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Overcoming barriers to breeding for increased lice resistance in farmed Atlantic salmon: A case study from Norway

G. Kristin Rosendal^a, Ingrid Olesen^{b,*}

^a The Fridtjof Nansen Institute (FNI), PB 326, NO-1326 Lysaker, Norway
^b Nofima AS, P.O. Box 210, NO-1431 Ås, Norway

ARTICLE INFO ABSTRACT Keywords: Lice is a persistent and major problem in the salmon aquaculture sector with serious environmental impacts and Salmon lice reducing growth potential and income of the salmon industry. This article discusses whether there is an untapped Genetic resistance potential in breeding for improved lice resistant of Atlantic salmon. To this end, three sets of factors that may Atlantic salmon impact the state of breeding for lice resistance are examined, using document analysis and key actor interviews. Selective breeding First, our data material indicates that market-based factors will hardly stimulate this type of breeding, as the Policy instruments benefits from breeding for lice resistance is predominantly a public good, and because the polygenic nature of Regulating gene editing lice resistance does not enable patenting as a powerful instrument to secure private goods or privatize the benefits of genetic improvement. Second, the regulation of gene editing technologies is in flux, and increase the risk of investments in technologies as selective breeding that could handle the polygenic challenges of lice resistance. Finally, policy instruments aimed at stimulating relevant innovation has been applied generously for other types of innovations to deal with the lice problem. For instance, new technologies for delousing have resulted in increased treatments and caused higher stress and mortality the recent years. However, none of these have targeted major root causes of the salmon lice problem (e.g. big monocultures or susceptible fish) or been exploited by breeding actors. Seen from a social and environmental point of view this could paradoxically lead to increased demand for fish that better endures harsh delousing treatments rather than demand for more lice resistant fish

1. Introduction

Lice is a costly and increasing problem in the aquaculture sector. In 2018, the costs associated with combating the lice *Lepeophtheirus salmonis* in producing 1.2 million tons of salmon in Norway was estimated at \notin 520 million, with a minimum cost of \notin 0.5 per kilo of fish (Holan et al., 2017).¹ The serious environmental impacts associated with lice create a barrier to increased growth in salmon production, incurring even higher costs in terms of reduced income from the salmon industry. According to the scientific board for salmon management (Anon., 2020), escaped farmed salmon and lice represent the most severe and increasing threats to wild salmon. As custodian of the bulk of wild Atlantic salmon, Norway has a specific international management responsibility.

Responding to the costly and increasing lice problem involves a broad range of activities and innovations specifically aimed at licereduction. Innovation can take place through various methods, which may be classified as *medicinal* (hydrogen peroxide and diflubenzuron treatments), *biological* (e.g. cleaner fish that eat lice and salmon breeding programs for lice resistance), and *mechanical* (production methods and equipment). Among these pathways, mechanical and biological innovations are presently considered to be the most promising, but only the mechanical pathway has received substantial targeted government intervention in terms of policy instruments to stimulate innovation (Greaker et al., 2020).

This is the background for our research question of whether there is an untapped potential for biological innovation in breeding for lice resistance, and if so, how this can be explained in the case of salmon farming in Norway.

We start by briefly presenting and comparing the various types of innovation directed at reducing the lice problem in the salmon breeding sector, then focusing on breeding for lice resistance through biological

* Corresponding author.

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E-mail addresses: krosendal@fni.no (G.K. Rosendal), ingrid.olesen@nofima.no (I. Olesen).

¹ https://www.dn.no/havbruk/gir-oppdrettsbransjen-en-lusing-for-52-milliarder/2-1-658103https://www.ssb.no/fiskeoppdrett

innovation. In the following section, we present three sets of factors that may impact the state of breeding for lice resistance in Norway: market demands and instruments; policy instruments aimed at stimulating relevant innovation; and the regulation of emerging breeding technologies. Next, based on our empirical data material collected from interviews and literature studies, we first examine the interaction between technological advances in breeding and the overall regulatory framework. Here, we look at evolving possibilities within gene editing using CRISPR technology and how the Norwegian Gene Technology Act (GTA) may affect such advances. In the second part of the discussion of the empirical results and literature, we inquire into the interaction between policy instruments and market mechanisms relating to breeding for lice resistance. We do not examine the full range of other policies and regulations aimed to reduce sea lice in aquaculture, as these are the same for all types of innovation and are, therefore, presumably less useful in explaining variation in breeding investments.

2. Data material and methods

Methodologically, our data material relies on the literature on breeding for lice resistance. This body of literature is not very large, so we are able to review most of it, as well as identify gaps in the knowledge. Adding to this, we conducted in-depth interviews with key actors in Norwegian salmon farming and salmon breeding programs using an interdisciplinary approach applied earlier (Rosendal et al., 2006; Olesen et al., 2007, 2015). This in depth and explorative methodology speaks in favour of focusing on one case country, which is likely to expose intrinsic characteristics. Hence, we do not expect a large scope for generalising our findings to other salmon producing countries, although we will discuss this matter in the discussion section.

Norwegian public breeding programs for salmon and trout were launched in 1971 (Gjoen and Bentsen, 1997). Following a period of cooperative organisation, and an economic crisis in the late 1980s that resulted in bankruptcy of one of the owners, the Aquaculture Sales Group AL, the breeding program was taken over by a new shareholder company, AquaGen in 1993 (Gjedrem, 2010; AquaGen, 2021). Here, the government became a majority owner, which also provided public control over the breeding material. In 2013, remaining public shares were sold to (German based) EW Group-a multinational and world-leading breeding corporation for poultry, pig, and aquaculture.² In 2014-15, SalmoBreed and Akvaforsk Genetics (also with majority government ownership) were sold to (UK) Benchmark Holdings, a multinational investment corporation.³ This implied that by 2015, 90% of Norway's breeding programs for salmon had been entirely transferred from domestic/public to foreign/private control.⁴ The two main breeding companies operating in Norway today are thus Benchmark Holding (SalmoBreed, Stofnfiskur and Akvaforsk Genetics Center) and EW Group (AquaGen). Another two breeding programmes are integrated as parts of (Norwegian) multinational corporation Mowi and the smaller Norwegian corporation, SalMar. These four actors constitute the universe of Norwegian breeding actors from which we draw our key actor interviews.

The main components of salmon breeding programmes are the three following tiers: i) a breeding nucleus that manages and develops the elite brood stock; ii) multipliers that propagate and disseminate improved and fertilized roe to tier iii) consisting of smolt producers and salmon farmers. For the two specialised breeding companies the breeding programmes operate as specialised entities. For Mowi and SalMar the breeding activities are integrated within the farming enterprise among activities covering the value chain from reproduction to the consumer product.

The interview method chosen is qualitative and in depth in contrast to a quantitative survey (or any other type of statistical data). As such the methodology is suited to draw out a range of perceptions and views from key actors and also allows for follow-up questions. As we conducted interviews with all four of the companies involved in salmon breeding programs in Norway, the results from these interviews are highly representative. The main challenge concerning results from these interviews is our respondents' requests for confidentiality, and thus our need to carefully handle sensitive information regarding corporate breeding strategies. In accordance with data-management practices, all of our interviewees were granted full anonymity and were not cited without consent. Still, the small number of companies constituting the full range of possible respondents, makes anonymisation difficult and implies that the data must be handled very carefully. Our approach to remedy this situation has been to generalise as much as possible, using phrasing such as, 'There is agreement among respondents that...', or 'Some respondents stress that..., while others point to ...'.

Our interviews in the salmon farming sector face the reverse methodological problem. Here, we needed to make a representative sample of interviewees from a much larger range of possible respondents. We included four interviewees from large and smaller companies; from integrated and independent companies; and from companies that experience the full brunt of the lice-problem in their specific locations, as well as those that are currently less hard hit. A majority of the major farming corporations, including the world's largest and second largest were represented, as well as a representative of small-scale producers of salmon in Norway. We were also wary of the effects of performing salmon farming in an area characterised by many competitors compared to those farming in locations with less competition and a lower density of farms. These differences are important for the representativeness of our findings as salmon farming takes place all along the Norwegian coastline, involving a variety of large and small-scale actors.

A central benefit of our approach is the multidisciplinary nature of our research, which also has methodological ramifications. Multidisciplinary studies compel extra attention to be paid to the validity and clarity of central concepts, which is also essential in interview situations. Combining insights from political science on legal and policy designs with knowledge of fish genetics and biology is expected to enhance our interpretation and understanding of how various factors affect the state of lice resistance in aquaculture.

3. Framework for analysing opportunities and constraints in lice resistance breeding

This section paves the way for discussing how market-based factors, the design of policy instruments and the state and availability of various breeding technologies may affect key actors' interests in and scope for choosing lice resistance breeding and lice-resistant roe.

3.1. Types of innovation aimed at reducing the lice problem

Before we focus on innovation in breeding strategies for lice resistance, we need to have a better idea of how the salmon sector is currently responding to the lice situation. The resistance of lice to *medicinal* treatments has increased more rapidly than the effectiveness of the treatments themselves, and negative environmental effect (on shellfish in particular) of medical treatments is increasingly being documented (Bechmann et al., 2019; Olaussen, 2018).

Mechanical innovations may have a more promising scope for further developments, although these methods also involve their own sets of pros and cons. Emerging mechanical technologies attract investors and inspire creative solutions to delouse farmed fish. Examples include developing more elaborate delousing methods using warm water or lasers, or by building bigger farming facilities on land or offshore that

² See History - AquaGenAquaGen accessed May 15, 2021.

³ Akvaforsk Genetics Center sold - FishFarmingExpert.comBenchmark to Acquire Two Major Players in Aquaculture Breeding | The Fish Site accessed May 15, 2021, see also Grydeland, 2015.

⁴ Interview Nofima, Ingrid Olesen and Hans B- Bentsen, December 16, 2016.

physically isolate the farmed fish from salmon lice, as well as from wild salmon. The latter mechanical solutions of closed farming have the added value of not only addressing the lice problem, but also providing better control over escapees, preventing less local pollution from feed residues, and protecting wild aquatic organisms from disease contamination, including pancreas disease (PD) and infectious salmon anaemia (ISA). The downside of mechanical innovation is that current technological trajectories, such as land-based closed fish production and offshore facilities, could undermine the natural competitive advantages of traditional Norwegian fish farming. Closed production on land and offshore facilities could weaken the competitiveness of small-scale, rural industries that are operating in coastal areas along the fjords (Greaker et al., 2020; Vormedal et al., 2019). These types of mechanical innovation would represent a mismatch with policy goals for rural employment, economies, and settlements (White Paper, 2019-2020) and involve land-use conflicts.

The *biological* pathways can target the problem of salmon monoculture by applying polyculture with cleaner fish (e.g. lice-eating lumpfish and various species of wrasse) or by e.g. strengthening the salmon own resistance to salmon lice. The biological measures can be regarded as environmentally sustainable methods to reduce lice. However, as its application of cleaner fish has rapidly increased, so has the criticism of overharvesting various wrasse species, as well as the concerns about the welfare, health and high mortality rates of millions of cleaner fish themselves (Olaussen, 2018).⁵ However, the potential of polyculture with other cleaner organisms such as mussels, filtering out larval forms of lice, as shown in laboratory scale (Molloy et al., 2011; Bartsch et al., 2013), have to our knowledge not been followed up by further field trials or development projects.

Similarly to the polyculture strategy, the biological pathway of selective breeding for lice resistance targets the causes rather than the symptoms of the lice problem. Furthermore, the genetic gain obtained over generations is cumulative and permanent given the long-term breeding goal and proper management of the breeding population. Therefore, genetic lice resistance could potentially have more long-term and, therefore, sustainable environmental and socio-economic effects (Gjerde, 2013). The addition of new traits in the breeding goal, such as seen in the case of resistance to infectious pancreas necrosis (IPN) since 2008, has already rid the salmon farming sector of very costly outbreaks.⁶ However, the more weight that is put on a new trait in the breeding goal, the higher the risk related to larger temporary loss in genetic gains in other traits. The inclusion of lice resistance as an additional trait in the breeding goal is likely to bring a temporary decline in the genetic gains of other profit-enhancing traits and functions-such as growth rate and the associated ability to utilise feed nutrients, as well as resistance to various diseases. The change in genetic gains for each trait following multi-trait selection is dependent on the population's genetic correlations between the traits, the heritabilities and their relative economic values (Smith, 1983). If the sign of the correlation with an additional trait is unfavourable and (or) the relative economic value is high, a decline in the selection response for each trait is expected. Estimates of genetic correlation between growth rate on one side and lice number or lice density on the other are low or moderate, showing that it is possible to improve both growth rate and lice resistance (Kolstad et al., 2005; Gjerde et al., 2011; Yáñez et al., 2014). Due to the low and not significant genetic correlation between growth and lice density of L. salmonis, one might however expect a decline in the gain for growth when adding a high economic value for resistance against salmon lice as also discussed in a project workshop with stakeholders (Nielsen, 2014). Based on the support from Norwegian households and the presentation on predicted selection responses from a

breeding program for both growth rate and lice resistance, most workshop participants concluded that breeding for fish welfare, as improved lice resistance, should be strengthened, and the industry representatives agreed it would benefit the industry in the long term in spite of reduced gain in growth rate. Due to such temporary declines in gains for other traits, the fish producers that choose a more lice-resistant roe would have to incorporate the added cost of impaired growth compared to other salmon farmers using roe with faster growth (Greaker et al., 2020). Still, selective breeding against salmon lice is applied to some extent in both major salmon producing countries, Norway (*L. salmonis* resistance as presented in section 4 below), Canada (Mowi) and Chile (*Caligus* resistance in e.g. SagaChile⁷ and Mowi).

Finally, research and innovation on genetic improvement of cleaner fish' lice eating, disease resistance and welfare have not received much attention or funding although promising results have been documented (Lopes, 2020).

There is a basic public-good character in biological innovation in fish health and welfare, in addition to environmental benefits for wild fish (Nielsen et al., 2010). The same applies to genetic improvement of lice resistance. The added public benefit is apparent from Norwegian households' high willingness to pay an extra tax to support breeding efforts for more lice-resistant salmon in Norway (Grimsrud et al., 2013). Most importantly, one producer's use of lice-resistant fish will be beneficial to all farmers, as it reduces lice pressure and infestations for surrounding salmon farms as well (Gjerde, 2018a). With a partly, but not completely, resistant fish type, this type of innovation might be effective only if all or almost all farms adopted the resistant fish. However, as one farmer's or breeder's loss may be another's gain, this type of innovation is less likely to be stimulated through market-based competition. The same features make relying on lice-resistant fish as the major trait in breeding programs resemble what is known to economists as a 'game of chicken' (Greaker et al., 2020). From a collective action perspective and based on its public-good character, biological innovation would then arguably need stimulation through the design of policy instruments and targeted government interventions: If all farmers and breeders chose to add and adopt lice resistance, the short-term reduction in growth would be carried equally by all, and everybody would contribute to and benefit from the positive effects of the ensuing lice reduction (Greaker et al., 2020).

3.2. Stimulating innovation: Market mechanisms and technologies

Lice puts severe constraints on the increased growth and, therefore, expansion of Norwegian salmon production, which would seem to be a strong incentive for lice-resistant roe. Nevertheless, we have seen that the market alone is unlikely to stimulate genetic breeding for lice resistance due to its public-good and game-of-chicken characteristics. This is the type of innovation where it does not pay to be a sole adaptor and where the public benefits, which are hard to privatize (for example through labelling and certification), tend to outweigh the private benefits of choosing roe with other production characteristics.

Another central market-based instrument is patenting, which ensures the recovery of investments through a temporary monopoly. Patents are, however, rarely suited nor applied to protect breeding results (Olesen et al., 2007; Rosendal et al., 2006). As shown by Rosendal et al. (2006), *continuous upgrading* is the most common method to protect results from selective breeding. Continuous upgrading is a much weaker form of protection than patenting, but it is feasible for securing benefits from cumulative selection responses and does not unnecessarily hamper access to breeding material for other breeders or farmers. Most of the patents in aquaculture relate to feed, vaccines and technical equipment. The last two years have witnessed an increase in patent applications in

⁵ See also: https://www.wwf.no/bibliotek/nyheter_fakta/nyhetssaker/?330 89/Krever-god-forvaltning-av-leppefisk accessed 02.10.2018.

⁶ See http://salmobreed.no/history/ [Accessed 8 May 2019].

⁷ https://www.benchmarkplc.com/sagachile-new-strain-of-salmon-ova-with -a-pedigree-of-excellence/

the aquaculture industry, particularly patents to protect measures combatting sea lice, such as bath treatments, mechanical solutions and offshore cages.⁸ There are a few examples of patenting in breeding, such as IPN resistance in Atlantic salmon (Patent application no. 20180127820) and rainbow trout (Patent application no. 20190241980), for which patenting has been possible through the application of a specific genetic marker, called a qualitative trait locus (OTL).⁹ In contrast to IPN, however, lice resistance involves far more genes, as lice resistance is a polygenic trait that can best be addressed by genomic selection (Tsai et al., 2016; Correa et al., 2017) and is, thus, less amenable to patenting. When first discovered and applied, modern selective breeding of salmon was still a predominantly public activity, and no patents were required or applied for. This may change with the privatisation and consolidation of salmon breeding companies, with the accompanied needs for protecting investments and breeding results through intellectual property rights.

Finally, an important driver for applying patents to stimulate this type of innovation could be changes in breeding technologies that counter the effect of the polygenic trait of lice resistance. Emerging technologies in marker-assisted selection (MAS), genomic selection (GS) and gene editing, such as CRISPR techniques, might potentially constitute such a driver (see Box 1), which might then also enhance the scope for producing more effective lice-resistant roe.

To explore this dimension, we need to gain a better understanding of the types of technologies available to breeders for obtaining liceresistant fish, including gene editing technology. Moreover, breeders are likely to factor in how the current regulatory framework accepts the kind of technology suitable to produce lice resistance through breeding. For instance, if the most promising breeding techniques include genetic engineering, this means that we need to explore the effects of the Norwegian Genetic Technology Act and gene technology regulations in the European Union (EU).

In Section 5.1, we examine and discuss key actor views about the effects of market mechanisms and emerging technologies on lice resistance breeding.

3.3. Stimulating innovation: Policy intervention

Commonly, costly, public-good types of innovation may depend on policy support for successful market diffusion because they are unlikely to receive sufficient private investment through market demands or through conventional market-based investment stimuli, such as patents (Greaker et al., 2020).

In effect, government intervention may be needed to ensure the early adoption and market penetration of a more, or rather, as close as possible to a "fully" lice-resistant salmon (Greaker et al., 2020). This type of government intervention would not be without precedence in the aquaculture and agriculture sectors. The government has already made it mandatory to introduce vaccination against fish-diseases such as PD.¹⁰ Such policies are also common in agriculture where the breeding of plant varieties with disease and pest resistance is strongly encouraged to reduce the use of pesticides. Another parallel is the pathogen-free and pathogen-resistant seed requirements in shrimp farming in countries such as India and Mexico (Briggs et al., 2004). The Norwegian Animal

Welfare Act demands that breeding programs enhance characteristics that provide the animals with good health and functions (§ 25). This could imply that when salmon suffer or die from delousing treatments, the government could decree that lice-resistant roe are made mandatory according to the Act. Alternatively, breeders and farmers could be required to possibly add lice resistance genes from the Pacific coho salmon to the Atlantic salmon breeding mix; coho salmon being genetically lice resistant.¹¹

Turning to potential policy instruments that might apply to stimulate lice resistance, one option would be to use the well-established permit arrangements. The Norwegian authorities have developed and applied Green permits,¹² Research permits, Development permits and Broodstock permits in the aquaculture sector (2013–2017). The value of these permits adds up to quite an extensive sum, which in many ways resemble subsidies (Vormedal et al., 2019). The Green and Research permits have hardly—and the Development permits not at all—been applied to biological innovation (Greaker et al., 2020; Vormedal et al., 2019). The Broodstock permits are focused on stimulating the development of high-quality salmon roe and could potentially be applied more directly to support breeding for lice resistance to enhance animal welfare and sustainable innovation, but this has not been the case so far.

The Development permits require a high level of innovation and significant investments (Lakseforskriften §23b). The accompanying ministry guidelines require a technology boost with solutions that are apt to solve the environmental and land-use challenges facing the salmon farming industry. The Development permits (2014-2017) are restricted to innovations in production/technological equipment and installations, and the totality of these permits (100%) is based on mechanical innovation. Each Development permit is given for 15 years and may then be converted (upon application) into conventional fish-forfood producing permits, independent of whether the innovation has been successful or not (Vormedal et al., 2019). Upon conversion, the applicant may exploit the added capacity irrespective of any farming taking place in the new installation. A Development permit allows for the production of 780 tons of biomass and a typical Development project involves a request for 8-30 permits (7-23,000 tons). Ordinary permits are very costly (auction prices per ton in 2018 ranged from € 13.200 in South Norway to € 25.200 in Northern Norway¹³; fixed price in 2020 was \in 15.600 per ton¹⁴), and there has hardly been any increase in salmon production outside of these permits. The value of a salmon production license has been estimated at € 12.000/ton assuming that the production can be maintained without new regulations imposing production restrictions (Misund, 2017¹⁵). Hence, the Development permits are highly attractive and potentially very effective policy instruments for governing innovation.

Of the Research permits, 26% have been granted to breeding (but not lice resistance) and 9% to other types of biological innovation; the largest bulk, 43%, went to mechanical innovation and 23% to medicinal innovation (Vormedal, 2019).¹⁶ Two new permits have been granted to

⁸ https://www.aquanor.no/oppdrettspatenter-bade-skaper-sikrer-verdier/?la ng=en

ng=en ⁹ The patent issue on fish genetic resources was hotly discussed among breeders in 2016 when AquaGen decided to apply for a patent on a QTL for IPN resistance in trout:https://ilaks.no/slik-bidrar-patenter-til-apenhet-og-innovas jon-i-havbruksnaeringen/ and https://ilaks.no/en-utbredt-bekymring-er-at-pa tenter-favner-for-bredt/

¹⁰ Administrative order from the Ministry of Trade and Fisheries to combat PD disease in aquaculture, 29 August 2017; based in legal Act on food production and food safety, 19 December 2003, no. 124.

¹¹ https://ilaks.no/coholaks-en-mulighet-for-norsk-oppdrettsnaering/

¹² Green permits require the farmer to demonstrate that concrete action is taken to reduce lice as well as escapees; unlike the Development permits, the activity does not need to involve innovation.

¹³ https://www.intrafish.no/pressemeldinger/liste-priser-og-kjopere-i-auksj onene/2-1-362342

¹⁴ https://ilaks.no/fiskeridirektoratet-offentliggjor-budgivere-til-lakseauks jonen-etter-arkiv-blemme/

¹⁵ https://www.intrafish.no/kommentarer/hva-er-verdien-av-en-konsesjo n-/2-1-228300

¹⁶ The latest data on permits (2020) show >6% to biological/genetic innovation, 31% to technology and operation, 12% to fish health and 36% to innovation on feed. https://www.fiskeridir.no/Akvakultur/Tildeling-og-till atelser/Saertillatelser/Forskningstillatelser/Alle-forskningstillatelsene

Box 1

Facts about selection using genomic information and genetic improvement using gene editing (such as CRISPR).

Aquantitative trait locus (QTL) is a locus (a section or region of DNA) associated with the phenotypic variation of a trait. A QTL is linked to (i.e., a marker of), or contains, gene(s) that control specific traits. In marker-assisted selection, information on OTLs is used and allows for more accurate and efficient selection for a trait (such as disease resistance) than traditional selection using only phenotypic information. The marker may be a gene or DNA sequence that is located very close to the desired trait, and is, therefore, inherited along with the trait. The method has proven efficient in increasing disease resistance for IPN in Atlantic salmon, where a single OTL was responsible for the bulk of genetic variation (Houston et al., 2008; Moen et al., 2009). Genomic selection is an advanced form of marker-assisted selection in which genetic markers covering the whole genome are used, and selection is based on the joint merit of all markers across the genome (Meuwissen et al., 2001). By this, traits that are challenging or very costly to measure on live candidates (e.g. carcass quality and disease resistance) can be selected for with higher accuracy, and within families. Traits can also be genetically improved using gene editing, such as through CRISPR technologies. This technology enables the immediate generation of genomic diversity for breeding, implying that a wide range of different genotypes with ample genetic diversity for selection could be generated within only one generation (Wolter et al., 2019). The latest gene editing technologies allow for making predefined changes to targeted positions of the genomes of terrestrial as well as aquatic species (West and Gill, 2016). It has been used extensively in different fish species from basic functional studies as well as applied research such as disease modelling and aquaculture (Zhu and Ge, 2018). In Norway CRISPR/Cas 9 has been used to make sterile salmon (Wargelius et al., 2016). Applications for disease or parasite resistance in salmon is currently under investigations in several research projects. Furthermore, knowledge on potential and impacts of gene editing for such polygenic traits is still lacking in farm animals.

biological innovation since 2015, but again, these are not related to lice resistance.¹⁷ Unlike the Development permits, the Research permits cannot be converted to ordinary commercial permits to produce salmon for food.

In summary, there has been little or no effort or effect from current policy instruments to instigate innovation against salmon lice (Greaker et al., 2020; Vormedal et al., 2019). This could imply that there is an untapped potential for highly potent policy instruments that are designed to enhance private actors' inclination to shoulder the risks of adding lice resistance to their breeding goal.

In Section 4.2, we present and discuss the results of our examination of the interests of and perceptions about policy interventions among key actors in the salmon farming and breeding industries.

Prior to this discussion, we present the state of breeding for lice resistance.

4. State of lice resistance breeding

Due to a great demand for secrecy, it is difficult to ascertain the precise situation of supply and demand for lice-resistant roe in the salmon sector. Also, there are yet no controlled studies comparing and documenting the effects of lice resistance to other lice-reducing instruments. Still, our data material suggests that there may be a greater potential for lice resistance breeding than has been presently achieved.

Three of the four salmon breeding companies operating in Norway have started selecting for lice resistance in addition to their standard breeding goals. SalmoBreed (bought by Benchmark in 2014) pioneered testing and selection in 2007 (Holan et al., 2017). Next in line was AquaGen (owned by EW Group since 2007), which started selection with its 2011 generation (AquaGen, 2017). Marine Harvest (now Mowi) started their first testing in 2014 and started selection in 2016 (Gjerde, 2018a), and SalMar will decide on a possible weighting of lice resistance in their salmon breeding program in 2020.¹⁸

GS (Meuwissen et al., 2001) is proven to be an efficient selection method to target traits affected by many genes (see Box 1) and is already or planned to be implemented by all breeding companies.

There are promising results from breeding for lice resistance. In a project supported by the Research Council of Norway and the Norwegian Seafood Research Fund (FHF) (Hægermark, 2012. Gjerde, 2013)

¹⁸ Interviews with breeders, Spring 2020.

predicted a 75% reduction in lice per fish after five generations of family selection for lice resistance only. AquaGen reported a 40–45% realised reduction of lice infestation in a selection group after only two generations of selection for lice resistance only (AquaGen, 2016, 2017; Jensen, 2018). SalmoBreed reported a 10% reduction in lice infestation after two and a half generations of selection for an aggregate breeding goal, including lice resistance (Hillestad et al., 2017). These results are consistent and show the difference between selecting for lice resistance only (rapid gains in lice resistance) and adding lice resistance to the aggregate breeding goal (slow gains in lice resistance). The former strategy is costly in terms of loss in conventional breeding goals, while the latter is costly in terms of delays in reaching lice resistance goals.

Although we have seen the occurrence of this type of innovation among the breeding companies, it may arguably be too little, too late. For example, in 2016, farmers' demand for lice-resistant roe was 6 million roe, while the breeders' supply was only 3 million roe.¹⁹ Our breeder interviewees confirmed that they cannot always meet farmers' demands for lice-resistant roe. This indicates that there may be untapped potential along this relatively sustainable innovation pathway. More could arguably have been achieved by providing public incentives to instigate an earlier start after the first publication on genetic variance in salmon lice resistance (Gjerde, 2013; Kolstad et al., 2005). Hence, we turn to our initial research question and explore and discuss what the main barriers are and how to explain the apparent gap in emphasis on ("full") lice resistance in salmon breeding goals in Norway, and the potential of future technological innovations, regulations, and policies.

5. Results and discussion

In this section, we examine how salmon farmers and breeding companies view the main barriers to and potential for innovation through the biological pathway of breeding. We apply the factors presented in Section 2 that may affect farmers and breeders' scope for and interest in choosing lice resistance breeding. Regarding scope, we look at the relationship between emerging breeding technologies and the legal acts regulating and constituting the framework for these technologies (Section 4.1). This also relies on scientific knowledge concerning the technological potential to develop a lice-resistant fish, taking the polygenic nature of lice resistance into consideration. Regarding interest, we examine how farmers and breeders consider the potential to encourage lice-resistant fish breeding either through market instruments (patents)

¹⁷ https://www.fiskeridir.no/Akvakultur/Tildeling-og-tillatelser/Saertill

atelser/Forskningstillatelser/Alle-forskningstillatelsene

¹⁹ Personal communication, Bjarne Gjerde, Nofima, 16 December 2016.

or through policy instruments (Section 4.2). Essentially, both patents and policy instruments concern how to recapture investments in lice-resistant roe.

5.1. Emerging technologies and changing regulations affecting lice resistance breeding strategies

Let us first look at the technological scope for producing lice-resistant roe and fish. Typically, breeding programs utilise phenotypic information from breeding candidates and their relatives together with pedigree information to estimate the genetic value of the parents of the next generation. In addition to family selection (traditional selective breeding), DNA technologies have promoted novel selection methods, such as MAS and GS to enhance the accuracy of selection (see Box 1). Both MAS and GS have been applied in selection for salmon lice (Lepeophtheirus. salmonis in Norway and Caligus Rogercresseyi in Chile). Still, selective breeding is a long-term approach of accumulating genetic selection response over several generations, up to 10 generations to halve or eliminate the number of lice treatments, depending on the selection intensity (0.2 or 0.01 selected proportion in simulations, Gharbi et al., 2015). More recently, genome editing technology has made it possible to make specific changes in the genome in a much shorter time. Genome editing can introduce favourable changes to the genome, such as fixing alleles at existing loci, creating new synthetic alleles, or introducing alleles from other strains or species (Doudna and Charpentier, 2014). Further, for widespread adoption, the genome editing technologies still need to be seamlessly integrated in well-managed selective breeding programs (Gratacap et al., 2019). Due to polygenic inheritance (Houston et al., 2014) and low-to-moderate heritability (Gjerde et al., 2011; Tsai et al., 2016), GS is still widely used for many traits and species, including lice resistance in Atlantic salmon.

There is increasing scientific knowledge concerning the successful effects from selecting for lice resistance. The complexity of polygenic inheritance has the upside that there is very little risk that lice would adapt to lice-resistant fish (i.e., lice adapting through natural selection to infect resistant fish). Although bacteria and viruses have much shorter generation intervals than salmon lice, there are many examples that selective breeding against infectious diseases in farm animals caused by such pathogens have shown long-term positive results (Heringstad et al., 2003; Storset et al., 2007). In sheep, selection for resistance against ectoand endoparasites has shown similar favourable responses without the experience of parasites with higher resistance adapting to hosts (Kemper et al., 2009). Based on a simulation study of gastrointestinal nematode parasites in sheep, it was concluded that it is unlikely that the sheep parasite will adapt to hosts with genetically improved resistance (resulting from selection) over a 20-year time frame (Kemper et al., 2013). Compared to medicinal treatments, which eradicate all but the hardiest lice (which proceeds to multiply as medicinally resistant), breeding strategies for lice resistance are long-term and dynamic, and have a broader spectrum of mechanisms (Gjerde, 2018b). Breeding also compares favourably to the development of a lice vaccine, which would target very specific biological mechanisms in the interaction between pathogen and host, and which remains unsuccessful after a decade of research.^{20,21}

Emerging technologies may have a broader scope for overcoming the challenges posed by the polygenic traits of lice resistance. Most of the actors we interviewed saw a significant potential for lice resistance through gene/genome-editing technologies. Several interviewees called it a potential game-changer, although there was also some hesitance regarding whether this technology may be overrated. CRISPR—currently the most relevant technique for gene editing—cannot altogether remove the problem of lice resistance being a polygenic trait. Although CRISPR may be less relevant for improving polygenic traits, it opens the possibility of going beyond the genetic variation of existing breeding populations of fish and utilises alleles from the wider genetic material of salmon; for example, DNA segments in liceresistant Pacific salmon species, such as coho salmon (*Oncorhynchus kisutch*) and pink salmon (*Oncorhynchus gorbuscha*). Unlike the Atlantic salmon, the Pacific coho and pink salmon are hardly susceptible to lice. On that note, the FHF recently called for and funded a project for this type of research (FHF, 2020).

While new technologies may, thus, carry lice resistance breeding forward faster, there may be regulatory barriers stunting the speed of its development. This is essentially a question of whether organisms resulting from gene editing technologies will be defined as genetically modified organisms (GMOs) and (or) transgenic (cross-species), in which case the roe and salmon could be problematic, both in terms of the current Norwegian GTA and consumer acceptance, both in Norway and in global markets.

The Norwegian GTA regulates GMOs, with mandatory impact assessments that ensure that the GMO in question is sustainable, benefits society and is ethically acceptable. The regulatory framework replies to the fact that most European consumers, including consumers in Norway, have been very hesitant to accept GMOs as a source of human food. This has resulted in some of the strictest regulations of GMOs worldwide (Myhr and Rosendal, 2009; Olesen et al., 2011). European GMO regulations are sensitive to public opinion and have affected regulatory regimes in many developing countries (Faulkner and Gupta, 2009). Recent surveys by the Norwegian Biotechnology Advisory Board (NBAB, 2020) and Consumption Research Norway (SIFO) (Bugge, 2020) show that most Norwegian consumers have positive opinions about using gene editing in plants and animals, provided that it is beneficial to society and contributes to sustainable development (NBAB, 2020, p. 6). Examples of acceptable gene editing are instances that help in the climate adaptation of crop plants, reduce the necessity of pesticides, reduce crop losses, and improve animal and fish health. At the same time, most respondents were somewhat or very worried that the use of gene editing in plants or livestock could pose risks to health and the environment (NBAB, 2020, p. 6). Compared to a similar study from 2017, an increasing percentage of respondents worried about the risks and consequences of GMOs regarding nature and ecosystems, and the health and welfare of animals, including fish and humans (Bugge, 2020). Consumers have negative opinions toward the use of gene editing when it is used to change the appearance of plant and animal products or increase the productivity of livestock. Both reports concluded that consumers want gene-edited products to be labelled, and an increase in the request for labelling was noted from 2017 to 2020 (Bugge, 2020; NBAB, 2020).

Our respondents were aware of consumer scepticism and were, therefore, rather pessimistic about a future market response to GMOlabelled salmon products (even when GMO technology might lead to health and welfare benefits for the salmon). The NBAB (2020) and SIFO (Bugge, 2020) reports suggest, however, that consumers could become more accepting of gene-edited fish if the gene editing resolves health and environmental problems represented by lice, including reduced lice pressure on wild salmon.

The GTA is currently under revision and will possibly be harmonised with EU legislation. The NBAB has suggested distinguishing between three categories of technologies and breeding methods, where softer versions of the GTA may apply at the first and second levels.²² The first level concerns products that are based on gene editing, but that could have taken place through traditional breeding, such as collecting and selecting the genetic material of salmon within and between Atlantic

²⁰ https://www.uib.no/bio/59037/nytt-lakselus-laboratorium Accessed 4 October 2020.

²² https://forskning.no/bioteknologi-dna-genteknologi/bioteknologiradet-vilmyke-opp-loven-om-genteknologi/1266816 Accessed 18 June 2020.

salmon breeding populations. In that case, the suggestion is for level 1 technologies to require notification only; there would be no request for labelling and there would be no obligation to assess the results in terms of sustainability, societal benefits, and ethics. For level 2, comprising other genetic changes within the species, a simplified request for consequence or risk assessment would apply. Level 3 applies to transgenic organisms where the genetic material has crossed species boundaries or synthetic DNA segments have been introduced, for which the full demands of the original GTA would apply. Introducing new gene segments from other organisms, such as Pacific or coho salmon, into Atlantic salmon genes would be an example of the latter and imply the original GTA demands.

It is hardly surprising that all the actors involved in salmon breeding agree that they would prefer to see this softening of the GTA take place. This was clear from our interviews and confirmed by the hearing replies from EW Group and Benchmark Genetics.²³ For the same purpose, the actors are taking collective action at the EU-level to advocate for a similar softening of the EU gene technology regulations.²⁴ Their aim is that gene editing should not automatically spell 'GMO' if it is not a case of trans-genetics. The most used platforms for this lobbying are the European Aquaculture Technology and Innovation Platform (EATIP) and European Forum for Farm Animal Breeders (EFFAB). Salmon breeders and farmers constitute a small part of the EATIP and EFFAB stakeholders, which could imply a limited impact on policies, compared to the much larger agriculture sector. Still, the Norwegian salmon breeders that supply the major bulk of roe to salmon farmers are part of very large multinational corporations (e.g., EW Group and Benchmark) and may arguably be expected to have substantial influence through their corporations in lobbying policy makers. Moreover, it seems that a significant part of the European agriculture sector concurs with the aquaculture sector on softening EU gene technology regulations.²

While waiting for Norwegian and EU regulatory frameworks on gene technology to soften up, most breeders are nevertheless actively engaged in research and development aimed at exploring the potential of the CRISPR technologies in both research (as a tool) and for application in the operation of breeding programs. Their rational is that if the regulatory framework on GMOs should soften, they wish to be prepared.

Currently, new genome editing technologies through CRISPR do not offer quick-fix avenues to full lice resistance in salmon, but the sector is nevertheless investing in improving this trait using selective breeding. Hence, the main message to be drawn from this section is that, for the time being, it is up to more traditional (and more long-term) methods and technologies to reach the consented goal of lice resistance in salmon breeding. This means that we must look beyond the barriers raised by the technology-regulatory framework to identify how innovation in breeding might close the gap between the perceived current supply of and need for lice-resistant salmon roe.

5.2. Market and policy measures stimulating (or hampering) innovation

Turning to farmers and breeders' economic deliberations and willingness to choose lice resistance, it is widely acknowledged that adding a new trait to the breeding goal is costly. For breeders, it requires extra recording, DNA analyses and, in some cases, costly challenge testing of animals. When a new trait is added to the breeding goal, an additional cost applies through an initial phase of reduced genetic gain in the other, existing traits in the breeding goal. This cost is mostly, but not solely, carried by the breeder in terms of poorer competitivity to other breeders targeting fewer traits, such as, for example, faster growth and sexual maturity. Farmers may also carry the costs of slower growth for a time, but with lice-resistant roe, they may save other costs by reducing the number of lice-cleaning operations and losses during delousing treatments. Somewhat paradoxically, the slower gain in growth brought on by putting more weight on lice resistance may also make the salmon more susceptible to sea lice, because slower growth increases the sea phase period and, hence, the lice challenge period. In the longer perspective, however, the benefits may outweigh the costs. Farmers would still save on more lice-resistant fish and reducing the lice problem would also help improve their green image. Further, reducing the lice challenge along the coast may further the number of permits for salmon production, representing a major value for the industry, coastal societies and possibly even for the wild salmon. Norwegian society will also benefit from the public goods associated with these changes (e.g., employment and increased tax income and other ripple effects resulting from increased production).

5.2.1. Breeders' market perspectives on lice resistance breeding

An inherent characteristic and an economic challenge in breeding is that bringing forth fast-growing, disease-free fish is very expensive, whereas the result can be copied at very low costs by just multiplying a few broodstock due to the high fertility of fish. This makes breeding a risky business for investors although it may-and indeed has-provided tremendous long-term benefit-cost ratios for the salmon producing sector. Hence, breeders need to find ways to capture investments in the added breeding goal, such as convincing customers to continue to buy their premium broodstock and roe Olesen et al. (2007). Studying access to breeding material in the salmon sector in the 2000s, (Olesen et al., 2007) found that most salmon breeders were confident in the superiority of their own breeders' lines and, hence, saw no need to patent their results if possible. At the same time, they acknowledged their vulnerability if access to new and improved genetic material or traits should become severely restricted by other breeders' patents (Olesen et al., 2007; Rosendal et al., 2013). It was evident that most breeders preferred and practiced continuous upgrading (biological superiority) rather than patenting for controlling access to their breeding results (Olesen et al., 2007; Rosendal et al., 2006).

Fifteen years later, despite the privatisation of the breeding sector, the view that patents have little utility is still prevalent among our respondents. First, due to the polygenic nature of most traits, including lice resistance, patenting is hardly applicable and, hence, not suitable to stimulate such innovation. Second, one breeding company worried that, in the long run, patenting could result in a situation where they cannot choose between all traits to be included in breeding programs because other companies might possess patents on other genes (through genetic markers of QTLs, see Box 1), in turn affecting some of the desired traits. In effect, farmers might have to choose roe with only a few favourable traits (e.g., either PD resistance or ILA resistance) rather than roe with a broader range of improved traits (e.g., both PD and ILA resistance).²⁵ Most corporations represented among our respondents would prefer to publish their results to prevent others from patenting, rather than seeking patents themselves. In practice, there are some recent examples of patenting of genetic markers, such as the IPN patents (in Atlantic salmon and rainbow trout), although earlier findings of IPN markers were published instead of patented. Even for IPN, there are several avenues open to 'invent around patents' through different genetic markers of QTLs (see Box 1) and, hence, the patent strategy is a weak protection here as well. Still, breeders concur that the current structure with a few

²³ http://www.bioteknologiradet.no/filarkiv/2018/04/Benchmark-Genetics. pdfAccessed 29 November 2020.

²⁴ https://www.fabretp.eu/statement-gene-editing.html

²⁵ ilaks, 7 October 2016. Jan-Emil Johannessen, SalmoBreed, on how patenting could hinder combining a variety of traits in a single fish. https://ilaks. no/en-utbredt-bekymring-er-at-patenter-favner-for-bredt/ilaks, 6 October 2016. Jan-Emil Johannessen, SalmoBreed comments https://ilaks.no/spillere glene-er-endret/

big multinational players is forcing everyone in the direction of securing their investments through patents.²⁶ The strong competition among the four breeding corporations is also mentioned as a factor that reduces the pace of innovation, as it hinders cooperation (and exchange of knowledge and aquatic genetic resources across research groups and breeding programs) on research and breeding for lice-resistant roe.

Despite the apparent lack of market incentives, all the breeding companies are set on breeding for lice resistance. However, they do not go all in by selecting for lice resistance only, which we have seen is the costlier short-term strategy, even though it would produce much more rapid gains in lice resistance. The breeders all want to be responsive to demands from the salmon farmers by supplying both fast-growing and lice-resistant salmon roe. With a view to the seriousness of the lice problem, breeding for lice resistance started arguably late and demands from farmers came even later. How do we explain this reluctance of the farmers to farm salmon roe with stronger lice resistance?

5.2.2. Farmers' demands and needs for lice-resistant roe

Farmers are generally interested in fast-growing salmon, also because it may shorten the sea rearing period, which in turn reduces the need for delousing. Our salmon farming interviewees concur that the current level of lice resistance selection is not strong enough to significantly reduce the number of delousing treatments. This limits their interest in buying or demanding more lice-resistant roe from the breeding companies. Until a "fully" lice resistant fish is on the market, *roe with high growth trumps lice-resistant roe*.

A central and somewhat paradoxical reason for the low farmer interest may be the low maximum mean level of sea lice (0.5 mature lice²⁷) required by aquaculture regulations. There are two reasons for this.

First, there is a lack of knowledge concerning the effect of genetic improvements in lice resistance on the number of treatments required for not exceeding 0.5 female adult lice per salmon. Due to the request for this very low maximum level of lice infestation, the farmers will probably not be able to measure any effects of salmon with higher genetic lice-resistance in terms of fewer delousing treatments required to obtain a mean below 0.5 adult female lice per fish. The variation in mean numbers is generally lower than individual numbers, and scale effect implies that the variation in lice number is even lower at this low requirement level (<0.5). The paradox is that the strict measures against salmon lice may itself present a barrier to lice resistance breeding: the maximum presence of 0.5 adult female lice per fish makes it difficult to document or measure the possible favourable effects from a less-than-perfect lice-resistant salmon by the farmers.

Secondly, it follows that the same number of (costly and harmful) delousing treatments are required, again making it difficult to see or experience the desirable effects of lice-resistant roe and fish. Typically, if the treatments are only reduced from four to three, this may not be likely to convince salmon farmers that they should invest heavily in lice-resistant roe, because it is hard to observe and note from farming operations data. Breeders and farmers seem to agree that at least one delousing treatment needs to be prevented in order to choose more lice-resistant salmon compared to faster growing salmon. One interviewee pointed to this as a 'hen and egg' situation that stops farmers from demanding and buying more lice-resistant roe, which again stops the breeders from making the necessary investments in lice resistance breeding. Breeding for lice resistance is currently a long-term process, and although results are promising, they do not represent quick-fix solutions in the current situation.

This 'hen and egg' situation leads to a mismatch between the actual (societal, environmental, and economic) needs for lice-resistant roe and the supply from the breeders. It also accentuates how the salmon farming industry has historically tended to pay less for the roe than its real value in terms of cost-saving and increased benefits. The late attention to lice-resistant roe from farmers may be that the gain in this trait is not yet sufficiently high, which, it could be argued, might lead to an underestimated market value of lice resistance in the breeding goal. This could call for (legal requirements for) implementing non-market values of lice resistance in the breeding goal, as discussed earlier for animal welfare traits and traits with environmental impacts (Nielsen et al., 2005, 2006, 2010; Olesen et al., 2000). Furthermore, there is a need for more research and knowledge on the effects of genetically improved lice resistance on the number of delousing treatments required to keep below different mean levels of adult female lice per fish, including the current 0.5 level.

Another related negative 'hen and egg' tendency may be evolving, with yet another effect on breeding goals. As the farmed salmon are increasingly and severely stressed by delousing treatments, many big fish become susceptible to death from cardiomyopathy syndrome (CMS) close to slaughter (Veterinærinstituttet, 2017, p. 18). The frequency of CMS is increasing and has recently moved up as the second-worst threat to farmed salmon, surpassing PD in 2018, and now only surpassed by the lice itself (Veterinærinstituttet, 2019). Unlike PD, CMS is present all over Norway. In 2018, the cost of salmon deaths due to CMS reached a NOK 16 billion loss to Norwegian salmon farmers (Veterinærinstituttet, 2019, p. 52–54).²⁸ In effect, farmers are now increasingly asking breeders for CMS-resistant salmon roe; they need more robust salmon that can tolerate the tough delousing treatments. If breeders start earning more from delivering CMS-resistant roe than from lice-resistant roe, a paradoxical situation may arise that exposes more salmon to stressful mechanical treatments, while the lice situation and threat to wild salmon remains the same. This hardly seems compatible with the Animal Welfare Act or any policy goal for animal and environmentally friendly innovations for sustainable aquaculture.

5.2.3. Apparent low demand for policy instruments

Our respondents agree that government support for biological innovation on lice resistance could amend this situation. Following the government's recent abandonment of introducing economic rent in aquaculture, the salmon farming sector has both been criticised and praised for effective lobbying for their interests.²⁹ The salmon farming sector has been characterised by strong linkages between salmon firms, authorities, and public actors, allowing an institutional specialization that is well adapted to meet the demands of the sector (Aarset and Jakobsen, 2015). In contrast, the salmon breeders concur that they are not collaborating in lobbying the government for support. Competition between breeding companies interferes with their joining forces for a common cause through lobbying.

The breeding companies agree that breeding receives too little attention and too little reward for its great contributions to value creation in the salmon aquaculture sector. It is also acknowledged that incentives through policy instruments might have increased the pace of lice resistance, which would enhance sustainability (societal, costefficiency and environmental) in the sector. There may be various reasons for the lack of requests/lobbing for such policy instruments: First, in

²⁶ See media debate: https://ilaks.no/slik-bidrar-patenter-til-apenhet-og-inn ovasjon-i-havbruksnaeringen/ and https://ilaks.no/en-utbredt-bekymring-er-a t-patenter-favner-for-bredt/ and https://ilaks.no/spillereglene-er-endret/

 $^{^{\}rm 27}$ The level is set at 0.2 lice during a few spring weeks, when the young wild salmon migrate out to sea.

²⁸ https://www.dn.no/havbruk/laks/veterinarinstituttet/brit-hjeltnes/dodeli g-laksesykdom-sprer-seg-til-stadig-flere-anlegg/2-1-541773 Accessed 27 April 2020.

²⁹ https://finansavisen.no/forum/thread/59873/view Acessed 2 October 2020. https://www.dn.no/havbruk/grunnrenteskatt/oppdrettslaks/sjomat/s tortinget-vil-utrede-lakseskatt/2-1-348561 Accessed 2 October 2020.https ://www.dn.no/innlegg/oppdrett/lakseoppdrett/skatt/oppdretternes-superprof itt-pa-niva-med-vannkraftens/2-1-698189 Accessed 14 October 2020.

addition to the competitiveness that prevents breeders from lobbying the politicians, the aquaculture sector is already subject to a great deal of government interventions as it is. Hence, some argue, there is fatigue and perhaps some trepidation about introducing more interventions. Some add that the market is likely to respond adequately and more flexibly through demand and supply, than would a publicly controlled regime. In effect, more government interventions are not widely in demand by the corporations. Some point out the risk that the lice problem might be solved through other means and then all the resources put into lice resistance breeding would be a waste of time and money. Delousing through laser-treatment could be one such new method³⁰; however, a comprehensive study found it to be less hurtful to fish, but also that it only had a limited effect on lice (Bui et al., 2020).

Nevertheless, respondents agree that the market has failed to have an ideal effect on the development and application of lice-resistant salmon. Respondents acknowledge that innovations in genetics and breeding are key to retain salmon production in Norwegian fjords, arguing for policy instruments to stimulate lice resistance breeding. Moreover, breeders and farmers concur that if breeding companies had had access to stimuli for innovation in lice-resistance salmon, such as the Development permits, the sector might have been closer to a fully lice-resistant salmon today. One pointed out that the presence of such policy tools favouring biological innovation would have made it easier to argue for including lice resistance in the breeding goal vis a vis their internal boards (who make decisions on breeding goals).

Following these deliberations, several interviewees called attention to how it is puzzling that Norwegian fisheries authorities have not considered aiming the Development permits (or other types of permits) at lice resistance through biological innovation. For instance, this could have been done through the Broodstock permits (which are issued free of charge), by adding legal requirements for breeders to prioritise lice resistance in their breeding goals. Issuing free Broodstock permits that simultaneously allow for commercial salmon production would mirror the Development permit arrangement. However, using Broodstock permits might not really be very effective for this purpose, as it is very costly to keep large quantities of biomass (fish) in cages. For parts of their fish stock (broodfish candidates) it is only later in the season (after the selection of broodfish) that it is possible to slaughter and market fish from the broodstock concessions. Moreover, the broodstock incentive would mainly be suitable for integrated companies (who engage in both farming and production) and be less applicable to non-integrated and specialised breeding companies. Still, also those that are not farming themselves may enter partnerships with salmon farmers to utilise the permits for the dissemination and marketing of roe and smolt. In any case, the popularity of the Development permits shows that there is a lot of money involved and that these policy instruments have been more than enough to instigate a lot of creativity and innovation along the mechanical innovation pathway. The biological pathways have a potential for similar success.

Finally: are our findings likely to apply in other salmon producing countries? Lice constitutes a significant problem where the Atlantic salmon is concerned, which makes it relevant to inquire about whether our findings could be generalised to breeding for lice resistance in other countries. Salmon production constitutes a very large and growing industry in Norway compared to most other salmon producing countries, and the sector is characterised by high levels of regulation (both sticks and carrots) and close interaction between producers and public authorities. In comparison, salmon production is a much smaller industry in Canada and Scotland and the regulatory framework is reportedly low in Chile. While the genetic and technological potential is likely to be similar, the variation in structural and political / legal traits would seem to warrant specific studies of the aquaculture sectors elsewhere.

6. Conclusions

The potential for lice resistance breeding is significant, however, while it is neither ignored nor unexploited, it is arguably underexploited. The results of our examination and inquiries are complex with ambivalent and inconclusive indications and opinions about what causes this. However, encouraging results on selection responses for lice resistance have certainly been obtained, although there is a need for more knowledge and research on the impacts on number of delousing treatments. There is also agreement among the stakeholders that more attention to breeding for lice resistance could be beneficial, and that policy instruments might help achieve that goal. The ambivalence stems from what appears as policy intervention fatigue in the salmon farming sector, which keeps actors from demanding additional interference from the government. This is compounded by a high degree of competitiveness among breeders, which keeps them from cooperating and demanding more engagement from the authorities. Thus, lice resistance breeding is not only characterised by being a public good 'game of chicken', it is also riddled by another poultry-related trait, the 'hen-andegg situation', where farmers and breeders are reluctant to make the first move on the full-scale application of lice-resistant roe.

Contrary effects of market competition and regulatory fatigue might help explain why the aquaculture sector has not lobbied for policy instruments aimed at stimulating lice resistance innovation. These factors do not, however, explain what seems like a lack of attention to lice resistance breeding from Norwegian fisheries authorities. The authorities have not made lice-resistant roe mandatory and they have not established specific permits to stimulate lice resistance innovation. A rather counter-innovative effect, but also a short-term benefit, from not having a fully effective lice-resistant salmon on the market is that a range of Norwegian delousing industries worth an annual ${\ensuremath{\, \in \, }}$ 500 million are kept busy and employed.³¹ In this perspective, the Development permits may have been expedient in strengthening less-sustainable industries at the expense of biological innovation, and at the expense of rural employment, economies, and settlements. Norwegian fisheries authorities, which have been governed by liberal parties for the last seven years, may be right in interpreting the companies' reluctance about demanding more government intervention. On the other hand, the lack of industry demand for policy intervention, is hardly an excuse for failing to respond to the urgent social and environmental needs for tackling the lice problem, for which our respondents agree that genetics and breeding are key to a solution. The call from the FHF in 2020 for research projects on innovation on lice resistance indicate rather late remedial action, initiated by the aquaculture sector itself.

This also reflects the need for more research and knowledge on both breeding technologies/strategies, as well as the short- and long-term impacts on the number of delousing treatments, increased resilience in fish to delousing treatments (through CMS resistance breeding, for example) and related aspects of animal welfare and ecosystems (including wild salmon and crustaceans) compared to other measures taken against salmon lice.

Author statement

The authors, Kristin Rosendal and Ingrid Olesen have contributed equally (approx. 50-50%) to all roles on Conceptualization; Data curation; Formal analyses; Investigation; Methodology; Validation; Writing – original draft; Writing – review & editing as well as Funding acquisition and Project management.

³⁰ Accessed 28 November 2020.

 $^{^{31}}$ As one farmer put it, 'If breeders succeeded in producing a fully lice-resistant fish, we would buy it, but then those employed in the delousing-treatment business would be out of a job'.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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- $\label{eq:constraint} \begin{array}{l} 7C9274ee3f94254109a27f9fb15c10675d\%7C0\%7C0\%7C637703173959159147\%\\ 7CUnknown\%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzIi\\ LCJBTil6lk1haWwiLCJXVCI6Mn0\%3D\%7C2000&sdata=SOF7JIn8eveP99gBrFC\%\\ 2FjnpJ5qWIwRMUDkJUNnLgOSw%3D&reserved=0. \end{array}$
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