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Derivation of economic values for important production traits in Atlantic salmon

Utrekning av økonomiske vekter for viktige produksjonsegenskaper hos laks

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Abstract

Atlantic salmon breeding programs selected several traits simultaneously. Lack of economic values may lead to inappropriate relative weighting of the traits selected for and with a suboptimal long-term genetic gain of the traits. Derivation of reliable economic values for important traits in Atlantic salmon is therefore necessary to optimize the economic benefits of the breeding program.

The objective of the thesis was to firstly to derive economic values for six important production traits of Atlantic salmon in the grow-out phase in seawater, and secondly to predict the genetic gain for each trait, and thirdly to calculate the relative contribution of each trait to the overall economic genetic gain. The studied traits were harvest body weight (HBW), feed conversion ratio (FCR), early sexual maturity (ESM), general mortality (GM), specific mortality (SP) and fillet yield (FY). Harvest body weight was modeled through the growth factor. The economic values for the traits were expressed as NOK/trait unit/kg round body weight produced.

HBW was the most important trait with an economic value of 1.95 NOK/kg; followed by the correlated trait FCR with -11.8 NOK/kg feed, FY with 0.82 NOK/%-unit; GM with -0.26 NOK/%-unit; SM with -0.37 NOK/%-unit, and ESM with -0.22 NOK/%-unit.

The magnitude of their contribution to the overall economic genetic gain was 48 % (HBW), 47 % (FCR), 5.3 % (FY), 0.9 % (GM), 0.1 % (SM) and -1.6 % (ESM). Given that records of feed intake could be obtained, the contribution of FCR to the overall genetic gain increased by 11 %-units while that of HBW decreased by 10 %-units.

The overall economic genetic gain per generation was estimated to NOK 2.20 and NOK 2.45 per kg fish produced without and with feed intake records, respectively.

This is the first reported study on the derivation of economic value for traits in Atlantic salmon. The predicted genetic gains for the studied traits and their relative contribution to the overall economic gain relies on reliable genetic parameters for the traits that are missing for most of the traits. Nevertheless, the results give some insight about the expected genetic gain of each trait their relative contribution to the overall economic gain.

Key words: Atlantic salmon, economic value, selection program, economic response.

Abstrakt

I avlsprogrammer for atlantisk laks blir det selektert for flere egenskaper trekk samtidig. Mangel på økonomiske vekter kan føre til ugunstig relativ vekting av egenskapene og dermed med en ikke optimal langsiktig genetisk endring av egenskapene. Pålitelige økonomiske vekter for viktige egenskaper hos laks er derfor nødvendig for å optimalisere et avlsprogram.

Målet med oppgaven var for det første å regne ut økonomiske verdier for seks viktige produksjonsegenskaper hos atlantisk laks i vekstfasen i sjøen, og for det andre å estimere den genetiske framgangen for hver egenskap, og for det tredje å beregne det relative bidraget av hver egenskap til den totale økonomiske framgangen for alle egenskapene. De studerte egenskapene var tilvekst fram til slakting (HBW), fôrutnytting (FCR), tidlig kjønnsmodning (ESM), generell dødelighet (GM), spesifikk dødelighet (SM) og filetutbytte (FY). Tilvekst ble modellert ved bruk av vekstfaktoren. De økonomiske verdiene for egenskapene ble uttrykt som NOK/enhet/kg produsert rund kroppsvekt.

HBW var den viktigste egenskapen med en økonomisk verdi på 1,95 NOK/kg; etterfulgt av den korrelerte egenskapen FCR med -11,8 NOK/kg fôr, FY med 0,82 NOK/%-enhet; GM med -0,26 NOK/% - enhet; SM med -0,37 NOK/% - enhet, og ESM med -0,22 NOK/% - enhet.

Størrelsen på deres bidrag til den totale økonomiske framgangen var 48% (HBW), 47% (FCR), 5,3% (FY), 0,9% (GM), 0,1% (SM) og -1,6% (ESM). Dersom en kunne fått registrert fôropptak på enkeltfisk ville FCRs bidrag til den totale genetiske framgangen øke med 11% -enheter, mens HBW sitt bidrag ville bli redusert med 10% -enheter.

Den totale økonomiske framgangen per generasjon ble estimert til henholdsvis 2,20 og 2,45 kroner per kg produsert fisk uten og med registreringer av fôrinntak. Dette er den første rapporterte studien om økonomiske vekter for egenskaper hos atlantisk laks. De forventede genetiske gevinstene for de studerte egenskapene og deres relative bidrag til den samlede økonomiske gevinsten er avhengige av pålitelige genetiske parametere for egenskapene, noe som mangler for de fleste egenskapene. Likevel gir resultatene noe innblikk i den forventede genetiske gevinsten for hver egenskap og deres relative bidrag til den totale økonomiske framgangen per generasjon.

Stikkord: atlantisk laks, økonomisk verdi, avlgsprogram, økonomisk respons.

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1. Introduction

The aquaculture production is using freshwater, sea water, brackish water to farm aquatic animals and aquatic plants. Global aquaculture production soar to 114.6 million tonnes in live weight in 2018, of which aquatic animal productions, including finfish, crustaceans, mollusks accounted for nearly 72% of it (FAO, 2020). Norway aquaculture industries produced about 1.4 million tonnes slaughtered salmon, which corresponds to a value of 68 billion NOK while it was 0.6 million tones to a value of 12 billion NOK in 2005 ("Atlantic salmon, rainbow trout and trout - Grow out production," 2020). Increased production comes from increasing number of grow-out licenses in the sea but decreasing numbers of operating sites with larger cages. More intensive culture must be a consequence of this situation, and the growing health risk follows. The constraint of such feeding conditions poses new breeding challenges even for those genetically improved stocks. Breeding program in aquaculture lag far behind most livestock breeding, even though the basic elements of breeding theory are same for fish and farmed animals. The most significant reasons for the difficulties in developing fish selection program are the complexity of reproductive biology cycle, like for anadromous species, and uncontrollable environmental factors to be taken into account in the fish breeding plans. The first selection experiment with farmed Atlantic salmon started in Norway in the early 1970s. In the mid 1980s the fish material was handed over to the industry which gradually developed it into a commercial selective breeding program. This fish material is now the material used by the breeding company Aqua Gen which is one of four selective breeding programs for Atlantic salmon in Norway. The other three are SalmoBreed, Mowi Genetics, Rauma Stamfisk/Salmar (Gjedrem, 2005).

The primary intent of these breeding programs is though selection increase the genetic potential of the animals for traits of economic importance. Selection is generally applied to several traits simultaneously. A lack of economic attention may lead to inappropriate relative weighting on the traits that selected for and with suboptimal long-term genetic gain for them. Thus, the economic efficiency of Atlantic salmon can be increased by the optimization of economic weights of the traits. The contribution of each trait to the overall economic gain of all traits is dependent on the relative weight given to each trait, the heritability of each trait, the phenotypic and genetic correlations among the traits and the number of fish recorded for each trait. The genetic improvement per generation obtained through selection for fish is remarkable (Gjedrem, Robinson, & Rye, 2012). Some traits like disease resistance and feed conversion ratio that are difficult or very expensive to measure can be improved by indirect selection, by using genetic and phenotypic correlation with body weight, both are -0.6.

Over the years, the number of traits selected for Atlantic salmon has increased markedly from 1-2 traits (growth, early sexual maturity) in the early 1970s and now maybe up to ten different traits in some of the most advanced programs; e.g., growth rate, early sexual maturity (McClure, Hammell, Moore, Dohoo, & Burnley, 2007; Mørkøre & Rørvik, 2001), carcass quality traits (e.g., fillet fat, fillet color) (Quinton, McMillan, & Glebe, 2005; Sutton, Bult, & Haedrich, 2000), specific disease traits (e.g., ISA, IPN, PD, salmon lice, amoebae gill disease) (Drangsholt, 2011; Gjøen, Refstie, Ulla, & Gjerde, 1997; R. Houston et al., 2008). Most of these traits cannot be recorded on the live breeding candidates and must therefore be recorded on their sibs from a costly slaughter test and costly disease challenge tests.

The objective of this thesis was to first derive the economic values for six important traits in grow-out phase in seawater of Atlantic salmon; and secondly to predict the genetic gain for each trait, and thirdly to calculate the relative contribution of each trait to the overall economic genetic gain of all traits. The six studied traits are harvest body weight (HBW), feed conversion ratio (FCR), early sexual maturity (ESM), general mortality (GM), specific mortality (SP) and fillet yield (FY).

The derivation of the economic values was obtained through the developing a weekly economic profit model at a grow out farm with two cages, and assuming relevant input data, production data during the grow-out period, a harvest strategy, and output production data at the time of harvest. From this the economic value of each trait (NOK/unit change in the trait/kg fish produced) was derived by the change in profit for a small favorable change in each trait, one at a time.

The predicted genetic gain for each trait was obtained by entering the derived economic values for each trait into a selection index program together with the assumed phenotypic and genetic parameters of the traits, the number of fish recorded for each trait, as well as the design of the breeding nucleus and the number of selection candidates; and from which we also obtained the relative contribution of each of the trait to the overall economic value of all traits.

2. Literature review

As a major aquaculture producing country, Norway has consolidated its share in world production to varying degree over the past two decades. As shown on the Directorate of Fisheris (2020), Norway aquaculture industries produced about 1.45 million tonnes fish for food, which corresponds to a value of 68 billion NOK in 2019. Atlantic salmon accounts for 93% of the total fish and also supply 45% of the salmon word market. Efficient breeding programs has been crucial to this development of salmon farming in Norway, not only to meet the industry production goal and to remain competitive in future food market (Jónasson, Gjerde, & Gjedrem, 1997). Farming of Atlantic salmon started at the end of the 1960s in Norway, and from the early 1970s with the development of efficient selective breeding programs to improve economically important traits (Gjedrem, 2005).

An early establishment of Atlantic salmon selective breeding program was the critical for developing salmon farm in Norway. The company MOWI, the largest Norwegian fish farm located close to Bergen developed rearing smolt technique and transferred them into sea-cages in the Fjords and exported its first farmed salmon in 1971 (Ford, 1984). In the year of 1975, the first selection of broodstock of fish was performed by AKVAFORSK at the research station at Sunndalsøra, with a general interval four years and four parallel nucleus breeding populations and a base population of a total of 4 x 120 full-sib families collected from more than 40 rivers to secure a broad genetic variation. During the first year, growth rate was the only trait selected for breeding program and followed by precocious male, early sexual maturity, and later by a number of other traits; furunculosis (Gjedrem, Salte, & Gjøen, 1991), fillet color (Gjedrem, 1997), Infectious Salmon Anemia (ISA) (Gjoen, Refstie, Ulla, & Gjerde, 1998), Infectious Pancreas Necrosis (IPN) (R. D. Houston et al., 2010).

This broodstock selection made it possible to supply the eyed eggs every year from four-year old broodstock to the industry (Gjedrem, 2010). In 1982, AKVAFORSK contacted the Fish Farmers Sales Organization (FOS) and Norwegian Fish Farmers Association (NFF) to take responsibility for the breeding program, named Norske Fiskeoppdretteres Avlsstasjon AS (NFA), in the second breeding station at Kyrksæterøra. In late 1992, breeding program was turned into a private company, now it is called Aqua Gen AS. Five years later, the SalmoBreed, a second breeding company was established. The genetic improvement of growth has made it possible to produce 0+ smolts instead of 1+ smolt which has made it possible to shorten the generation interval from four to three years (Thodesen & Gjedrem, 2006).

The extremely fecundity with thousands of eggs per spawn in aquaculture species brings some advantages and disadvantages. The advantages, for example, are the cost of rearing breeding fish is cheaper than farm animals, mating strategy is more flexible and makes the intensive selection possible, high fecundity can be fully utilized at the multiplier level when disseminating the improved genetic material to the industry. The disadvantages are high fertility causes a rapid of inbreeding rate and fish cannot be tagged immediately after hatching, they must be reared separately until reach a size big enough to be tagged. Although modern technology breaks through the limitations of body size, but it is relatively expensive (Pine, Pollock, Hightower, Kwak, & Rice, 2003). In light of those advantages and disadvantages, process of fish breeding program was developed well.

2.1 Atlantic salmon industry structure in Norway

The value chain of the Atlantic salmon production industry includes eyed eggs production at multiplier stations, smolt production at smolt farms, production of the fish until marketing size at grow out farms and slaughtering and processing. The multiplier stations are mostly owned by the breeding companies.

The whole production cycle is around three years, i.e., about 10-16 months in freshwater and 1-2 years in seawater. The eggs are fertilized, and the resulting fry/fingerlings reared in freshwater tank/pond until an average body weight of about 100 grams at which the fish are smoltified and transferred into net-cages in the sea. After a site is harvested, the site is fallowed for 2-6 months before next groups of salmon are released into same location. The successful sea farming production depends on good quality smolt that depends both on good genetic quality of the fertilized eggs and good production environment and management.

The breeding station as the first stage of genetic development where the breeding nucleus and selection takes place. The breeding nucleus in fish consist of full-sib family groups that may reared in separate tanks until an average body weight of 15-18 g at which a random sample of the fish in each tank from each family are tagged by physical methods. The tagged fish are raised as test fish or breeding candidates in a commercial rearing environment. Alternatively, without access to a large number of tanks, a given number of eyed eggs may be pooled and reared in a common tank and later be traced back to their parents through genotyping of a tissue sample of each fish and their parents.

To make sure the sufficient year supply of the eyed eggs and smolt productions to the fish industries, multiplier stations were set up. Each multiplier station is equipped with facilities for the production of smolt and for rearing the fish to the sexual maturity for the production of a new generation of eyed eggs that are sold to the smolt production farms. As an alternative option, fry may be supplied directly from the breeding nucleus to the smolt production farms. The smolt production farms rear the fish until the fish reach the suitable body size to be stocked into the net-cages at the grow-out farms. In order to shorten the times of grow-out phase to minimize the risk of infectious disease, like sea lice, the larger smolts (around 150 g – 500 g) have become more common.

The sea farming subsegment is the largest part in the salmon production line. The sale of smolt production for sea farm was 372 million fish and to a value of 5.6 billion NOK while the sale of salmon production was 1.4 million tonnes to a value of 68 billion NOK in 2019 ("Atlantic salmon, Rainbow trout and Trout - Juvenile production," 2020b). Although production has increased significantly, it is not unlimited. The main two original reasons of how much should be produced and by whom and how to protect environment made the regulating access to the fish industry and made aquaculture regulation. The regulation illustrates two limitation on the license and the locality. The license is used to regulate access to the fish farms and the locality is used to allocate the space of coastal area for them (Hersoug, 2015). In 2018, the license applied to grow-out farm was 1041 and the total number of localities was 587 with an average number of cages in each locality was six. The maximum allowed biomass (MTB) is 945 tonnes as an upper limit in the Troms and Finnamark counties, while it is 780 tonnes for standard license for the rest of Norway (Hersoug, 2015).

Based on the developed product industry chain, well-designed fish breeding programs can realize its economic value. However, before selection programs can be started, the breeding objectives integrated breeding company must be defined exactly.

2.2 Breeding objectives

A good breeding objective definition is the pre-requisite to maximize the economic return for any selection program. The traits are characterized by its breeding value and economic weight, which are the two components of the breeding goal. In the breeding goal, the accumulated genotype (H) is a linear function of breeding values with economic values:

$$H = V_1A_1 + V_2A_2 + \cdots\cdots + V_nA_n, \quad (1)$$

where the V is the economic value and A represents the true breeding value. So, the total genetic gain is the sum of the economic values and their related true breeding values. The optimization of the animal breeding program using genetic improvement can be a more sustainable and long-term process that need not only the economic values as same as those are considered in short-term genetic changes but also consider the non-economic values (Ingrid Olesen, Groen, & Gjerde, 2000) that include the biological, ecological, sociological importance. In other words, for the traits to be considered in the breeding goal should meet the economic and ethical importance that makes breeding program more holistic prospective. Also, as the non-economic factor, some of them already fetch a price. For example, the fillet fat and fillet color which are the critical standard to grade the fish. The breeding goals frequently different among species, among countries, but for fish, the most common traits with high economic importance with longer stability in the market are growth rate, food conversion ratio, mortality, fillet yield, and early sexual maturity. After the definition of breeding goal has been established, the selection criteria should be considered.

2.2.1 Growth rate

As Atlantic salmon is marketed by its flesh product, the highest economic importance trait is growth rate. Two measurements, on the body weight and body length, can be used as the indicators of growth rate. However, harvest body weight (HBW) is directly influencing the price paid to industry, and also body weight doesn't have to be measured on each single fish compared to the measurement on the body length, which makes measurement more effective. Thus, frequently body weight has been used as the indicator of growth rate. In today's rearing practice, the smolts are transferred to sea cage in spring around 16 months after hatching (1+ smolts) or around 8 months (0+ smolts) during autumn (Duston & Saunders, 1995; Thrush, Duncan, & Bromage, 1994). The completion of smoltification of 0+ smolts depends on the growth that is gained by the heated water and longer photoperiod (Kristinsson, Saunders, & Wiggs, 1985; Thorpe, Adams, Miles, & Keay, 1989). Although, some studies have shown that there is no significant change on the feed utilization and product qualities between 1+ smolts and 0+ smolts (Mørkøre & Rørvik, 2001; Roth et al., 2005), the overall benefit of the out-of-season smolts (0+ smolts) still need to be further tested.

At present, the weight of Atlantic salmon at harvest time is vary, ranged between 4-8 kg. Optimal management of fish farm to arrive optimal gain involves the calculating optimal level of production variables in terms of initial stocking numbers and size of the smolt, feeding method and harvest time, taking into account local climate, sea water temperature and sunlight exposure. Body weight until harvest body size is a trait with moderate heritability and ranged from 0.2-0.3 in 2-3 years of Atlantic salmon (Gjerde, Simianer, & Refstie, 1994; I Olesen, Gjedrem, Bentsen, Gjerde, & Rye, 2003; Quinton et al., 2005). However, other commercially important traits that correlated with body weight also need to be considered, otherwise it may bring unexpected correlated side effects on carcass quality and health trait (Kankainen et al., 2016). The effects of selection for increased body weight on other economically important traits is not fully understood and need to be considered when applying selection for several traits.

2.2.2 Fillet yield

Fillet yield (FY) is the ratio of the fillet weight and carcass weight, it shows a large variation about 62-69% in Atlantic salmon (salmon salar) (Powell, White, Guy, & Brotherstone, 2008). In addition to the body weight, the fillet yield is an important criterion on which the processing company pay for the fish, because the fillet is the most valuable products in salmon. However, the price per kg for the fillet is generally determined its weight and quality like fat content and fillet color, which means those product qualities should be included in most breeding programs as an apart of selection criteria (Gjedrem, 1997; Rutten, Bovenhuis, & Komen, 2004; Sapkota, 2010). Fillet color is important for grading the fillet quality, the retailers will downgrade or reject to buy the inferior color fillet. However, the fat content in salmon is essential for the texture and flavor but not related with fillet yield and the chemical analysis on fillet fat is consuming and costly (Van Sang, Thomassen, Klemetsdal, & Gjøen, 2009). With the technology improvement, most industries use the filleting machines instead of the hand-filleting. Modern filleting machine is fast, effective, can be adapted to specific species. However, the disadvantage is the shape and size beyond the scope of machine that is designed before will result in reduction of fillet yield or even worse the machine and fillet will be damaged. From the perspective of economic loss, the whole processing loss was arrived to around 31-35%, including around, 16.8-23.8% was from filleting process and 10.7-12.4% loss was from trimming (Rora, Morkore, & Einen, 2001). Large variance in fillet yield output and in the heritability, which ranged from 0.05-0.17 (Powell et al., 2008; Tsai et al., 2015), indicate potential improvement of grading and selection on fillet yield.

2.2.3 Early sexual maturity

If fish become sexual mature before desired harvest size, called early sexual maturity (ESM) is a problem for Atlantic salmon farm. Early maturity lead to economic losses, in New Brunswick Canada, 12% grilse caused \$11-\$24 million losses, the total gross revenue was \$250 million, in 2002 (McClure et al., 2007). In the early stages of sexual maturation, fish appetite increases, energy is accumulated. To the contrary, later in maturation, appetite decreases. Thus, the energy source of the body now is taken from the viscera and the meat of the fish. It leads the fillet fat and protein content is decreased by 3-7%-units, produce the poor meat quality (Aksnes, Gjerde, & Roald, 1986). In farmed Atlantic salmon, the trait early sexual maturity may happen during the first wither in the sea (jacks) or after one winter in the sea (grilse) while the trait normal sexual maturity happens after two winters in sea. The early maturation is attributed to many factors, like nutritional, water temperature, and photoperiod and so on. Male fish tend to be more precocious than female fish, because higher threshold size is found on the female fish (Adams & Thorpe, 1989). From nutritional perspective, the higher water content moist feed is associated with becoming grilse (McClure et al., 2007), and extra 0.3% phosphorus in feed is found to decrease the early maturation rate (Fjelldal, Imsland, & Hansen, 2012). In addition, the continuous light (LL) on the sea cages during winter and spring also used to reduce the rate of early maturation

(Hansen, Stefansson, & Taranger, 1992; Taranger et al., 1999). Conversely, the good growth during first summer in sea brings the higher grilse proportion (Duston & Saunders, 1999). For the present studies, not only the early maturation proportion in grilse is available, but also the estimation of the genetic parameters of this trait is carried out, but both are very variable from one study from another study. Heritability, for instance, is varied considerably from 0.07-0.34 (Gjerde et al., 1994; Wild, Simianer, Gjøen, & Gjerde, 1994). Above information indicate that the optimization of the early unwanted sexual maturity needs to be improved, not just only for economic reasons but also about for animal welfare issue.

2.2.4 Feed conversion ratio

In fish species, feed cost makes up more than half of the production costs per kg of fish produced. Changes in this cost item are therefore of great importance for the development in production cost per kg fish. According to the Norwegian aquaculture data survey over one year (2014-2015) , the average feed cost per kg of fish produced increased by 12.8% ("Økte kostnader ga redusert lønnsomhet i 2015," 2016). The increase in feed costs per kg is primarily due to an increase in the average feed price in the same period. The most effective and simplest indication of the feed utilization is feed conversion ratio (FCR) that is the ratio between the feed eaten and fish produced (Dvergedal, Ødegård, Øverland, Mydland, & Klemetsdal, 2019), like shown in following formula:

$$(2) \qquad \text{FCR} = \frac{\text{Feed eaten}}{\text{Fish produced}}.$$

Atlantic salmon has low FCR (around 1.3-1.5) with the heritability around 0.2 (Aas, Ytrestøyl, & Åsgård, 2019; Einen & Roem, 1997; Omasaki, Janssen, Besson, & Komen, 2017) . The reasons for low FCR are maybe because fish feed have a high energy content and salmon are very efficiently user of protein and amino acids contained within the protein and essential fatty acid (Lall & Tibbetts, 2009). FCR is a combination function including animal genetics, age, feed quality and ingredients, farm management, and so forth. FCR in small fish is generally lower than older fish, because of relatively high speed of growth: good quality with high protein content feed, bring a lower FCR, can be used to feed more fish; using the continuous light (LL) also can improve the salmon FCR (Nordgarden, Oppedal, Taranger, Hemre, & Hansen, 2003). In summary, the selection and feed optimal profitability can be improved through FCR. However, it is difficult and costly to calculate uneaten feed to estimate feed intake by per fish. The measurement on the feed consumption in family is possible but costly, while to obtain individual feed intake is not possible (Houlihan, Mathers, & Foster, 1993). Thus, using indirect selection through selection for other traits correlated with feed conversion ratio is preferable.

2.2.5 Mortality

Sustainable management of fish farming requires the potential to overcome all stages of fish development, including eyed eggs, juvenile rearing, and adult Atlantic salmon. Infectious diseases and non-infectious disorders affect the fish at each life cycle, causing mortality with inevitable economic losses. It is not possible to quantify the economic loss of diseases purely from mortality rate, because the low appetite and growth rate caused by the sickness of fish, the waste of feed, the treatment of infected fish and even the removing of dead fish have indirectly caused large number of economic losses.

Mortality of juvenile during fresh-water phase

In 2019, the number of losses juveniles was 100 million out of 482 million hatched eggs ("Atlantic salmon, Rainbow trout and Trout - Juvenile production," 2020b). The most sensitive stage is from hatching to juvenile, with the highest organ development and growth rates. Any unfriendly condition in living density, feed ingredients and water environment, may push beyond juvenile tolerance: From rearing density aspect, the juvenile of Atlantic salmon is strongly territorial, salmon fry appears to distribute quickly and evenly over the nursery area after spawn. Such fierce competition will result in death for the vulnerable fry in site or on the way of immigration (Gee, Milner, & Hemsworth, 1978); Lack or excesses of any nutrient content, like vitamins, proteins and fats maybe make fish in the condition of predisposing of infection through impairment skin and tissue and reduction on muscle secretion (Lall & Tibbetts, 2009). Too high water temperature adversely affect the growth rate of juveniles, thereby decreasing overall productivity of Atlantic salmon (Swansburg, Chaput, Moore, Caissie, & El-Jabi, 2002). In general, the implementation of management policy of fresh-water phase is important, because ensuring the healthy growth of juveniles not only reduces mortality and economic losses but also contributes to salmon growth in the following grow-out stage (Gee et al., 1978).

General mortality during grow-out phase

The entire salmon production line encompasses juvenile production, grow-out production and processing. This implies that there is a need for transfer the fish to the next stage of farming. It is achieved by moving fish to well boat from fresh-water ponds to sea locality, and again being moved to well boat to the processing industry on shore after fish reach the harvest size. The Norwegian aquaculture statistics showed that the annual loss during transportation was on average approximately 10 % over the 12 years (1994-2006) and even higher (21 %) in Scotland (Aunsmo et al., 2008). The exact cause of death during transport is not yet known, it could diseases or die from accident and aggressive behavior due to physiological stress response, due to higher densities (over 200 kg/m^3) and water degradation at el. Such death from unknown causes, named general mortality, also occur throughout the following grow-out phase. In Norway, up to 12 % of the yearly losses for 1997-2007 were reported as non-specific mortalities (Waagbø, 2008). For the individual farm, cause of the fish's death cannot be determined because of the complexities of the etiology. However, larger aquaculture companies have more detailed data of their own, but those data are not open to the public.

Specific mortality during grow-out phase

The death from a particular disease maybe defined as a specific mortality. During the year of 2017, the dead fish physically taken out from sea cage was up to 53 million, including the fish dead from disease and injury, and it was accounted for 88% of sea-cage losses (Svendsen & Fritsvold, 2018). The ways and causes of disease infection vary and cannot be counted precisely. Transportation, for example, is the one of the high-risk factors for spread of diseases for post sea-transfer salmon, because latent disease is hard to be identified before the fish are released into sea-cage. The bacterial disease, furunculosis, and the viral diseases are the main causes for the high mortality; the most common viral diseases are infectious salmon anemia (ISA), cardiomyopathy syndrome (CMS), infectious pancreatic necrosis (IPN), pancreas disease (PD). CMS is a severe cardiac disease for farmed Atlantic salmon and will cause large economic losses, because it normally affects the large fish that are in the second year in sea-cage and infected fish will die suddenly without any clinical signs (Wiik-Nielsen, Alarcón, Fineid, Rode, & Haugland, 2013). Since the PD first found in the Scotland in 1976, it has been revealed that there are six virus subtypes that can cause PD and Salmonid alphavirus SAV2 and SAV3 are the main virus affect salmon in Norway. Norwegian fish farm lose 55.4 millions of kronor due to outbreak of PD in 2013 (Hjeltnes, Walde, Bang Jensen, & Haukaas, 2016). The condition of the fish infected by ISA and IPN is inverse, because the mortality during the IPN-outbreak reaches as high as 90% while it during the ISA-outbreak is very low like daily mortality is 0.05-0.1 (Hjeltnes et al., 2016). But ISA cause severe fish welfare problem and waste a lot of feed by feed the sick fish.

Sea Lice

The sea lice are a greatest challenge for Atlantic salmon during grow-out phase. The salmon lice will raise the risk of problem on the osmotic balance and salt balance by damaging the physical barriers when the fish are transferred from fresh-water ponds to the sea-cage farm (Muhammed, 2018). Due to the development of chemistry, the drugs for sea lice are developed well to prevent from the spread. High number of lice not a problem today. The problem relates to the low action limit (less than on average 0.5 adult female lice) that results in frequent delousing events and mortality and thus an animal welfare issue (Hjeltnes et al., 2016).

So far, vaccines for many viral diseases have been developed (Caruffo, Maturana, Kambalapally, Larenas, & Tobar, 2016; Ding, 2019; Jensen, Kristoffersen, Myr, & Brun, 2012). While the specific reasons for why the fish, especially those being vaccinated for some diseases, become infected are unknown. Some studies have shown that cardiac diseases, for instance, are more likely exposed in high density and stressing feeding condition (Vassgård, 2017). Moreover, whatever the vaccines or the drugs were developed with many negative side effects related to carcass quality and welfare aspects (Caruffo et al., 2016; Trimonyte, 2016). Therefore, no matter what kind of disease has occurred in any fish life cycle, the effective control and even reduction of the occurrence of the diseases will enhance fish welfare and fish farm profit simultaneously.

2.3 Relationship among the traits

Relationship between two traits could be expressed by the correlation. It is a statistic analyzing method used to study the strength of two continuous variable traits, expressed as:

(3) $$\text{Correlation} = \frac{\text{cov}_{(x,y)}}{\sigma_x \times \sigma_y},$$

where the cov(x,y) is the covariance of trait x and trait y, σ_x is the standard deviation of x and σ_y is the standard deviation of y. The covariance is a linear relationship that describes how two traits change together, increasing on one trait may influence another trait to increase or decrease. The correlation also could be expressed by the genetic correlation and phenotypic correlation. Phenotypic correlation determines that if a fish with high value of one phenotypic will have high or low phenotype value for another trait. The phenotypic correlation is sum of the additive genetic and environmental effect. Genetic correlation illustrates how the genetic values for two traits associates. In the other words, a gene mainly effects one trait, but normally this gene also effects other traits. Another condition is when two genes are linked together on the same chromosome will causes genetic correlation.

However the neither the genetic correlation not the phenotypic correlation for many traits in the fish breeding are still not clear or unreliable. Eventhough, the body weight, for example, as the most economically important trait have studied until now still has a lot of uncertainty correlation with other traits like the phenotypic correlation between body weight with early secual maturity and specific mortality, like ISA PD et al. Because of lack of data about general mortality fish, the correlation of it with body weight is unclear. According the research from Tsai et al. (2015) the phenotypic correlation between body weight and fillet yield was 0.35 and genetypic correlation was 0.02. The genetic and phenotypic correlation between body weight and early sexual maturity was 0.49 and 0 respectively, but there was larger standard error (±0.56) (Gjerde et al., 1994). The mean family (number of family was 28 with 30 fish per family) correlation between harvest body weight and feed conversion ratio was 0.79 (Thodesen, Gjerde, Grisdale-Helland, & Storebakken, 2001). Thus, the genetic correlation between them were higher when more family or fish per family invloved. Except those correlation, the relationships among other traits are unknown.

2.4 Derivation of economic value

The economic weight or value of a trait reflects the contribution to change in profit per unit change in the trait while keeping the other traits constant (Shook, 2006). The is to maximum economic improvement for all the traits included in the breeding objective and is obtained through selection index on which the animals are selected (Gibson & Kennedy, 1990). The relative contribution of each trait to the overall index is determined by their economic weight, the heritability, the phenotypic and genetic covariance among the traits. In other word, economic weight determines the distribution of the selection response among traits, and the number of phenotypic records on per trait. The increasing weight on one trait implies a decreasing the weights on the other traits and thus redistribute the trait responses among the traits. Derivation of the economic value by using profit equation is the most common method and has been applied for some aquaculture species (Besson et al., 2014; Janssen, Berentsen, Besson, & Komen, 2017; Omasaki et al., 2017). Bio-economic models are more suited to estimate the economic values, because it gives a better description on the relationship in different levels, including trait level, cage level and farm level (Besson et al., 2014).

2.5 Bio-economic model

Bio-economic model simulates the situation an annually operation of a farm, including three hierarchical structure: fish model, cage model and farm model (Janssen et al., 2017). The information for the fish model is the inputs of the fish situation that are including stocking date, stocking weights, weekly temperature of sea water. The outputs of the fish model are the mean and total body weight in per week, harvest date, the number of fish that dies due to unknown causes (general mortality) and specific diseases (specific mortality), and early sexual mature fish. Inputs of the cage model is made up of the outputs of fish model, cage volume and feed price. Outputs of it are number of fish harvested, total harvest body weight, feed cost. Inputs of the farm model are formed from the outputs of the cage model, cage numbers, price of smolts, price of different classes of round body weight and fillet yield, fixed cost. Outputs of the farm level model are the numbers of fish, total harvest body weight, total smolts used at stocking, feed cost, fixed cost, revenues in farm level and marginal change for one production cycle from stocking day to harvesting day. The economic value for a trait can be obtained as the partial derivative of a profit function with respect to each of the trait (Komlósi et al., 2010), or by change in the overall profit due to a small change in each of the trait, one at a time.

2.6 Prediction of breeding value

2.6.1 Prediction response

The selection response per generation (ΔG) is the change in the population mean in the desired or not desired direction. For a single trait this can be written as:

(4) $\Delta G = i \times r \times \sigma_A$,

where i is the selection intensity, r is the accuracy of selection and σ_A is the additive genetic standard deviation of the true breeding values. Thus, the predicted selection response is directly proportional to each of the three parameters.

2.6.2 Selection strategies

Purebreeding is the selection strategy for obtaining selection response due to additive genetic effects over a long period of time within the breeding nucleus population. The individuals with higher breeding value are selected as parents for next generation. Additional genetic gain may be obtained at the multiplier level through non-additive genetic effects that may be capitalized due to some crossbreeding strategies. The true breeding value of the individual is not known, the prediction of it can be obtained based on measured phenotypic values of the traits on the breeding candidates or on their relatives, e.g., full- and half-sibs.

2.6.3 Selection methods

The available selection methods for fish breeding are individual selection, sib (family) selection and within family selection, or a combined of these methods. The accuracy and the selection response predicted by given set of genetic parameters could be the criteria of the efficiency of the selection methods. Individual selection is a type of method that breeding candidates selected based on their own performance. The greatest advantage of individual selection is its simplicity. However, it can only be applied for the traits with medium to higher heritability and that can be recorded on the alive breeding candidates. For traits with low heritability, either discrete traits or traits that cannot be measured on the candidates while still alive, sib selection or genomic selection (López, Neira, & Yáñez, 2015) is to be used. In principle, the combined sib and within family selection is always the best option, because it collects all available information from on animal itself, full- and half-sibs. The high reproductive capacity makes sib selection important for fish breeding, as different subsample of fish from each of the families can be tested for different traits (e.g., specific disease challenge tests, or in different type of rearing environments) and a large number of breeding candidates per family that allow for high selection intensities. The larger number of tested fish implies high selection accuracy and high selection intensity but also high rate of inbreeding and thus loss of genetic variation and inbreeding depression (Meuwissen, 1997). For traits impossible or difficult and costly to record (e.g., feed efficiency) an option is to select for a correlated trait such as growth rate, which is called indirect selection method.

2.6.4 Best Linear Unbiased Prediction (BLUP)

The ultimate goal for all selection methods is to maximize the accuracy of selection, i.e., to maximize the correlation between the true and the predicted breeding values. Different genetic evaluation procedures are used to derive predicted breeding values. The Best Linear Unbiased Prediction (BLUP) is the most powerful procedure. In BLUP, the fixed effects like environment condition and random effects like breeding value are obtained simultaneously, and the variances of the population parameters are assumed to be known (Haffray et al., 2018).

2.7 Mating design

A good long-term breeding program should include maximization of the long-term overall breeding goal at an acceptable rate of inbreeding. Accumulated inbreeding reduces fitness of fish, performance of traits and genetic variability. For a fish finite population, breeding scheme inevitably cause inbreeding to some extent. The implementations of the reduction of inbreeding rate can be executed from several aspects, for example the increasing of effective number of parents and individuals and appreciate mating design. The different mating design result in different selected candidates and effective population and bring different inbreeding rate. Nowadays, four kinds of mating designs used, they are full factorial (D'agaro, Woolliams, Haley, & Lanari, 2007), partial factorial (Dupont-Nivet, Vandeputte, Haffray, & Chevassus, 2006), nested (Dupont-Nivet, Vandeputte, & Chevassus, 2002) and single pair mating (Engström, McMillan, McKay, & Quinton, 1996). However, a 2x2 factorial design may be a more efficient design under some conditions (Dupont-Nivet et al., 2006) but in some conditions it is not (Dupont-Nivet et al., 2002). The nested mating design, one male mated with two females, is the most commonly used in fish breeding plan. Comparing to the full factorial mating method, nested mating makes it possible to produce same numbers of offspring by using more males, the greater the sires the greater the accuracy and more precise the heritability.

2.8 Testing strategy

The purpose of the test fish is through phenotypic trait records obtain more accurate breeding values of the breeding candidates. Important pre-requisites are reliable data obtained on fish reared under as optimal and similar environmental and feeding conditions. The testing environment should be similar to a common and commercial environment with respect to e.g. water temperature and rearing density (Bentsen, 1990). The death fish should be counted including time of death. In specific challenge tests the surviving fish should not be considered as breeding candidates as they maybe carrier of the actual disease. Therefore, their untested breeding candidate are to be selected as the parents for the next generation.

3. Materials and Methods

3.1 Developing of the economic model

3.1.1 Input data of the farm

The assumed farm was a rescaling of an actual farm with two grow-out localities, one with MTB of 3900 tonnes that is calculated by five licenses multiplies by 780 tonnes per licenses, and the other with MTB of 3120 tonnes that means four licenses multiplies by 780 tonnes per license. Eight cages on the first locality and five cages on the second one, each cage with a circumference of 157 m and the volume is 30 000 m^3. The farm released the total of 2.4 million 0+ smolt with mean weight varying from 90 to 200 g into the 13 cages of two localities. The two main constraints are not higher biomass on the locality than the given MTB, and not more than 15 kg fish/m^3 in any of the cages. According to two constrains, the first time of slaughtering is about 12 months after stocking and finish in the December or January around 15 or 16 months after stocking.

The assumed farm used in this study has two cages, each of them with 30 000 m^3 and the 157 m circumference. The stocking numbers of +0 smolts for each cage were 200 000 with an average body weight of 150 g. The stocking date was in the week 14 for cage 1 and week 18 for the cage 2. The total MTB for two cages was calculated on the basis that the grow-out locality of the mentioned above farm locality has five cages with four licenses each of 780 tonnes MTB. The MTB for two cages was, therefore, 1248 tonnes. The harvesting constrains were illustrated followed:

- When the fish density of each cage exceeds the maximum fish density (20 kg fish/m^3) then 30% of the fish will be harvested.
- When the average body weight of the fish reaches the maximum of 10 kg then harvest all fish.
- The last harvesting time was on the week 51 of the second year.

The inputs of the simulation statistics included the following data:

- The weekly seawater temperature over the grow-out period (Figure 1).
- The accumulated proportion of the mortality (Figure 2 and Figure 3).
- The proportion of the sexual mature fish in week 30.
- The growth rate determined by the growth factor and temperature (Figure 4).
- The price (NOK) per kg round body weight for different body weight classes (Table 1).

Throughout the rearing period, the standard sea water temperature fluctuated between 4°C to 14°C and originate from a similar rearing period at Akvaforsk (now Nofima) Marine Unit at Averøy, Møre and Romsdal. As shown on Figure 1, temp(0) represented the standard temperature, temp(-1) showed a 10 % decrease in temperature, and temp(+1) was a 10 percent increase. The YearW represented the year and the week of the year in cages.

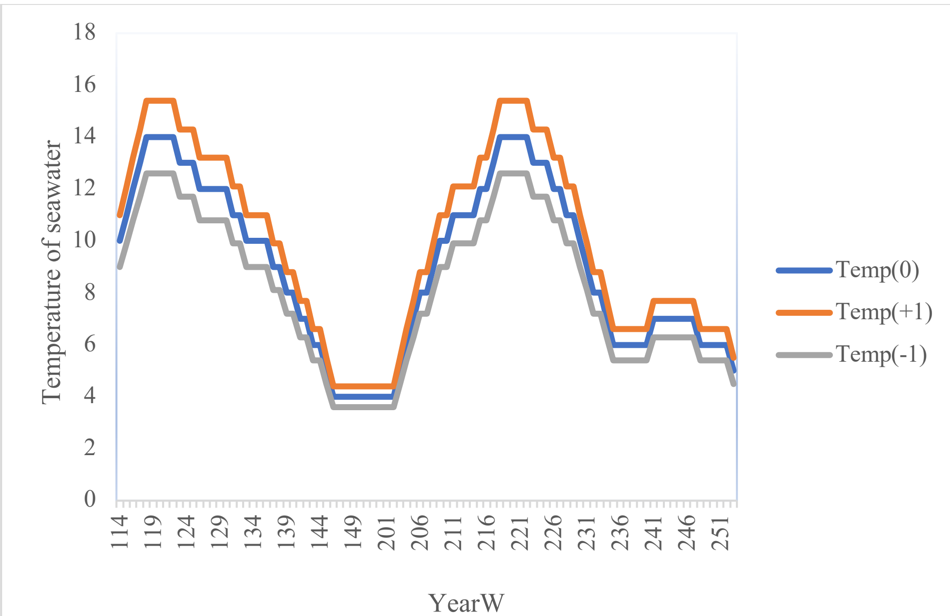

Figure 1. The standard seawater temperature and with its marginal changes on the temperature.

The accumulated proportions of the general mortality and specific mortality for the two cages are showed in Figure 2 and Figure 3, and represent assumed and not observed mortality rates at a specific farm. The general mortalities for each cage were documented from first week, whilst the specific mortalities occurred from 53rd week of the first year.

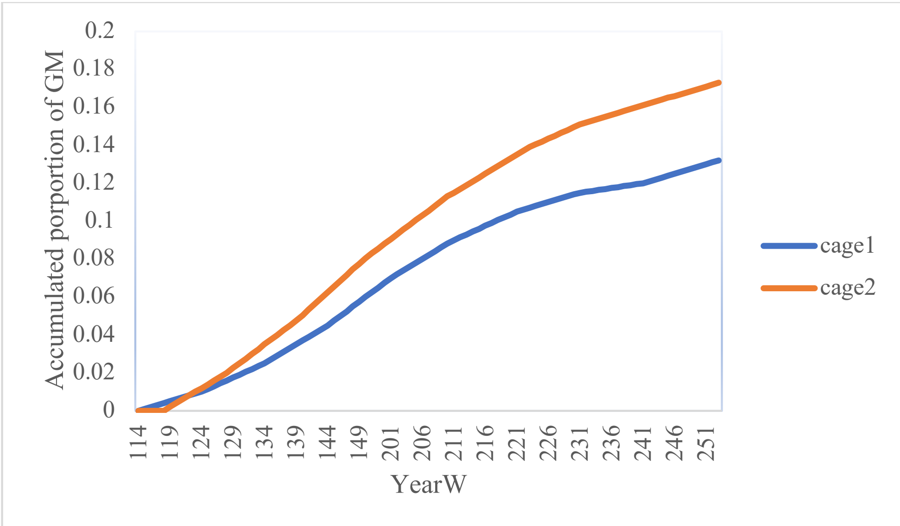

Figure 2. Accumulated proportion of general mortalities in the two cages.

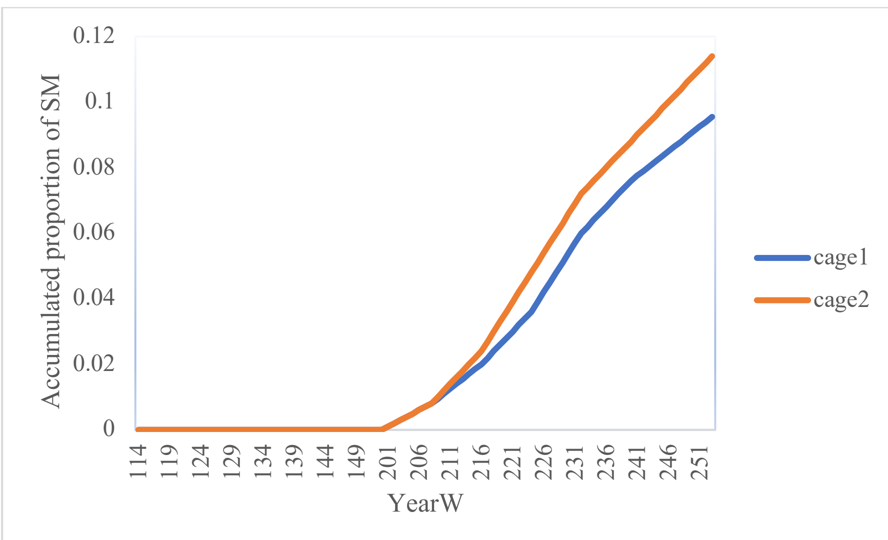

Figure 3. Accumulated proportion of specific mortalities in the wo cages.

The proportion of early sexual maturity ratios for cage 1 and cage 2 was 0.1 and 0.075 respectively.

For a fixed growth factor, three different growth curve were assumed one for each of the three temperatures, temp(0), temp(-1) and temp(+1), as illustrated in the Figure 4.

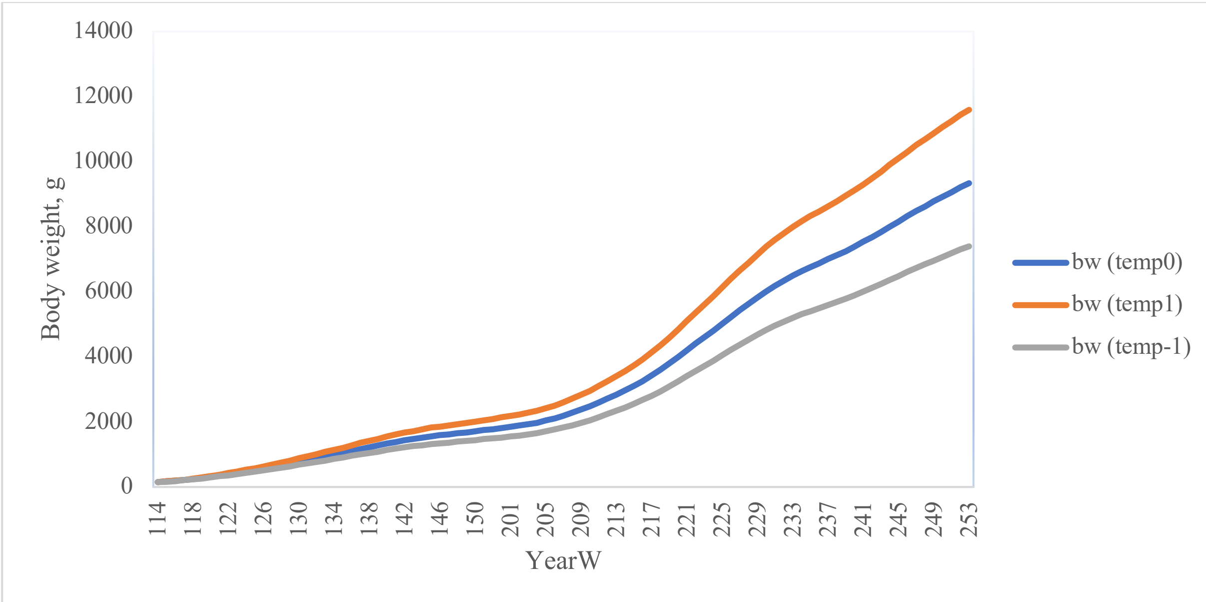

Figure 4. Increase in body weight under different temperatures with growth factor growth factor = 2.7.

The fillet yield and the price per kg round body for different body weight classes are shown in Table 1.

Table 1. The prices (NOK/kg) for different classes of round body weight and fillet yield.

Mean RBW	**Fillet yield**	**Price** (Nok/kg RBW)	**Price** (NOK/kg fillet)
0.5	0.6	0	0
1.5	0.64	30.57	47.77
2.5	0.647	33.17	51.27
3.5	0.654	38.58	58.00
4.5	0.661	42.01	63.56
5.5	0.668	44.77	67.02
6.5	0.675	52.75	78.15
7.5	0.682	55.94	82.02
8.5	0.689	58.78	85.31
9.5	0.69	52.93	76.71
10.5	0.69	52.93	76.71
11.5	0.69	52.93	76.71

RBW: round body weight.

3.1.2 Developing of the bio-economic model

The bio-economic model is made up of 3 parts, the fish model, cage model and farm model. The processes of each model completion involve the description of inputs and outputs from fish model to farm model. The output of the fish model is the input of the cage model and the output of the cage model is the input of the farm model. Finally, combined all the above data can calculate the profit in farm level. The parameters of each model are showed in the Figure 5.

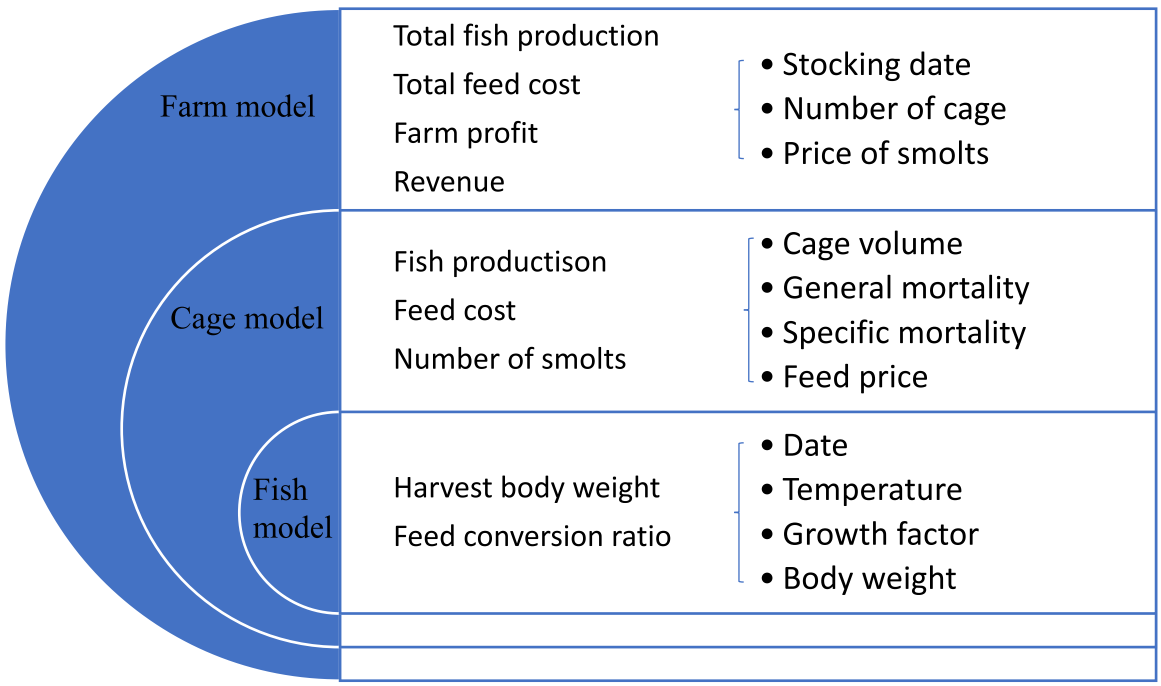

Figure 5. The schematic overview of the bio-economic model (Janssen et al., 2017).

<u>Fish model</u>

Seasonal variation in weekly seawater temperatures during the whole year affect the growth rate, which in turn affects the harvest body weight (kg). The harvest body weight is defined as:

$$\text{(5)} \qquad HBW_{[i,\,j]} = \frac{N[i,j] \times \text{proportion of harvest} \times BW[i,j]}{1000},$$

where i stands for the recorded time of the year, and j represents the cage. $N_{[i,\,j]}$ is the number of the fish in the cage 1 or cage 2 from the beginning until the time i. Analogous to $N_{[i,\,j]}$, $BW_{[i,\,j]}$ is the accumulated body weight until time i. The $N_{[i,\,j]}$ is from the equation of

(6) $N_{[i, j]} = N_{[i-1, j]} - N \text{ of } ESM_{[i, j]} - N \text{ of } GM_{[i, j]} - N \text{ of } SM_{[i, j]}$,

where the N of ESM, GM, SM is the number of early sexual maturing fish, general mortality fish and specific mortality fish, respectively.

The model to describe $BW_{[i,j]}$ is:

(7) $BW_{[i,j]} = \left(\frac{GF}{1000} \times temp_{[i, j]} \times 7 + BW_{[i-1,j]}^{\frac{1}{3}}\right)^3$,

where $BW_{[i-1,j]}^{\frac{1}{3}}$ represent the cube root of accumulated body weight until previous week *i*. Temp is the average weekly temperature (°C). GF is the abbreviation of grow factor.

The body fat of the fish was assumed to increase with body weight of the fish according to the following equation (B. Gjerde, personal comment.):

(8) $\text{Body fat} = b_1 + \frac{b_2 \times BW_{[i,j]}}{1000} + \frac{b_3 \times BW_{[i,j]}^2}{1000\,000}$,

where b_1 (6.21 %) is intercept fat of the fish at stocking time, b_2 (3.38 %) and is b_3 (-0.21 %) are the regression coefficients of the 1st and 2nd degree polynomial of the body fat on body weight respectively, i.e., the curvilinear increase in percent body fat per kilogram increase in body weight.

The feed conversion ratio (kg) was assumed to increase with increasing body fat (%) according to the following equation:

(9) $FCR = b_1 + b_2 \times \text{Body fat}_{[i, j]}$,

where the intercept $b_1 = 1.1$ is the FCR at stocking and b_2 is the increase in FCR per %-unit increase in body fat.

<u>Cage model</u>

The mortality of each cage includes two parts, the general mortality and specific mortality.

The number of dead fish due to general mortalities was calculated as:

(10) $N \text{ of } GM_{[i, j]} = N_{[i-1, j]} \times \text{proportion of } GM_{[i, j]}$.

The number of dead fish due to specific mortalities was calculated as:

(11) $N \text{ of } SM_{[i, j]} = N_{[i-1, j]} \times \text{proportion of } SM_{[i, j]}$.

The number of early sexual maturing fish was calculated as:

(12) $N \text{ of } ESM = N_{[i-1, j]} \times \text{proportion of } ESM_{[i, j]}$.

We assumed that the price for per kg feed is 11 NOK. The total price (NOK) of used feed is:

(13) Price of feed = price per Kg × total feed,

where total feed is for the whole production cycle for per cage, e.g., is the sum of the feed consumed by the harvest fish, the dead fish and the fish that were early sexual mature. Thus, the total feed could be estimated from the following formula:

(14) $\text{Total feed}_{[i, j]} = \text{Feed harvested}_{[i, j]} + \text{Feed dead fish}_{[i, j]} + \text{Feed ESM}_{[i, j]}$.

Farm model

The derivation of the farm model is:

(15) Farm profit = Revenue from the harvested fish – Smolt cost – Feed cost – Fixed cost,

where fixed cost in the profit equation that we assumed was 24 NOK/kg of Atlantic salmon, includes transport, operating cost and labor cost, etc. except smolt cost and feed cost according to the reports from FISKERIDIREKTORATET(2020). According to the market in Norway, price of smolt was around 10 NOK/smolt in 2019 ("Atlantic salmon, Rainbow trout and Trout - Juvenile production," 2020a). The price of feed we assumed is 11 NOK/per Kg feed. Fixed cost, smolt cost are assumed to be not influenced by the genetic change of the traits.

3.1.3 The derivation of economic values

The economic value (EV) for each trait was expressed per kg of fish produced as:

$$(16) \qquad EV = \left(\frac{Profit_A - Profit_B}{Trait_A - Trait_B}\right)/\text{fish harvested}_B,$$

where the subscripts illustrate before (B) and after (A) are the marginal (1%) change in the actual trait. Fish harvested_B is the sum of the total harvest body weight.

The growth factor is not an appropriate breeding objective trait as the revenue comes from the amount (kg) of harvested fish. Therefore, a marginal increase in the growth factor was converted into a marginal increase in the mean harvested body weight and thus to the economic value for the body weight was shown as:

$$(17) \qquad EV_{bw} = \left(\frac{Profit_A - Profit_B}{meanbw_A - meanbw_B}\right)/\text{fish harvested}_B,$$

where the $meanbw_A$ and $meanbw_B$ was the mean body weight after and before a marginal change in a growth factor. Fish harvested_B is as defined in formula (16).

3.2 Prediction on the genetic gain

3.2.1 Structure of the breeding program

Assume was a selective breeding program with a total of 300 full-sib family group (the offspring of 150 sires and 300 dams), with a total group of 12 000 breeding candidates (20 males and 20 females per family). Based on the data recorded on the breeding candidates and 6 000 test fish (20 fullsibs of the breeding candidates from each of the 300 families) (see Appendix), breeding candidates with high breeding values, i.e. the top 5 % males (in total 150 males, through truncation selection of the overall estimated breeding values for all traits) and the top 10 % females (in total 300 females, through truncation selection of the overall estimated breeding values for all traits), were selected among the breeding candidates to become the parents of the next generation. In total, 6 000 (10 males and 10 females) sexual mature candidates were selected as breeders (see Appendix). Both of the candidates and breeders were reared in a commercial net-cage grow-out environment. The structure of the baseline breeding program is shown in Figure 6.

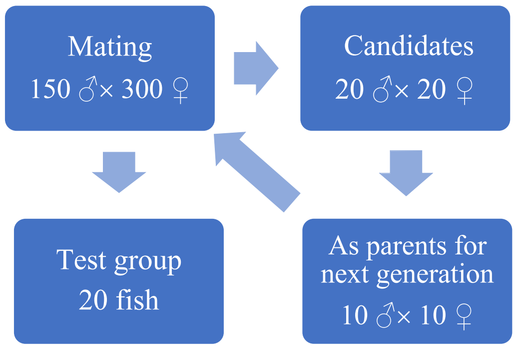

Figure 6. Schematic overview of the baseline breeding program.

Identical index for sires and dams as all traits were recorded on both sexes and with no sex effect on the trait. As illustrate in the Table 2, it was assumed that the body weight, general mortality and early sexual maturity could be recorded on both the breeding candidates and test fish, and that fillet yield, specific mortality and feed conversion ratio (feed intake) could be measured on the test fish only.

Table 2. Illustration of the index of the traits.

	Candidates	Test fish
Harvest body weight	√	√
Fillet yield	×	√
General mortality	√	√
Specific mortality	×	√
Early sexual maturity	√	√
Feed conversion ratio	×	×

3.2.2 Genetic parameter of traits

The assumed mean value and phenotypic and genetic parameters of the studied traits are shown in Table 3. For harvest body weight in Atlantic salmon there are many published estimates of heritability (Gjerde et al., 1994; Quinton et al., 2005), but few for early sexual maturity (Wild et al., 1994), filet yield (Powell et al., 2008) and feed conversion ratio (Omasaki et al., 2017), and none for general and specific mortality in the seawater phase. With respect to phenotypic and genetic correlations among the studied traits there are very few published estimates.

Therefore, the set genetic parameters in Table 3 and 4 are to a large extent chosen based on the experience of Professor Bjarne Gjerde. The parameters of three either or traits general mortality, specific mortality and early sexual maturity were assumed to be defined on the non-observable liability scale with a phenotypic variance of 1.0. This was done so that the heritability for the traits do not need to be changed when the mean value of the trait changes.

Table 3. Traits and their relevant mean values, phenotypic variances and heritability.

Traits	Mean value[1]	Phenotypic variance	Heritability
Harvest body weight (kg)	4.5	1.25	0.25
Fillet yield (%-units)	65	16	0.05
General mortality (%-units)	12.6	1	0.1
Specific mortality (%-units)	6.0	1	0.09
Early sexual maturity (%-units)	8.5	1	0.25
Feed conversion ratio (kg feed/kg fish)	1.1	0.09	0.2

The superscript 1 means the mean values are assumed.

Table 4. The genetic correlation (above the diagonal) and phenotypic correlation (below the diagonal) between the studied traits.

trait	HBW	FY	GM	SM	ESM	FCR
HBW		0.02	-0.20	0.00	0.49	-0.60
FY	0.35		0	0.20	0	0
GM	-0.20	0		0	0	0
SM	0.00	0	0.2		0	0
ESM	0.00	0	0	0		0
FCR	-0.60	0	0	0	0	

HBW= harvest body weight; FY = fillet yield; GM = general mortality; SM = specific mortality; ESM = early sexual maturity; and FCR = feed conversion ratio.

3.2.3 Prediction of the genetic gain

In this study, the overall breeding goal or the aggregate genotype (H, in monitoring units, in this case NOK) is a linear function of the true breeding value of six trait weighted by their economic values:

(18) $H = V_1A_1 + V_2A_2 + \ldots\ldots + V_6A_6$,

where the A's are the true breeding values and the V's the economic values for each trait. As the true breeding values and H cannot be known, an estimate of the A's (EBVs) and H (I) was obtained from a multi-trait selection index through the SelAction software (Herselman & Olivier, 2010), then:

(19) $I = b_1P_1 + b_2P_2 + \ldots\ldots + b_6P_6$.

where P's are the phenotype of the traits and the b's are regression coefficients or the weights to be given to each source of information that maximizes the correlation between the overall all true (H) and estimated (I) breeding value.

SelAction software provide the predicted genetic gain of the overall genotype (ΔG) through the following equation:

(20) $\Delta G = i \times r \times \sigma_A$,

where *i* is the selection intensity, r is selection accuracy and σ_A is the additive genetic standard deviation of the selection index (I). The I was assumed to be normally distributed, then *i* can be simply derived from the proportions of individuals that is selected as parents and offspring.

The change on curve for the different magnitude of genetic gain, $\Delta G_0 < \Delta G_1 < \Delta G_2$, showed in the Figure 7. When the ΔG become smaller after genetic improvement, then the curve will move to the left direct, and if the ΔG become bigger than it was before then the curve will move to the right.

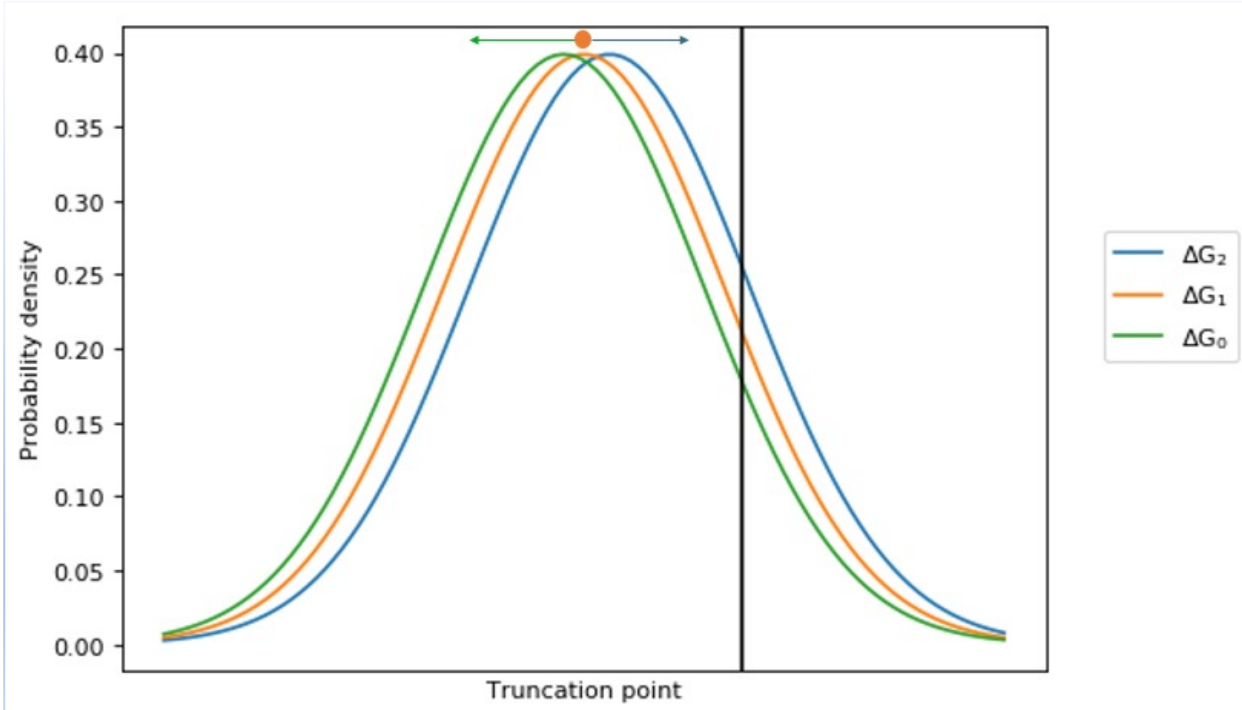

Figure 7. The change on the curve for different magnitude of genetic gain.

In addition, SelAction also provide the predicted genetic gain in actual trait units for each of the trait in H as well as the relative contribution of each trait in monitoring units to the overall breeding objective.

4. Results

4.1 Descriptive statistics for the fish harvested in the two cages

The fish were harvested over four (Cage 1) and three (Cage 2) harvesting events (Table 5). The total fish weight harvested from cage 1 was 992.6 tonnes with an average body weight of 6.198 kg, and that from cage 2 904.8 tonnes with average body weight of 6.065 kg.

Table 5. Number of fish harvested, mean body weight and total kg fish harvested at each harvest event.

Cage/ Harvest no.	YearW	No. fish harvested	Mean body weight, kg	Total body weight, kg
Cage 1				
1st	217	53 154	3.419	181 757
2nd	225	36 215	5.023	181 898
3rd	247	21 379	8.484	181 369
4th	251	49 387	9.062	447 559
Total		160 135	6.198	992 583
Cage 2				
1st	222	50 151	3.683	184 723
2nd	236	30 659	5.901	180 913
3rd	251	68 384	7.885	539 220
Total		149 194	6.065	904 856

4.2 Economic values

The derived economic values (NOK/kg fish) for the traits are shown in the Table 6. The economic value for the harvest body weight was 1.95 NOK/kg fish, which means the 1 % marginal increase in the growth factor (from 2.7 to 2.701) gave rise to the economic value in the harvest body weight 1.95 NOK/kg. The economic value for the growth factor reached to 9.49 NOK/kg fish. The second economically important trait was FCR. The economic value of it was -11.8 NOK per kg fish, while the mean value of FCR was 1.1 FCR units, the marginal change, therefore, was 0.011 FCR units. The economic value for the fillet yield means that for every percent-unit increase in the fillet yield, the total profit increases by 0.82 NOK. The economic values for general and specific mortality and early sexual maturity were negative, means that for every percent-unit decrease in them, the profit would increase by 0.26, 0.37 and 0.22 NOK per kg fish produced, respectively.

Table 6. The derived economic values for the studied traits in Atlantic salmon.

Trait	Economic value, NOK/ trait unit/ kg fish produced
Growth factor	9.49
Harvest body weight (kg)	1.95
Fillet yield (%-unit)	0.82
General mortality (%-unit)	-0.26
Specific mortality (%-unit)	-0.37
Early sexual maturity (%-unit)	-0.22
Feed conversion ratio (kg feed/kg gain)	-11.8

4.3 Predicted genetic gain for each trait and total aggregate genotype

The predicted genetic gain for the aggregate genotype (NOK/generation) and for each trait (in trait unit/generation), as well as the relative contribution of each trait to the aggregate genotype are presented in Table 7 where the gain for general and specific mortality and early sexual maturity are given in standard deviation units.

For the baseline scenario, selection without FCR records, the economic value of the harvest body weight accounted for 48 % of the total economic value; the second big proportion of the economic response was feed conversion ratio that was 47 %; the third one was fillet yield but contributed only 5.3 % to the variation in the overall breeding objective, while sum of the general and specific economic values contributed was 0.7 %; the percentage of early sexual maturity was -1.6 %. Genetic per generation for the harvest body weight was biggest (+0.546); the FCR was the unfavorable trait is needed to be decreased, then the genetic gain was -0.088; the general and specific mortality were also unfavorable traits, as same as FCR, thus the genetic gain was -0.047 and -0.009, respectively; as the third most important trait, the genetic gain for the fillet yield reached to +0.142.

Comparing the second scenario with the baseline scenario, the adding information on the feed intake both in candidates and test fish made the economic proportion of the feed conversion ratio increased by 11 % and lower genetic gain (-0.123) than it in baseline scenario (-0.088), became the most important trait. Conversely, the economic proportion of harvest body weight fell by 10.5 % and decreased to 0.482 in the genetic gain. The contribution from the fillet yield was also decreased by 0.9 % to 4.4 % from 5.3 %. The remaining traits, general mortality, specific mortality and early sexual maturity changed little. The validity of the feet intake records increased the accuracy to 0.59 from 0.51 that made the outputs much closer to true breeding value.

In the baseline scenario, the genetic gain on the FCR was -0.088 FCR unit, and the mean body weight was 4.5 kg. The genetic gain for per kg fish would be 0.0196 FCR units while it was 0.027 FCR units after improvement on the feed intake. Based on these estimates, the farmer could save 386 million NOK every year on the feed consumption with the feed intake record comparing to the baseline scenario.

The total economic value (NOK/kg fish) was 2.20 NOK/kg fish in baseline scenario, and it was 2.49 NOK/kg fish after gaining feed intake records. According to the report from Directorate of Fisheries (2020), the weight of sale of slaughtered Atlantic salmon was 1.36 billion kg in 2019. Under the baseline situation, the total profit farmer could save about 3.0 billion NOK through artificial selection, and it would grow to 3.4 billion NOK if the feed intake technology is developed.

Table 7. The predicted genetic gain per generation for each trait (in trait unit) and for the aggregate genotype (monitoring unit, NOK), and the relative contribution of each trait to the aggregate genotype for the two scenarios with and without FCR records.

	Without FCR records		With FCR records	
Trait	Genetic gain per fish	% of total gain	Genetic gain per fish	% of total gain
HBW (kg)	+0.546	48.3	+0.482	37.8
FY (%-unit)	+0.142	5.3	+0.135	4.4
GM (SD-unit)	-0.047	0.6	-0.039	0.4
SM (SD-unit)	-0.009	0.1	-0.009	0.1
ESM (SD-unit)	+0.160	-1.6	+0.121	-1.1

FCR (kg feed/kg gain)	-0.088	47.3	-0.123	58.3
Total, NOK/kg	2.20	100.0	2.45	100.0
Variance of I	1.34		2.49	
Variance of H	5.16		4.85	
Accuracy	0.51		0.59	
Rate of inbreeding	0.90		0.83	

HBW= harvest body weight; FY = fillet yield; GM = general mortality; SM = specific mortality; ESM = early sexual maturity; and FCR = feed conversion ratio; Variance of I = variance of index; Variance of H = variance of breeding goal; SD=standard deviation unit

In Table 8, the gains for general mortality, specific mortality and early sexual maturity are converted into actual observed traits units. The results of general mortality, specific mortality and early sexual maturity included or excluded FCR records were similar; therefor only the results from baseline are explained more details here. The proportion of the general mortality and specific mortality for next generation after genetic gain was decreased by around 1.1 %, from the input 15.3 to 14.2 %, and by 0.2 %, from the 10.5 % at the beginning to 10.3 % at the end. To the contrary, the percentage of the early sexual maturity was inversely increased by 2.8 %, up to around 12 %.

Table 8. Percentage of general mortality, specific mortality and early sexual maturity before and after one generation genetic change.

	Without FCR record			With FCR record		
Traits	Input, %	Genetic gain	Output, %	Input, %	Genetic gain	Output, %
GM (%-units)	15.3	-0.047	14.2	15.3	-0.039	14.4
SM (%-units)	10.5	-0.009	10.3	10.5	-0.009	10.3
ESM (%-units)	8.8	+0.160	11.6	8.8	+0.123	10.9

GM = general mortality; SM = specific mortality; ESM = early sexual maturity.

4.4 Effect of a different genetic correlation between early sexual maturity and harvest body weight

The genetic correlation between early sexual maturity and harvest body weight in Atlantic salmon is not well documented. The predicted gains for three different levels of this correlation are shown in Table 9. When it was assumed to be +0.49 (base scenario) percentage of early sexual mature fish increased from 8.8 to 11.6 % over one generation of selection. If the genetic correlation was assumed to be zero or -0.49, the percentage of early sexual mature fish decreased to 8.4 and 6.4 %, respectively.

Table 9. The predicted genetic gains in early sexual maturity for three different magnitude of the genetic correlation between early sexual maturity and harvest body weight.

Genetic correlation ESM and HBW	Input, %	Genetic gain, %	Output, %
-0.49	8.8	-0.167	6.4
0	8.8	-0.023	8.4
+0.49	8.8	+0.160	11.6

HBW = harvest body weight; ESM = early sexual maturity.

4.5 Effect of body weight on FCR

The estimated economic value for FCR was NOK -11.8 /kg fish produced, when assuming 1.1 kg feed/kg round body weight gain. If FCR was assumed to increase with increasing body fat according to a theoretical calculation (+0.034 FCR/%-unit increase in body fat; T. Åsgård, Nofima), the economic value increased to NOK -19.8/kg fish produced; and to NOK -15.8/kg fish produced if the increase in FCR was reduced to +0.017 FCR/%-unit increase in body fat). This illustrates the importance of a reliable estimates of FCR for fish of different body fat.

4.6 Sensitivity analyses

The plan was to investigate the effect of different seawater temperatures, growth factor, general mortality (Figure 2), specific mortality (Figure 3), and sexual maturity on the estimated economic values, one at a time. However, as it was found that relatively small changes (e.g., 5, 10 and 15 %) in the mentioned input parameters had a not varying and mot systematic effect on the economic values, this exercise was dropped. The reason for this is not known but may be due to the harvesting strategy that may result in different amount (kg) and sizes of fish to be harvested at different times. Maybe harvesting a given proportion of the total biomass, rather than a given proportion of the number of fish (30 %), would have been a better strategy. This needs further investigation.

5. Discussion
5.1 General discussion

The selection index developed by Hazel and Lush (1942) has been the appreciated method for multiple traits selection. This was later used for various specific purposes, like the restricted selection index (Kempthorne and Nordskog (1959) and the selection index for quadratic models for nonlinear effect of profit on traits selected for Wilton, Evans, and Van Vleck (1968).

Today fish breeding selection also more focus on the estimating multiple traits BLUP breeding value simultaneously by means of mixed model equation, but the advantages of multi-trait selection cannot be fully obtained due to scares of reliable genetic parameters for the traits, not only the genetic correlation among traits, but also heritability.

In addition, there are very few published estimates of economic values for traits in aquaculture species; one is the economic values for several traits in gilthead seabream (Janssen et al. (2017), another for Nile tilapia (Omasaki et al. (2017), and none for any trait in Atlantic salmon. In lack of reliable genetic parameters and economic values, a desired gain approach is often used where EBVs for each trait are often obtained using a single trait approach, and thereafter weighted to get the desired genetic change in each trait, in which the relative weighting reflects a combination of genetic correlations among the traits and their market and non-market (strategic) economic values (Olesen et al., 2000). E.g., if the predicted genetic change in a trait is in an unfavorable direction, an extra (strategic) weight may have to be given to this trait to prevent this to happen.

This is therefore the first reported study on the economic values for traits in farmed Atlantic salmon. The economic value of a trait reflects the contribution to the change in profit per unit change in a trait while keeping the other traits constant (Shook, 2006), and thus the partial regression coefficient of profit on the traits included in the selection index.

Reliable economic values for traits in the grow-out phase can only be obtained from a grow-out farm with a realistic scale and environmental and management factors and strategies. Given this, the derived economic values may also be of great value in order to optimize farm profit, while at the same time used in a selective breeding context to study the relative importance of the traits selected for and their expected changes per generation of selection. The assumed grow-out farm herein was a simplified farm with two sea-cages with a maximum MTB of 1248 tonnes but with stocking density and harvesting strategy similar to that which can be found at a commercial farm, and input parameters obtained from official statistics.

The studied traits were harvest body weight (HBW), feed conversion ratio (FCR), early sexual maturity (ESM), general mortality (GM), specific mortality (SP) and fillet yield (FY). Harvest body weight was modeled through the growth factor. The economic values for the traits were expressed as NOK/trait unit/kg round body weight produced.

5.2 Genetic gain and relative contribution to overall economic weight of each trait

HBW was the most important trait with an economic value of 1.95 NOK/kg; followed by the correlated trait FCR with -11.8 NOK/kg feed, FY with 0.82 NOK/%-unit; GM with -0.26 NOK/%-unit; SM with -0.37 NOK/%-unit, and ESM with -0.22 NOK/%-unit. The magnitude of their contribution to the overall economic genetic gain was 48 % (HBW), 47 % (FCR), 5.3 % (FY), 0.9 % (GM), 0.1 % (SM) and -1.6 % (ESM). Given that records of feed intake could be obtained, the contribution of FCR to the overall genetic gain increased by 11 %-units while that of HBW decreased by 10 %-units.

Comparing all above percentage of economic response of each trait, the improvement in feed cost makes up more than half of the total economic gain per kg of fish produced, improving the cost item is thereby of great importance for development in production cost per kg fish. If feed intake records could be obtained, the genetic gain per generation increased from -0.088 to -0.123 FCR units per fish per generation, the overall genetic gain per generation increased from 2.20 to 2.45 NOK per kg fish produced, and the contribution of FCR to the overall breeding objective increased to 58.3 %, thus becoming the biggest contributor among traits, while that for harvest body weight was reduced to 37.8 %. Based on these estimates it can be calculated that the genetic improvement in FCR without feed intake records will reduce the total amount of feed needed with 25480 tonnes (1.8 %) worth 280 million NOK per year while producing the same number of fish (1.3 million tonnes), while with feed intake records this will increase to 35100 tonnes (2.45 %) worth 386 million NOK.

The economic selection index should combine all available information that helps to increase the accuracy of breeding objective on each breeding candidates. For the scenario with feed intake records, if feed intake was just taken on the sibs, omitting the own performance of candidates, then the genetic gain on the FCR per fish will be reduced by 3.3 % to -0.119 FCR units per fish, and with a 378 million NOK in the feed cost to produce same fish production (in Norway 1.3 million tonnes) as compared to the cost when the FCR was recorded both on own performance and sibs.

This illustrates that the improvement on the FCR will save feed purchasing cost, and furthermore the whole farm profit will increase with decreasing the feed cost. However, this advantage can only be achieved by the development of methodology to obtain individual feed intake records both on the selection candidates and their relatives.

5.3 Effect of genetic parameters on economic value and genetic gain

Within economic selection index, reliable estimates of genetic gain for the traits selected for and their contribution to the overall economic gain is dependent on reliable genetic parameters (heritability and genetic correlations) and economic values for the traits.

The predicted gain in FCR for the baseline scenario (without feed intake records) was a correlated gain due to selection for increased harvest body weight. If the genetic and phenotypic correlation was assumed to lower (-0.5) than it in the baseline scenario (-0.6) the percentage of the economic response in FCR decreased from 47 % to 42 % and the genetic gain changed from -0.088 to -0.073 FCR units per fish. At the same time the contribution of harvest body weight to the overall economic gain would increase from 48 % to 53 %.

The estimated economic value for FCR was NOK -11.8 /kg fish produced, when assuming the mean FCR kept constant on 1.1 kg feed/kg round body weight gain. However, if FCR increases with +0.034 FCR/%-unit increase in body fat (a theoretical calculation by T. Åsgård, Nofima) the economic value for FCR increased to NOK -19.8 per kg fish produced. and the contribution of FCR to the total economic gain increased from 47 to 62 %. If the above theoretical regression coefficient was half of the at calculated by Åsgård, the economic value for FCR was -15.8

NOK/kg fish. These results illustrate the importance of reliable input parameters when deriving reliable economic values.

The assumed genetic parameters not only influence the magnitude of the genetic gain and the relative contribution of each trait to the overall genetic gain but may also change the genetic gain from an unfavorable to a favorable direction, or vice versa. In the baseline scenario the genetic gain ESM was unfavorable (Table 9) when the genetic correlation between harvest body weight and early sexual maturity was assumed to be +0.49 (the only reported estimate found so far; (Gjerde et al., 1994)). However, if the genetic correlation was -0.49, the genetic gain become favorable with 2.4 %-unit decrease (from 8.8 to 6.4 %) in ESM in one generation of selection, as compared to a 2.8 %-unit increase when the genetic correlation was +0.49. If the genetic correlation between e.g., an important trait like growth rate and another trait is unfavorable, it is important to record and select also for the other trait to prevent this other trait to change in an unfavorable direction.

The magnitude of the predicted genetic gain in fillet yield is uncertain, not only due to the uncertain genetic correlations to the other traits but also the uncertain on the heritability of FY. E.g., if the heritability of FY was assumed to 0.23, as reported by Acharya (2012), and not 0.05 as reported by Tsai et al. (2015), the predicted genetic gain in the fillet yield would increase to 0.92 %-unit as compare to 0.14 %-unit when the heritability was 0.05, and its contribution to the total economic gain would increase from 5.3 to 29.5 %. Therefore, investigation on the genetic parameters for fillet yield is imperative for obtaining reliable genetic gain for fillet yield. The only reported genetic gain for fillet yield is that reported in Nile tilapia and rainbow trout (Vandeputte et al., 2019).

Fillet yield is the ratio between the two very highly genetic correlated (0.97) traits fillet weight and body weight (Tsai et al., 2015). This makes fillet yield, a difficult breeding objective trait as the heritability for FY and genetic correlations of FY to other traits are very sensitive on measurements error in the two traits from which it is calculated (Gunsett, 1987). In addition, the farmer is not paid by yield itself but by body weight or fillet weight. Consequently, it may be better to replace fillet yield with fillet weight as a trait in the breeding goal, in addition to round body weight, or preferably gutted body weight, as an informant trait as these are easier to record than fillet weight.

5.4 Argument on the specific mortality as a breeding objective

In this study the trait records for specific mortality were assumed to be obtained from a commercial grow-out environment. However, a specific disease does not occur every year at a grow-out farm. Therefore, estimated breeding values for specific diseases must be based on mortality records from specific challenge tests. In that case the predicted genetic for the breeding objective trait (specific disease in a grow-out environment) may be obtained as a correlated trait assuming a genetic correlation between the breeding objective trait and the trait recorded in the challenge test. In a study with furunculosis this genetic correlation was found to be very high (0.95) (Gjøen et al., 1997), but may be lower for other diseases. The lack of reliable genetic parameters and scientific research is inevitable as specific mortality traits are very important trait for the current selective breeding programs for Atlantic salmon and that also show substantial genetic variation (Ødegård, Baranski, Gjerde, & Gjedrem, 2011).

5.5 Sensitivity analysis on input parameters

The sensitivity analysis on the input parameters, like sea water temperature, mortality rate, smolt cost, fixed cost, etc. need tom be investigated. The temperature, for example, have large effect of the growth factor and thus when the biomass in a cage or at the farm reach the allowed constraints and some of the fish need to be harvested. The growth rate may be also be dependent of the genetic material used. The same is the case for an increase or increase in general and specific mortality.

6. Conclusion

In today's selective breeding programs for Atlantic salmon selection are performed simultaneously for several traits. Appropriate weighting of the traits requires reliable economic values as well as reliable genetic parameters. This is the first study on economic values for traits in Atlantic salmon that and that gave some insight about the expected genetic gain for each of the six studied traits and their relative contribution to the overall economic gain. The harvest body weight and the correlated trait feed conversion ratio was by far the two most important trait followed by the fillet yield, general mortality and early sexual maturity, while the specific mortality was the least important trait. However, these results are to a large based on the assumed genetic parameters that are missing and this not reliable for most of the traits.

The derivation of the economic value for the traits not only can improve the efficiency of breeding program, but also optimize the management decisions and economic benefits at the farm level.

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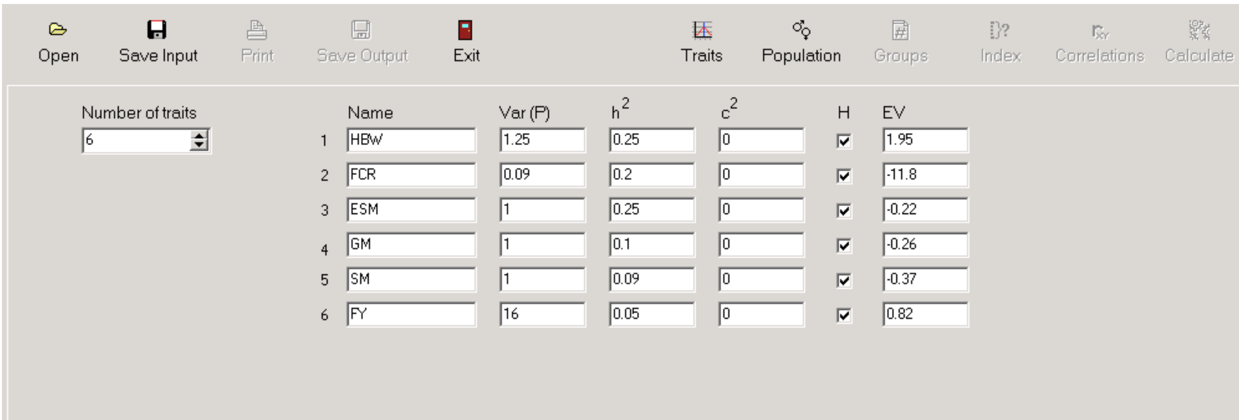
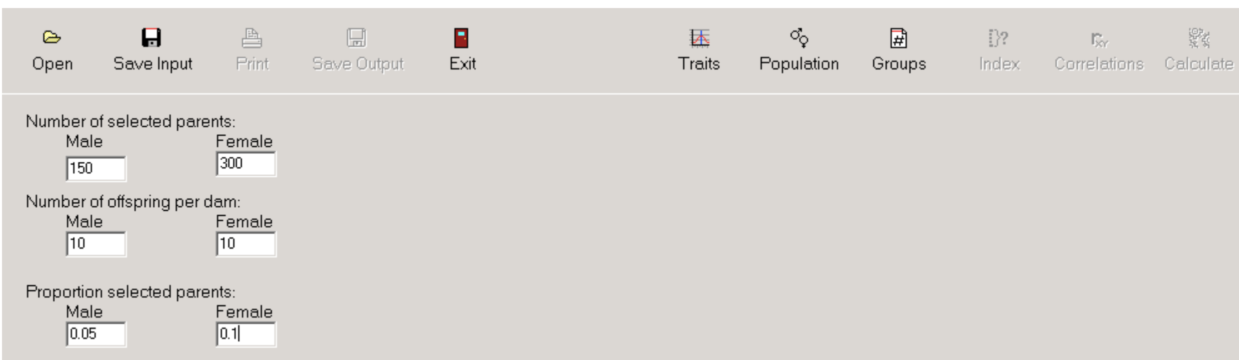
Appendix

Each window from SelAction program about setting for the baseline scenario, as shown in the following pictures.

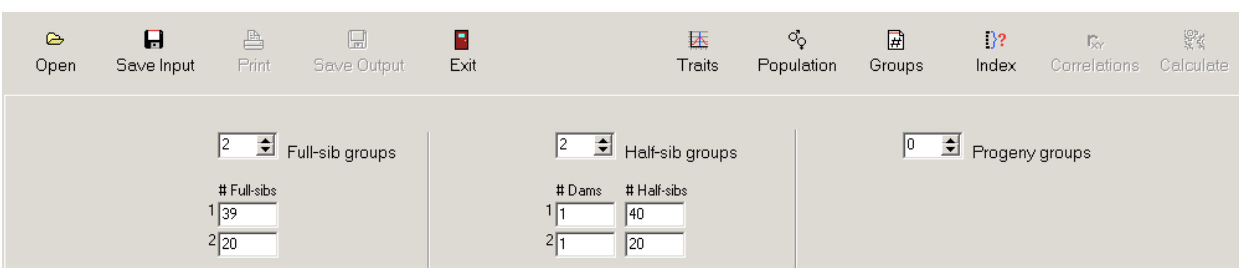
1.The traits window



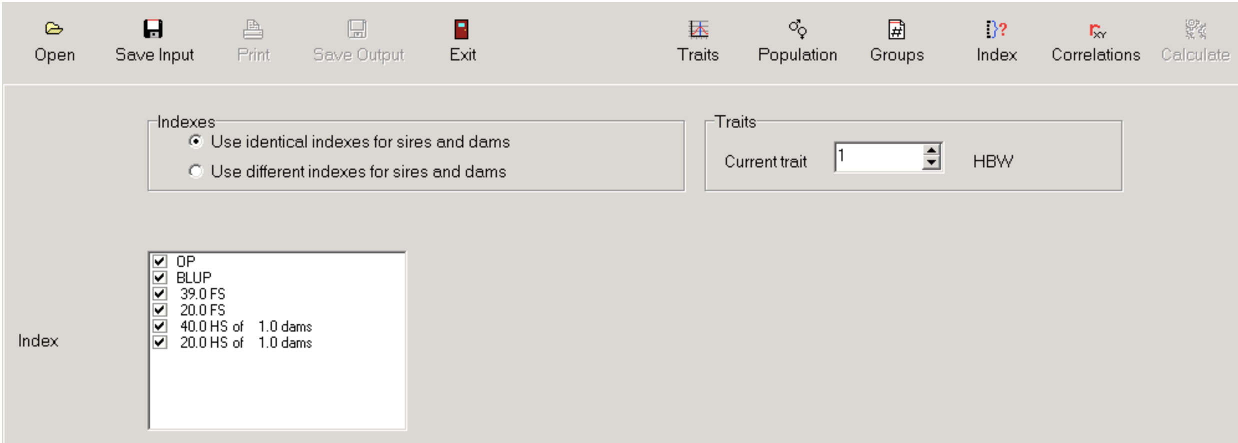
2.The population window



3.The groups window



4.The index windows for each trait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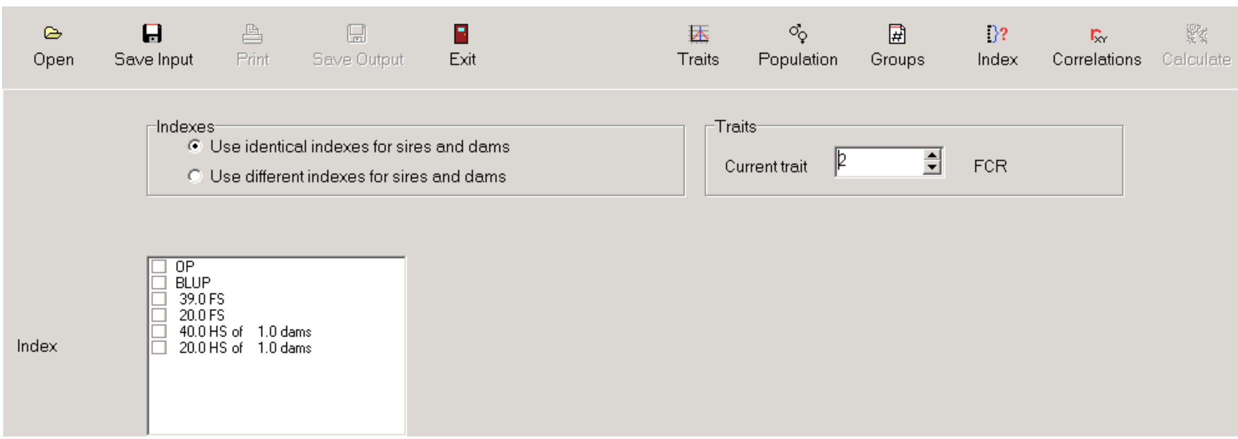
Save Input
Print
Save Output
Exit
Traits
Population
Groups
Index
Correlations
Calculate
Indexes
Use identical indexes for sires and dams
Use different indexes for sires and dams
Traits
Current trait
1
HBW
Index
OP
BLUP
39.0 FS
20.0 FS
40.0 HS of 1.0 dams
20.0 HS of 1.0 dams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Groups
Index
Correlations
Calculate
Indexes
Use identical indexes for sires and dams
Use different indexes for sires and dams
Traits
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Index
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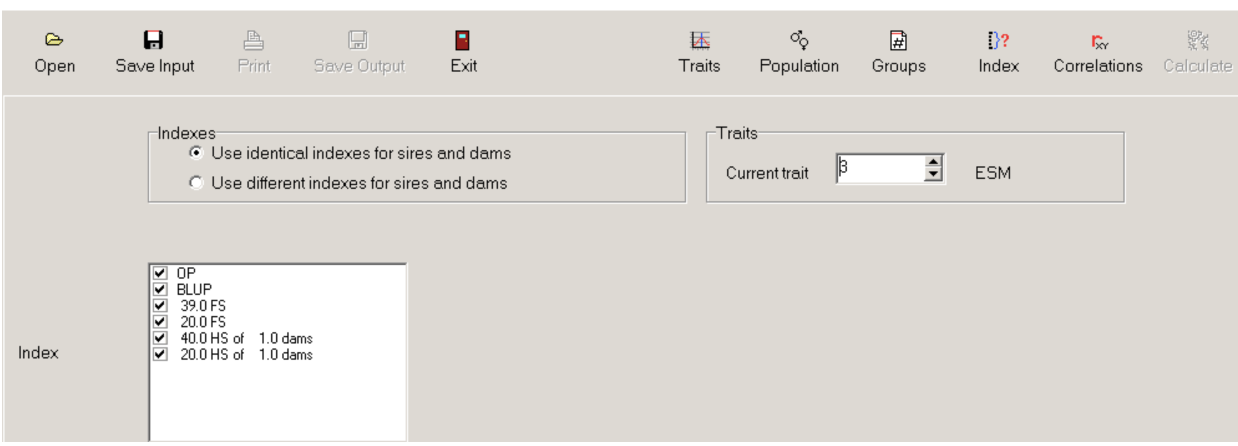
BLUP
39.0 FS
20.0 FS
40.0 HS of 1.0 dams
20.0 HS of 1.0 dams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Groups
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Correlations
Calculate
Indexes
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Use different indexes for sires and dams
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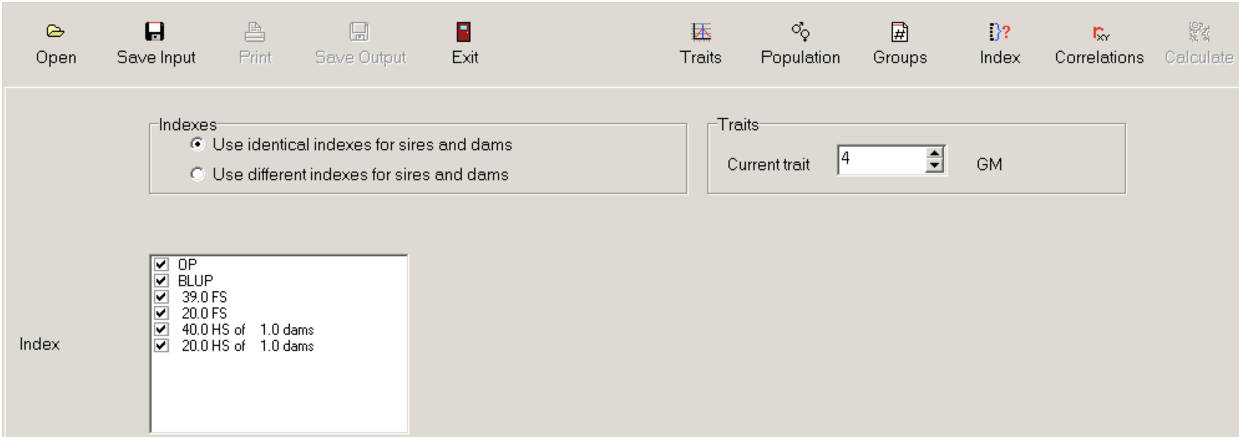
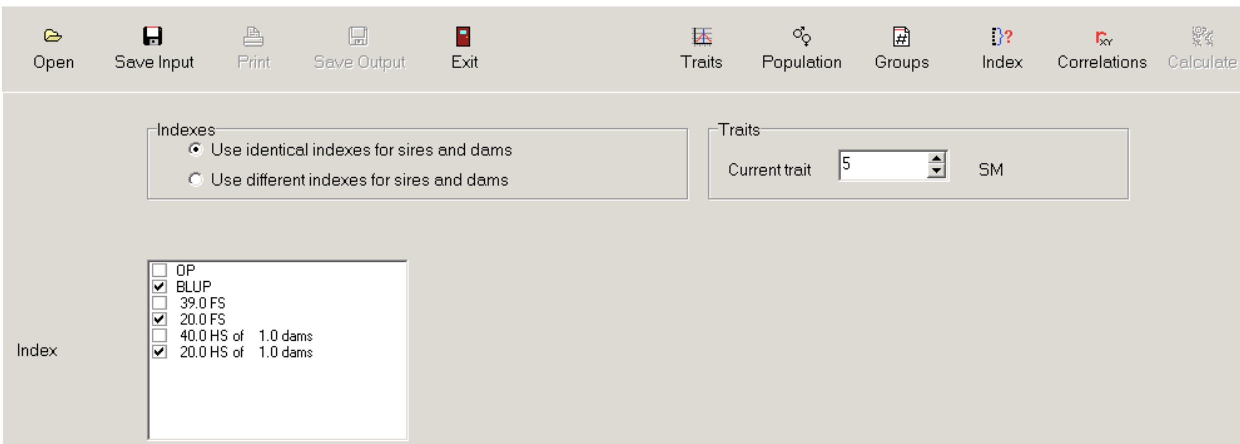
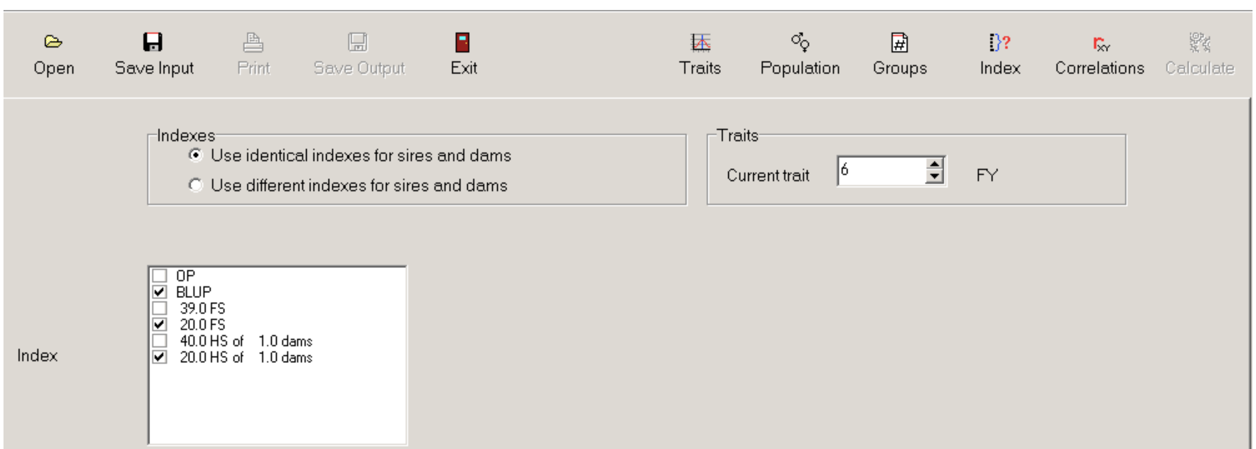
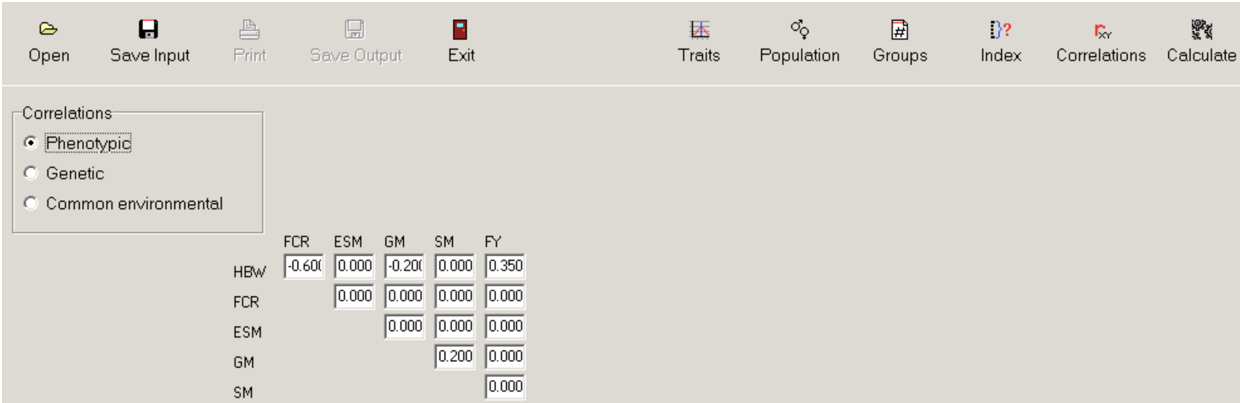
40.0 HS of 1.0 dams
20.0 HS of 1.0 dams







5.The genetic and phenotypic correlations windows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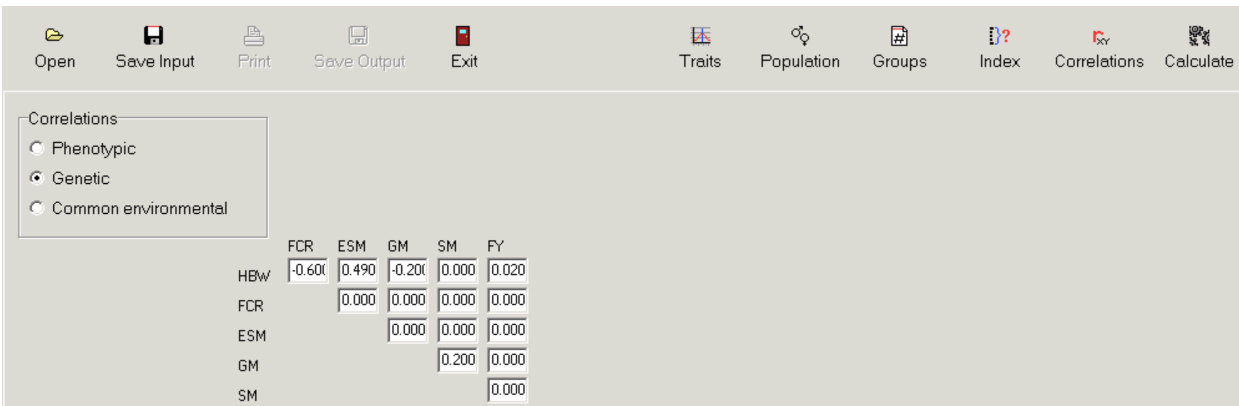
SM 0.000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ESM 0.000 0.000 0.000
GM 0.200 0.000
SM 0.000

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