were collected to compose a European total. Per country data were collected on the number of eggs produced, the import of eggs, the export of eggs and the number of eggs used in domestic production. However for all countries some of the data were missing and these had to be derived from the other data. The data were related as follows:

National egg production = eggs used for domestic production + export – import [1]

When no data on the number of eggs used for domestic production could be obtained, this figure was estimated from national fish production data, the yield per smolt and egg to smolt survival, according to:

Eggs for domestic production = fish production/ yield per smolt/ egg to smolt survival [2]

In this equation the means of national fish production statistics of 2012 according to FEAP (2014) and the FAO (2014), were used as fish production data. The yield per smolt was 4.39kg and 5.49 kg for Norway and the Faroe Islands respectively (Marine_Harvest, 2014) and it was assumed to be 4.5kg for Iceland. An egg to smolt survival of 80% was assumed (Bakke, 2014). Remaining missing data were composed using equation 1.

[1] AQUATRACE - https://aquatrace.eu/ - 7th Framework Programme for research (FP7)

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2.3. Market share of breeding companies

The market share is defined as a firm's sales relative to the total sales of all firms in the same industry (Ghosh, 2004). Here it is used as the total egg production of European breeding companies relative to the national and relative to the total European egg production. On a national level the market share of breeding companies was determined by comparing the pooled egg production of breeding companies per country to the national egg production. As the pooled reported egg production of breeding companies was higher than the total European egg production, the market share of breeding companies could not be determined by comparing the pooled egg production of breeding companies to the total European egg production. Instead the market share was estimated as 100% minus the part of the egg production that could not be attributed to the breeding companies.

3. Results

3.1. Characterisation of breeding companies

All seven breeding companies in the survey employed family selection. In this type of selection artificial fertilisation is applied to create full sib families, which are reared in separate tanks and part of them is used for field and challenge tests. In addition to phenotypic records the information from full and half sibs is used in selection (Gjerde et al., 2007). Most of the breeding companies selected on growth performance, processing yield, product quality and disease resistance (table 2). All companies monitored the rate of inbreeding. Genetic fingerprints for parentage assignment, marker assisted selection and genomic selection were commonly applied. Most companies used genetic traceability as a protection strategy and two companies applied sterilisation.

Table 2. Traits in selection of Atlantic salmon breeding companies in Europe

Selected traits	Applied by [a]
Growth performance	7
Processing yield	6
Product quality	6
Disease resistance	6
Reproduction (sexual maturity, fecundity)	2
Morphology	3
Feed efficiency	2

[a] Number of respondents that performed selection on a trait. Seven companies participated in the survey

The egg production grouped according to the original strains is presented in table 3. Instead of exact values, ranges are presented to obscure company specific details. The major contributions to European aquaculture are from the Mowi and Aquagen strains, accounting for 27-36% and 36-54% of the reported egg production respectively.

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Table 3. Atlantic salmon egg production in Europe in 2012 grouped according to the original strains

Original strain	Generations in mass selection	Generations in family selection	Total selected generations	Egg production (million)	Proportion (%) [c]
Bolaks	4-5	4	8-9	75-90	13-16
Jakta	3-4	4	7-8	50-60	9-11
Mowi	6-7	4	10-11	150-200	27-36
Mowi mixed [a]	?	4	?	10-15	2-3
Aquagen	0	10	10	200-300	36-54
Total				513-558 [b]	

[a] Mowi mixed with other strains than Bolaks, Jakta or Aquagen
[b] Based on more exact but confidential figures
[c] 100% = 558 million eggs

3.2. Egg production

The total European egg production was 473 million of which the majority was produced in Norway (table 4). The number of eggs used in European production was 441 million, corresponding to the number of eggs produced minus the export to non-European countries.

Table 4. Production and trade of eyed eggs of Atlantic salmon within Europe in 2012

Country	Used in domestic production (million)	Import (million)	Export (million)	Production (million)
Faroe Islands	17 [C]	4.5 [C]	0 [R1]	12.5 [R1]
Iceland	1 [C]	0 [C]	54 [R2]	55 [R2]
Ireland	7.4 [R3]	0.6 [R3]	10.1 [R3]	16.9 [R3]
Norway	352 [C]	22 [R4]	30 [C]	360 [C]
UK-Scotland	63.2 [R5]	44.7 [R5]	0 [R5]	18.5 [R5]
UK-rest	0 [R6]	0 [R6]	10 [R5]	10 [R5]
Total	441	72	104	473

R = Values from references: [1] Patursson (2013); [2] Jonasson (2014); [3] Robinson (2014); [4] Bakke (2014); [5] Munro and Wallace (2012); [6] Poseidon (2008)
C = Calculated (equation 1 and 2 in text)

Although the official statistic for the number of eggs used in production in Norway was 598 million (Directorate_of_Fisheries, 2014), this figure is assumed to overestimate the actual number of eggs used in production. Kontali Analyse estimated that 370 million eggs were used in production in 2013/2014 (Hosteland, 2014). For 2012 the Norwegian egg production was derived as follows. The number of eggs used in domestic production in the Faroe Islands, Iceland and Norway was calculated with equation 2. For the Faroe Islands and Iceland the egg imports were calculated according to equation 1. Successively the total quantity of imported eggs on a European level could be calculated. It was assumed that on a European level the exports were 32.3 million higher than the imports, as imports from non-European countries were insignificant (Bakke, 2014) and 32.3 million eggs were exported to Chili (Sernapesca, 2014). The exports of all countries except for Norway were known, hence the Norwegian export could be derived from the difference between the total export on a European level and the sum of exports of the other countries. The Norwegian egg production could then be calculated with equation 1 and equalled 360 million.

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3.3. Market share of breeding companies

Figure 1 shows the reported egg production of each of the breeding companies. The three biggest breeding companies together produced more than 80% of the total egg production by breeding companies. Summed up the total egg production by breeding companies was 513-558 million eggs, which was 40-85 million higher than the total European egg production according to table 4. The production of 26-31 million eggs in the UK and the Faroe Islands could not be explained by the egg production of the seven major breeding companies. This egg production originated from a few small companies that did not have a breeding program (Tinch, 2014) and from a breeding program that was terminated in 2005 (Patursson, 2015). Therefore the market share of breeding companies was 93-95% in 2012. Since 2013 the broodstock in the Faroe Islands was replaced by broodstock of one of the seven breeding companies and the market share of breeding companies has increased accordingly to 96-97%.

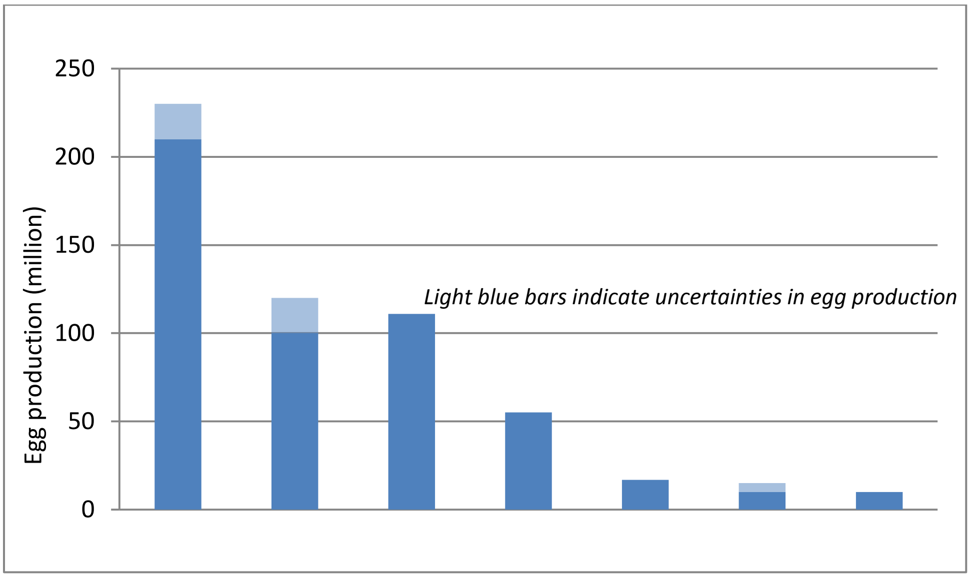

Figure 1. The egg production of the seven Atlantic salmon breeding companies in Europe in 2012.

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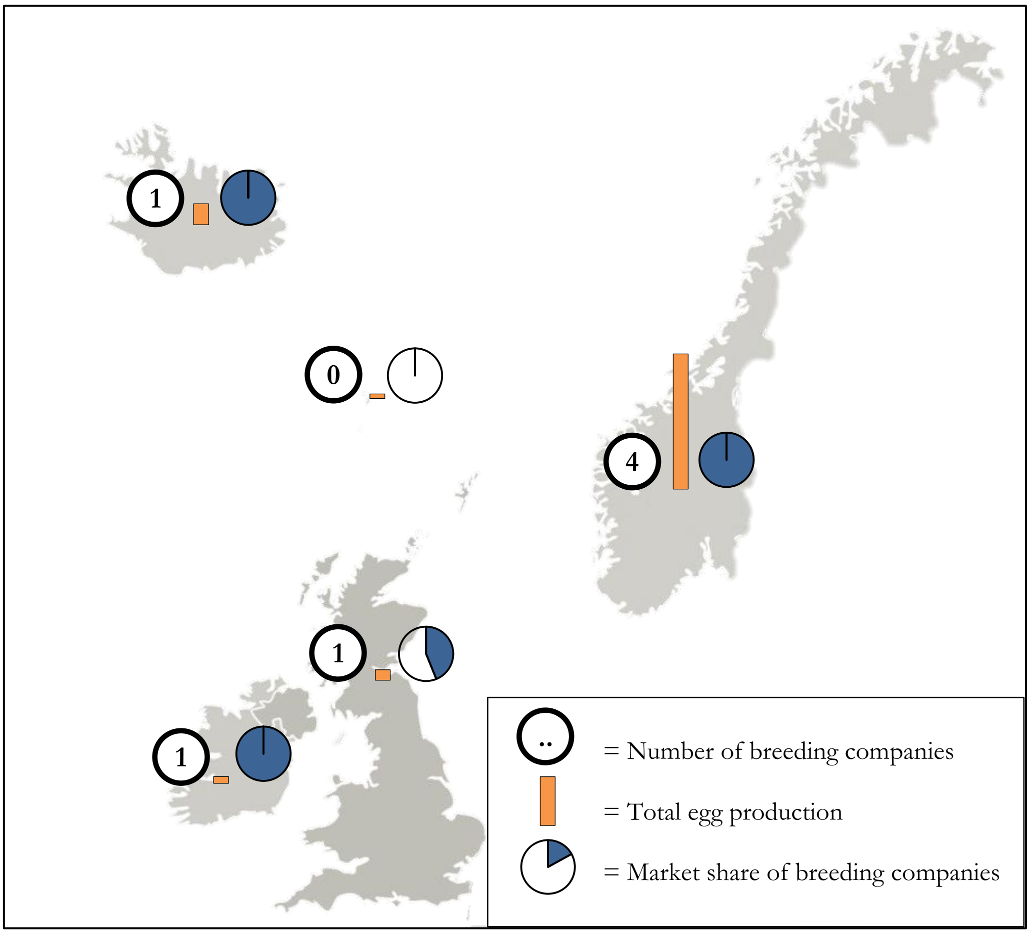

Figure 2. The distribution of Atlantic salmon breeding companies across Europe, the egg production per country and the national market share of breeding companies in 2012.

4. Discussion

It was evident from the survey that most breeding companies select on a diverse set of traits. Several of these traits cannot be recorded on the selection candidate itself, hence information of related individuals is required to estimate breeding values. Only two companies indicated to select on reproduction related traits, including age at sexual maturity. Nevertheless most breeding companies do select against precocious maturation (Gjerde, 2015). Selection against precocious maturation has for a long time been considered an important trait in the breeding goal (Gjøen & Bentsen, 1997). Precocious maturation occurs mainly in males and negatively affects flesh quality. It has been suggested that the incidence of precocious maturation may reduce as an effect a shorter growing period in seacages due to improved growth performance (Gjedrem, 2005 ; Gjøen & Bentsen, 1997), but the relationship between growth rate and sexual maturity is not that evident (Taranger et al., 2010). The incidence of precocious maturation ranges from 1-10% (Arge et al., 2014) and it has a medium heritability of 0.10-0.17 (Wild et al., 1994). Thereby selection against it is relatively ineffective (Gjedrem, 2005).

The quantity of eggs used in production in 2012 was calculated from fish production data of 2012, while fish produced from these eggs were harvested in 2014 which may have caused some minor inaccuracies in the egg production data. The cumulative reported egg production of the breeding

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companies was 40-85 million higher than the total European egg production. This difference can be explained by the difference between the eggs produced and the actual number of eggs used in production. As breeding companies want to be able to guarantee a sufficient amount of eggs, they produce more than what they expect to need (Gjerde, 2015).

In European finfish aquaculture, salmon production is by far the biggest in terms of volume and value (FEAP, 2014). Considering the size of the industry, compared to other aquaculture species, relatively few companies operate a breeding program. This can be explained by several factors. The first factor is the large size of fish producing companies, which gives them much power to demand stocking material with the best genetic attributes from their suppliers. The second factor is the ease of transporting eggs, due to which a high level of international competition exists. This forces breeding companies to compete on genetic gain for a wide array of traits, which is achieved by family selection based breeding programs. The high cost associated with a family selection based breeding program is the third factor. This selection strategy requires the separate housing of full and half sib families and is often combined with separate challenge test facilities, both of which are capital intensive. The cost to operate such a breeding program requires large egg production volumes to maintain egg prices competitive. Together these three factors have resulted in a sector consisting of relatively few and large breeding companies applying advanced selection schemes.

Selective breeding has resulted in improvements of many different traits and most illustrative for the achieved genetic gain may be improvements in growth performance. Glover et al. (2009) compared the performance of the Mowi strain which had been selected for 7-8 generations to a wild strain in the same conditions. After a 3 year period from egg to harvest the wild strain reached a weight of 2kg while the Mowi strain weighed about 4.5kg. They reported a 121-131% increase of bodyweight at harvest in the Mowi strain compared to the wild strain, i.e. an average increase of about 11-12% per generation. Solberg et al. (2013) reported a 196% higher bodyweight of juveniles of the Mowi strain, which had been selected for 9-10 generations, than that of a wild strain after an equal growing period. Salmon that is currently used in production has been selected for about 10 generations (table 3). Assuming an continued increase in bodyweight at harvest of 12% per generation, it is estimated that after an equal growing period currently produced salmon reaches a three times higher bodyweight than that wild salmon would in the same conditions. This huge improvement in growth performance is evidenced by a reduction in growing period to 2-3 years from egg to harvest and an increase in harvest weight to about 5kg (Marine_Harvest, 2014), which rather represents an industry average than the even higher actual growth potential (Bakke, 2015).

5. Conclusion

1. All seven major breeding companies perform family selection
2. Commonly selected traits include growth, processing yield, product quality and disease resistance.
3. Most of the salmon has been selected for about 10 generations in 2012.
4. The market share of breeding companies in total European egg production was 93-95% in 2012 and 96-97% as of 2013.
5. After an equal growing period currently produced salmon reaches a three times higher bodyweight than that wild salmon would in the same conditions.

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