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REVIEW

REVIEWS IN Aquaculture

Development of cod farming in Norway: Past and current biological and market status and future prospects and directions

Velmurugu Puvanendran[1,2] | Atle Mortensen[1,2] | Lill-Heidi Johansen[3] | Anne Kettunen[4] | Øyvind J. Hansen[1,2] | Edgar Henriksen[5] | Morten Heide[6]

[1]Production Biology, Nofima AS, Tromsø, Norway
[2]Center for Marine Aquaculture, Nofima AS, Tromsø, Norway
[3]Fish Health, Nofima AS, Tromsø, Norway
[4]Breeding and Genetics, Nofima AS, Ås, Norway
[5]Industrial Economics, Nofima AS, Tromsø, Norway
[6]Marketing Research, Nofima AS, Tromsø, Norway

Correspondence
Velmurugu Puvanendran, Production Biology, Nofima AS, Muninbakken 13, 9019 Tromsø, Norway.
Email: Velmurugu.puvanendran@nofima.no

Present address
Atle Mortensen, Kanakva, Alta, Norway

Funding information
Nærings- og Fiskeridepartementet

Abstract

Atlantic cod is a historically abundant species in the North Atlantic region and has contributed to the prosperity of many nations. But a decline in stocks in the last century has prompted to initiate commercial farming of cod in captive conditions. Several approaches have been employed ranging from stock enhancement, capture-based aquaculture and intensive cod farming. However, except for the enhancement efforts which were carried out for almost a century, efforts on other methods were intermittent coinciding with lower quotas. Intensive farming was attempted in Norway, Scotland, Ireland, Canada, Iceland and Faroe Islands in the 2000s. But it was carried out hastily to cash in the demand for cod in the market even though there were many biological knowledge gaps that are required for a successful aquaculture venture. The reasons for the failure of commercial farming in Norway during the 2000s were not only because of limited knowledge of the biology of cod but also the economic meltdown in Europe in 2008. Cod farming came to a halt; however, the Norwegian National Cod Breeding Program (NCBP) initiated in 2003 continued to operate and produced a fifth generation of a domesticated cod in 2019. Efforts to fill the gaps and the selective breeding for better growth and disease resistance within NCBP have improved the quality of the juveniles produced. We will discuss the past efforts and reasons for failure in farming of cod, how the current situation looks and the future direction in terms of cod biology, political atmosphere and market.

KEYWORDS
Atlantic cod farming, breeding programme, challenges, cod biology, history, Norway

1 | INTRODUCTION

Atlantic cod (*Gadus morhua* L.) has historically been the most important species for fisheries in the North Atlantic, and it has been of major importance for the settlement along the coasts on both sides of the ocean. The history of cod and cod fisheries is nicely described in the award-winning book: 'Cod: A biography of the fish that changed the world'.[1] Cod is an unpredictable food source, and large fluctuations

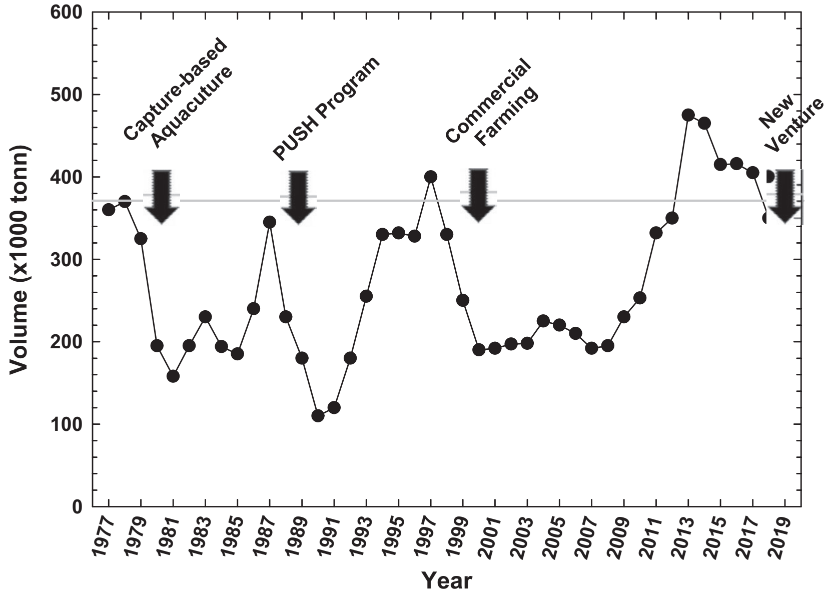

FIGURE 1 Swinging interest in cod farming in Norway and significant events during 1977–2018

in quotas have been experienced over the years. The traditional cod fishery in Norway is also very seasonal, with most of the catch taken during the spawning season from January to May. Several solutions have been proposed to overcome the challenges of unpredictable and seasonally variable access to wild cod. These include stock enhancement, catching and holding cod alive, capture-based aquaculture (feeding live caught cod) and intensive cod farming.

The first stock enhancement project with cod started in 1878 in Massachusetts, USA. It was followed by a similar project in Flødevigen in the south of Norway in 1882. In this extremely long-lasting project, yolk-sac cod larvae were released in Norway almost every year until 1967.[2] None of these two projects gave significant increase in the mature populations of cod in the release area, but they have contributed with valuable knowledge of reproduction and larval biology of cod.[3,4] However, the projects failed in producing larger cod juveniles. The breakthrough came in the 1970s when Øiestad et al[5] were able to produce cod juveniles in a 4400 m^3 constructed basin with natural plankton as feed. In 1980, they started mass production of juveniles in a 60,000 m^3 enclosed saltwater pond.[6] The purpose of this project was still restocking and not commercial aquaculture.[2]

Feeding of live caught cod in sea cages represents another step in the direction of commercial cod farming. This started in Norway in the mid-1980s with the purpose of selling high-quality cod outside the ordinary harvest season. In contrast to capture-based aquaculture of other species, cod is caught not as juveniles but as adults of more than four years old.[7] Because of the migration pattern of cod, they can be caught close to the coast at low cost during spring in Northern Norway and then be fed for some months and sold at significantly higher than normal price during autumn. Still, capture-based aquaculture of cod only accounts for a minor part of the wild catch, and the interest in doing this is inversely related to the extra cod quotas as a reward for landing live cod.[8]

The Norwegian Research Council launched a large programme for 'Development and promotion of sea-ranching—PUSH' in 1990, where cod was one of the four species included.[9] The others were Atlantic salmon (*Salmo salar*), Arctic charr (*Salvelinus* alpinus) and lobster (*Homarus gammarus*). The ambition was to develop sea ranching as a new coastal industry. But the initiative challenged the existing legislation and triggered conflicts of interest. The programme was terminated in 1997 without reaching the original goals. However, the programme improved the technique for intensive production of cod juveniles in tanks, using artificially produced rotifers (*Brachionus plicatilis*) and *Artemia* instead of natural plankton as feed. That was an important stepping stone for the commercial cod farming, which boomed some years later.

With a renewed interest in cod farming now in Norway, in this review we will discuss the factors that triggered the start of the commercial farming in early 2000s in North Atlantic countries and highlight the events responsible for the collapse of all farming activities in late 2000s followed by the improvements made in solving the biological challenges in the last 10 years. Then, we will explain the new cautious and smooth approach related to solving biological challenges, securing investments and developing new marketing methods.

2 | START OF COMMERCIAL COD FARMING—TRIGGERING FACTORS

The efforts which have been made to minimize the effects of the unpredictable wild catch of cod show a conspicuously concurrence with falling quotas for wild cod (Figure 1). A natural explanation for this is that prices for cod tend to move in the opposite direction of the quotas, giving higher price when the supply to the market is reduced. Around the millennium shift, the Norwegian cod quotas had

TABLE 1 Production of farmed cod (in tons) in different North Atlantic countries from 2005 to 2018

Year	Canada	Denmark	Iceland	Norway	UK	Russia
2005	0	0	636	7409	69	7
2006	0	0	1598	11,087	543	0
2007	0	0	1467	11,104	1111	0
2008	0	5	1502	18,052	1822	0
2009	0	0	1805	20,924	0	0
2010	0	0	1317	21,240	1	0
2011	0	0	877	15,273	0	0
2012	0	0	893	10,033	0	0
2013	0	0	482	3770	0	0
2014	0	0	310	1386	0	0
2015	0	0	74	5	0	0
2016	0	0	59	450	0	0
2017	0	0	29	492	0	0
2018	0	0	29	495	0	0

Source: OECD Statistics; https://stats.oecd.org/Index.aspx?DataSetCode=FISH_AQUA

sunk to a low level of around 200,000 tons per year, and it was expected that the quotas would stay low for several years to come.

At the same time, the Norwegian salmon farming had laid behind a difficult period in the early nineties and is now in a period of fast growth, with a production increase of around 8% per year.[10] The interest to join the salmon farming industry was therefore high, but the restrictive concession policy in Norway prevented access to this profitable profession. However, access to cod farming licences was not regulated by the Fisheries Directorate, and therefore appeared to be an attractive alternative. Not at least since the challenge of producing high numbers of juveniles under controlled conditions seemed to be solved.

3 | POLITICAL BACKGROUND/'PUBLIC ROLE'

Reduced cod quotas in the 80s and after the millennium actualized the necessity of political strategies to secure employment and settlement along the coast and especially in northern Norway. Cod farming came up as an alternative to meet the challenges, and the idea was supported by the scientific community. The Norwegian Industrial and Regional Fund (Statens Nærings og Distriktsutbyggingsfond, SND) carried out a study that recommended a large-scale industrial investment in cod farming from fry, via farming in good localities, to slaughter. In 2001, SND together with the Research Council presented a national action plan for cod farming. Estimated potential was 400,000 tonnes of farmed cod annually. However, the known biological bottlenecks such as fry production, growth rate and early sexual maturation, disease resistance, lack of cod specific feed and breeding technology had to be refined.

The need to strengthen the business community on the coast to compensate for reduced cod quotas, and especially in Finnmark (Norway's northernmost county), became a further reason for investing in cod farming. This led to political promises being made about investing in the north, and the University of Tromsø, together with the NORUT group, seized the opportunity. The Norwegian government decided to start a national cod breeding programme in Tromsø to support the emerging cod farming industry with genetically improved fish material. The task was given to the research institute Fiskeriforskning (now Nofima), which should also carry out applied research connected to the breeding programme. At the same time, a private company, Marine Breed, has also started a breeding programme for Atlantic cod in Norway in 2002, however, became defunct in November 2011 with the collapse of the cod farming.

SND and the Ministry of Fisheries both had far-reaching strategic plans and contributed to the financing of actors, research and breeding stations. When banks considered the risk too great to make capital available for biomass build-up at sea, the obvious answer to the lack of inflow of private capital was to turn to the state to put in place schemes that both made capital available directly and that relieved risk. The banks were still reluctant, but SND and various marine public investment funds were established.[11,12]

4 | WORLDWIDE STATUS OF COD FARMING IN THE 2000S

There has been great interest in cod farming in several countries in North Atlantic region, namely Norway, Canada, United Kingdom (Scotland), Iceland, Ireland and USA in the 2000s. Among these countries, Norway had 16 hatcheries and capable of producing more than 4 million juveniles and a harvest volume of 1500 tons while other countries had 1–3 hatcheries with production capability of 0.1 to 0.5 million juveniles and 200–1000 tons of harvested fish.[13] Table 1 summarizes the production of farmed cod (in tonnes) in different North Atlantic countries from 2005 to 2018 (Source: OECD Statistics). In Newfoundland, Canada Sea Forest Plantation pioneered cod farming in the late 1990s having their own hatchery and met with success producing large number of cod juveniles[14] but was destroyed in fire accident in 1997. Later, another company Northern Aqua Ventures built a hatchery capable of producing 10 million cod juveniles but due to failing to secure the investor support. Cooke Aquaculture Ltd, In New Brunswick, Canada, entered into sea cage cod farming in 2003 purchasing the cod juveniles from Great Bay Aquaculture in Portsmouth, USA, and successfully harvested more than 1000 m.t. of cod in 2009. However, the economic crisis in the late 2000s, production challenges and loss of government support ended this venture.[15]

In Iceland, Marine Research Institute of Iceland and a company (Fisky Ltd.) has produced cod juveniles for farmers, but the quantity was not sufficient to support the on-growing. In Iceland, sea ranching of cod was the dominant cod farming activity during the 2000s.[16] In UK (Scotland), the Shetland organic cod farming brand of 'No Catch fish' was launched by Johnson Seafarms in 2006 controlling entire value chain from hatching to marketing. However, it went into administration in 2008.[16] Ireland started a pilot cod faming in the early 2000s with a partnership between Martin Ryan Institute (MRI) in Galway (producing juveniles) and a company Trosc Teo (sea cage farming) but never took off to a larger commercial farming.

5 | REASONS FOR THE FAILURE OF COD FARMING IN THE 2000S

As mentioned previously, the cod farming boomed in the early 2000s with several companies involved as juvenile producers in land-based system and on-growers in sea cages in Norway, Scotland, Iceland, Canada and Faroe Island. However, the growth was short-lived and in the late 2000s the farming activities dwindled down due to several reasons. We will discuss the reasons for this decline in cod farming activities below.

5.1 | No existing/limited knowledge of intensive cod juvenile production

One of the reasons for rushing to huge farming efforts in the 2000s involving several companies was the success of producing better quality cod juveniles in extensive pond systems in the 1970s and 1980s in Norway[2,5,6] and optimism due to the rapid and successful development in salmon farming. In the ponds, the cod larvae fed with their natural prey (mainly copepods) and it is well known that copepods have superior nutritional quality compared with the cultured livefeed that are used in intensive production of all marine finfish species.[17,18] Although good quality juveniles were produced, the volume of production was not enough to support a commercial cod farming industry. Further, difficulties of producing large quantity of copepod nauplii to support the production several millions of cod larvae in intensive systems necessitated to use other common cultured livefeed such as rotifers and Artemia.[19] Both these livefeed were successfully produced in large quantity and have been used in the production of other marine finfish species such as seabream, seabass and turbot.[20] Although rotifers and *Artemia* easier to be produced, their nutritional quality is far inferior to the copepods even after nutritional enrichments.[21,22] Thus, the failure to produce robust cod juveniles created cascading effects and led to the downfall of the cod farming along with other reasons that are discussed below.

5.2 | Larval mortality

Research on intensive production of cod juveniles has been ongoing since the mid-1990s in the North Atlantic region but mostly in a stop and go fashion. Several studies were undertaken aiming to improve the growth and survival of larval and juvenile cod through manipulating prey quality,[21,23–26] prey concentration,[27] temperature,[28] light regime,[29–31] weaning and on-growing diets.[32] These efforts improved the growth of cod larvae about 50% and increased the survival from 5% to 10%. Similar research in Europe and North America has helped in developing reliable larval and juvenile rearing protocols,[33,34] and these protocols have been further refined in the last few years.[18,35,36] Still variable survival of embryo, larvae and early juvenile among different egg batches within a season exist. Differences in survival between egg batches of Atlantic cod related to egg quality have also been reported.[37] Further variable growth within the same cohort of larvae and early juveniles created discrepancy in size and increased cannibalism-related mortalities.[38,39] It is reported that the cannibalism-related mortality could reach above 30%.[40] This necessitated the commercial producers to size grade the juveniles to reduce the cannibalistic mortality; however, this practice increased the handling of the juveniles repeatedly and weakened the fish[41] and subsequently could have increased the mortality. Several husbandry tactics were used to minimize the size variation such as increased feeding and increased water velocity to reduce interactions among large and small fish, however, with limited improvement.[38,40]

5.3 | Feed/feeding

Cod larvae require livefeed during start-feeding, thus livefeed is a vital part of the cod larval production. In intensive cod larviculture, enriched rotifer and *Artemia* are used as livefeed. Several studies have attributed the quality of juveniles to the nutritional quality of livefeed during the larval stages.[42] To meet the nutritional quality of the larvae, rotifers and *Artemia* need to be enriched with nutrients before feeding the larvae. Lipid has been identified as one of the most important nutritional components that affects the cod larval performance.[25,43–45] These early studies have identified the basic requirement of polyunsaturated fatty acids (PUFA) such as arachidonic acid (ARA; 20:4ω6), eicosapentaenoic acid (EPA; 20:5ω3) and docosahexaenoic acid (DHA; 22:6ω3) for neural development, pigmentation, growth, survival and reproduction of marine finfish. Cultured rotifers and *Artemia* lack several of these essential fatty acids both in required amount and in proportion, even after enriching with commercially available lipid emulsifiers. Several studies have been carried out to improve the nutritional quality of the cultured livefeed but could not match the nutritional quality of the copepods which are the main natural prey for cod larvae in nature.[18] That was reflected in the growth and quality of the larvae and juveniles, where larvae fed on the copepods had significantly higher growth and quality than the larvae fed with cultured livefeed.[18,46,47] Recently, it has been showed that type of prey during the first feeding (Copepod and cultured livefeed) differentially affects the microRNA expressions and their targets in cod larvae.[48] They also suggested that these targets control the proliferation of myoblasts, thus affecting the growth in cod larvae. Nutritional content of dry diets is easily manageable, and thus, development of suitable dry diets with different feeding techniques combined with cultured livefeed has been suggested as a strategy to improve the quality of cod juveniles.[36,49] Some improvements in developing the dry diets were made in the 2000s but stalled after the crashing of commercial production of cod.[32,50] All these issues in live feed and inert feed development resulted in poor quality cod juveniles which eventually would have affected the performance of the juveniles in sea cages.[46]

5.4 | Juvenile quality—Deformities

In the early 2000s, it was reported that more than 50% of the cod juveniles produced in Norwegian commercial hatcheries had severe skeletal deformities.[51] This was attributed to egg incubation and larval rearing conditions such as temperature and water quality[52] and poor nutritional quality of the livefeed and formulated diets[53] such as deficiencies in phosphorus and vitamin C,[54] excess vitamin A[55] and oxidative degradation of lipid but also to genetics.[56] Wild-caught cod juveniles have lower skeletal deformities compared to intensively reared cod juveniles fed with cultured live feed, and 20–75% of skeletal deformity was reported in cultured cod.[57] However, wild cod juveniles with deformities may have lower survival due to their reduced capabilities in escaping from predators and this could be one of the reasons for lower incidence of deformities in wild-caught juveniles.[58] Cod larvae fed with copepods had significantly lower skeletal deformities compared to rotifer fed cod larvae[46] which shows the importance of early larval nutrition on the development of skeletal deformities in juveniles and failure of the cultured live feeds in meeting the nutritional requirements of developing cod larvae. Further due to poor nutritional quality of cultured live feed and weaning diets, in the 2000s quality of the cod juveniles produced was below par[13] and resulted in severe deformities, poor growth and survival in sea cages (Figure 2). This resulted in discarding majority of the juvenile cod produced and loss of resources.

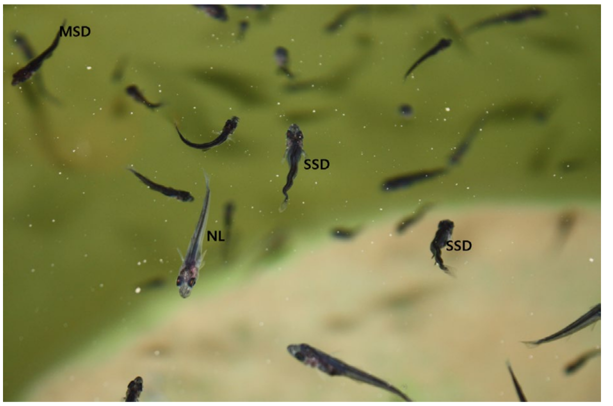

FIGURE 2 Farmed cod larvae with skeletal deformities in 2010. NL, normal larva; MSD, mild skeletal deformity; SSD, severe skeletal deformity

5.5 | Broodstock development

During the 2000s surge of commercial cod production, production logistics were concentrated solely on mass production of cod juveniles. Cod is a mass spawner, and an adult cod of 5 kg can produce one million eggs.[59] Due to this unlimited supply of eggs, broodstock development was neglected and resulting in poor quality eggs and subsequently produced poor quality juveniles. Broodstock nutrition did not get much attention, and fish were fed with fresh or frozen fish with vitamin supplementation and the available broodstock dry diets during this time did not meet the nutritional requirements of the broodstock.[60] Broodstock were photomanipulated to spawn year-around; however, temperature was not controlled. Temperature is an important environmental variable that affects gonadal development, and poor temperature management has resulted in poor gamete quality.[61,62] Besides the ovarian development, male broodstock development was also neglected. It is known that the sperm quality can affect the fertilization success and consequently the hatching success and larval quality.[62–64] While egg quality was visually inspected (bad eggs have cloudy appearance) and discarded, no such visual quality control has been used in determining the sperm. Overall, broodstock management was neglected during this period of commercial development of cod production.

5.6 | Escapes

During the heightened commercial farming activities of Atlantic cod in the 2000s in Norway, farmed cod escapes from the sea cages were frequently reported.[65] The main reasons for these escapes appear to be behaviour of the cod (net biting),[66] inferior technical standards of the nets and increased predator activity around the sea cages who damage the nets.[65,67] Based on their interviews with cod farmers and observations, Moe et al. suggested that technological improvements of net pens and cage nets are required to withstand the physical forcing of extreme storms and the biting of cod and their predators (seals).[65] Hansen et al showed that genetic variability in cod escape behaviour exists[68] and suggested that selective breeding for this trait could reduce the incidents of escape.

5.7 | Sexual maturation

One of the unsolved issues in the 2000s (even today) was early sexual maturation of cod. Early sexual maturation is a troublesome because it can result in reduced growth[69] (energy reserves diverted to gonadal development rather than to growth), increased post-spawning mortality and poor flesh quality. Thus, it represents economic loss to the farmer but may have ecological and genetic impact on wild fish. Controlling light conditions in tanks and sea cages can delay sexual maturation in farmed cod but it cannot stop the maturation.[70,71] In tanks, controlled light conditions can postpone the gonadal maturation for longer periods but in sea cages the success is limited. Nearly 100% of all cod mature at two years of age under normal farming conditions,[72–74] whereas wild populations generally mature at a higher age. Although not documented, the early sexual maturation of farmed cod could have reduced the profit margin of farmers during the 2000s cod boom and partly responsible for the collapse of the cod farming.

Spawning activities of mature adult cod in sea cages have been discussed in the 2000s and possible mixing of these farmed origin gametes, embryos and larvae with the wild origin.[75] Further, an increase in spawning activities year to year has resulted in a 20–25% increase in larval occurrence of farmed fish origin in adjacent fjords.[76] The embryonic survival through hatching is relatively low (0.5–14%) in North-east Arctic cod and North Sea cod,[77] and it is known that odds of a newly hatched cod larva to survive through adulthood is very minimal and only one in a million cod egg survives to the adulthood.[78] Thus, the long-term effect of the cage spawning on the wild population is unclear.

5.8 | Economic meltdown and increase in total allowable catch (TAC) for cod

The economic meltdown in Europe[79] and increase in TOC[80] in Norway were the two major contributors apart from the biological shortcomings for the collapse of the cod farming in the late 2000s. While the economic meltdown hampered the credit access for importers in EU, increased TAC flooded the supply chain of cod and eventually brought down the price of fresh cod in the market. With the reduced price, farmed cod could not make any profit and cod producers went bankrupt. This issue will be discussed in detail below in the 'Business and Market' chapter.

6 | BUSINESS AND MARKET

This section describes the background to the great public involvement that has been in developing cod farming as an industry, as well as which instruments have been used. Furthermore, the market challenges in both the product market and the capital market are described, both important for profitability and for being able to finance growth in the industry. The market prospects, and the industry's ability to compete for valuable and scarce farming areas are discussed as conditions and limitations for growth in production of farmed cod.

6.1 | Developing a new industry

As described in the Introduction, political ambitions to develop large-scale commercial cod farming were triggered by the socio-economic consequences of an overexploited and weak population of the important North-east Atlantic cod stock in the late 1980s and 1990s. The Institute of Marine Research presented 'Perspective outline for the aquaculture industry', and The Norwegian Technical-Science Research Council (NTNF) followed up with 'Perspective analyses for aquaculture'. This increased the interest in fish farming overall including cod farming. Optimism among potential business actors and authorities also increased. Optimistic forecasts predicted that cod farming would be as large as the traditional cod fisheries by 2010. The governmental purpose was to secure employment and settlement in rural coastal areas, and the strategy was used actively in electoral campaigns to win seats in Parliament.

Entrepreneurs in other countries (UK, Denmark, Iceland, Canada) backed by the authorities also launched ambitions for growth in cod farming. In Norway, it was important to secure its share of a potentially large industry. While the FAO in 2000 presented forecasts of cod farming around the North Atlantic at 2 million tons by 2015, the Norwegian forecasts from the National Industry and Rural Development Fund (precursor to Innovation Norway) and the Research Council of Norway were the same value creation from cod farming as for salmon farming within 20 years. The government built up its expectations with strategies for investing in a governmental owned breeding programme for cod followed up by marine development research programmes. The banks, however, were reluctant to invest in cod farming, and this led to SND and governmental 'seed grain funds' had to be awarded an active role in the development of the industry.[11]

Private entrepreneurs were inspired by successful salmon farming, optimistic prognosis regarding cod farming from the research community and government. They expected profitable production and a limited number of transferable, and hence, valuable, production permits to be granted by the authorities. This led to a proven and long-term commitment from the early 1990s to about 2010 that involved research, public funding and private entrepreneurs. Despite the strategy being consistent with the triple helix model of innovation (interactions between universities engaging in basic research, commercial industries and governments),[81] the cod farming industry collapsed over a period from 2008 to 2012 (Figure 3). The explanations are complex, and, in the following, we will shed light on the elements that we perceive have the greatest significance. This will also point in the direction of what it takes to make it possible to obtain a profitable cod farming industry. In rough terms, in addition to the biological challenges described above, the potential bottlenecks for the re-establishment of the industry are market challenges, access to venture capital and access to well suited marine areas for cod farming.

6.2 | Market challenges

Farmed cod has mainly been exported fresh, gutted with or without head. The first major batch of farmed cod, hatched from roe, was exported to England in 1998. At the beginning of the 2000s, exports of farmed cod were below 1000 tons a year, before increasing sharply from 2350 tons in 2005 to 10,500 tons in 2010. Subsequently, exports fell rapidly until it came below 2000 tons in 2014 (Figure 4). During the period 2002–2008, farmed cod achieved an average export price of between 38 and 33 NOK/kg. The price then dropped to around 25 NOK/kg in the period 2009–2015. From 2015 to 2017, the price for wild cod increased to above 35 NOK/kg (Figure 4). In 2020, the price for wild cod increased to over 39 NOK/kg, but in the first 4 months of 2021, it decreased to 33 NOK/kg.

Farming cod has mainly been exported as fresh whole fish (gutted). As previously shown, the largest export volumes of farmed cod were in the period 2009–2011. In the same period, large volumes of wild cod were exported from Norway. To see how these products affected each other, it would be interesting to compare the exports of fresh whole wild-caught and farmed cod during this period (Figure 5). The seasonal profile of export of fresh whole wild and farmed cod in the period 2009–2011 shows that the overall export volume of whole wild cod is much larger than farmed cod. The largest proportion of wild cod was exported in February to April. The largest export months for farmed cod were October to February / March. The largest quantities of farmed cod were largely exported in months when exports of wild-caught cod were low.

A comparison of the export prices of fresh whole wild-caught and farmed cod in 2009–2011 shows that the price of wild-caught cod was lowest in February–May (except February 2009) and highest in August-January (except November 2011) for the entire period (Figure 5). For farmed cod, the picture was more complicated. In 2009, farmed cod achieved the highest price in January, April–June and July–September. In October-December, when export volumes for farmed cod were high, they reached the lowest price and at the same time lower prices than wild-caught cod. In 2010, farmed cod was best paid in the period May–December, peaking in July–August. During this period, the price of farmed cod was equal to or slightly higher than wild cod. In 2011, farmed cod was also best paid in the period May–December, peaking in August–October. Farmed cod achieved a significantly better price than wild cod in the period August–December 2011. As previously shown, the largest volumes of farmed cod were sold in October to February/March, which largely coincides with when it achieves a high price in the market. In 2010 and 2011, prices of farmed cod to a large extent followed the same trend as wild cod. The price of farmed cod increases as the price of wild-caught cod increases and vice versa.[82] As larger volumes of wild cod are exported during this period, this indicates that the price formation of wild-caught cod controls the price of farmed cod and thus that wild-caught cod and farmed cod are sold in the same sales channels. This shows that farmed cod was a supplement to wild-caught cod during periods when the catch volume of wild-caught cod was low, and prices were high (Figure 5).

The cod prices were also negatively influenced by the financial crisis in 2008 and by the increase in total allowable catch for Atlantic cod from 2008. As we have shown, the price of farmed cod was dependent on the price of wild cod. The effect of this was that

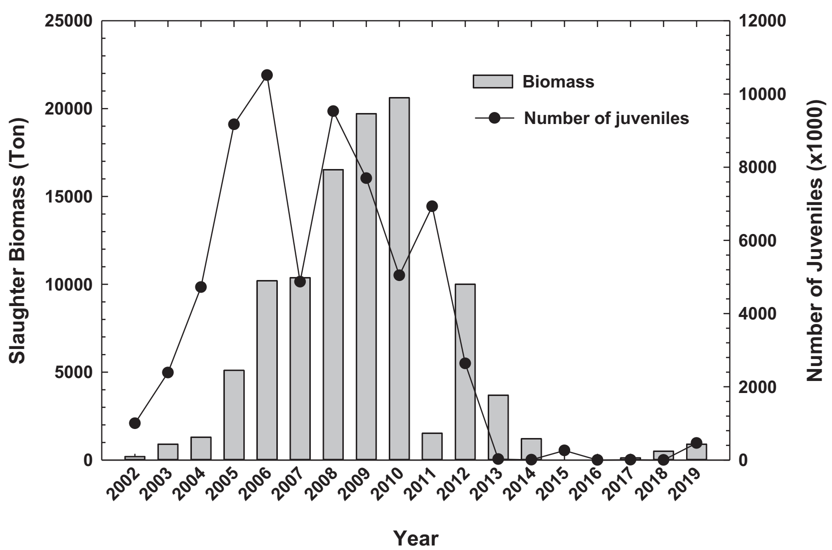

FIGURE 3 Number of cod juveniles produced and the biomass of slaughtered cod from 2002 to 2019, showing the collapse of cod farming during 2008–2012. Source: Norwegian Fisheries Directorate

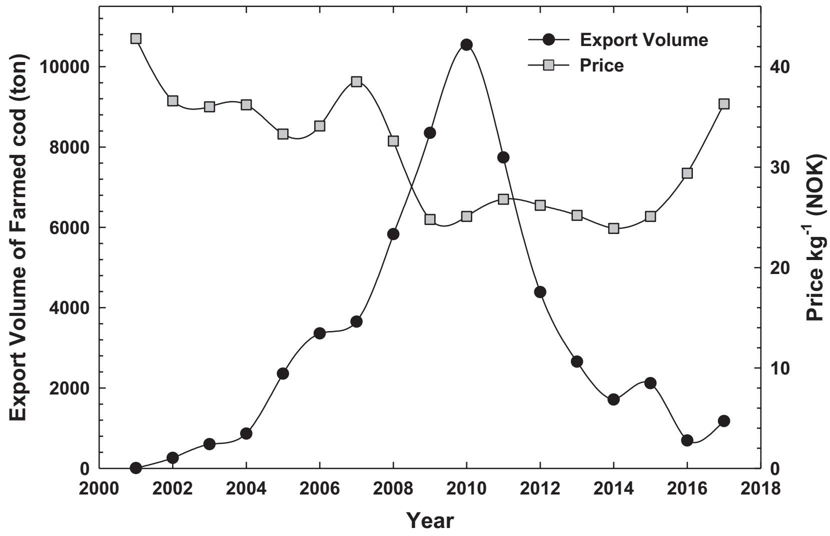

FIGURE 4 Export volume and unit price per kg (NOK) of farmed cod from 2001 to 20017 (Norwegian Seafood Council)

the average price of farmed cod decreased by almost 14 NOK/kg (36%) from 2007 to 2009, making profitable production of farmed cod very difficult.

6.3 | Access to venture capital

Through successful emissions, entrepreneurs raised venture capital, encouraged by politicians and backed by public venture funds. This led to rapid growth in the production of farmed cod from 2000 and the next ten years, but still far below the optimistic predictions that farmed cod would be equivalent to cod from the catch sector. Several companies located along the cost of Western and Northern Norway were established, which signalled plans for future growth of the cod farming. Major financial players and investors provided capital to the industry with strong expectations of profitability and return on their investments. Mergers were also discussed, and the companies signalled ambitious plans to grow. In the autumn of 2006, two of the cod farming companies, Codfarmers and Marine Farms, were listed on the Oslo Stock Exchange, and several companies signalled that they were ready to follow. The banks, however, did not share the investors' optimism and were reluctant to grant loans.

It also turned out that the biological challenges mentioned above led to high production costs. The breeders also had market problems related to small size of the fish and that farmed cod often were brought to the market during winter, when it was 'flooded' by cod from the rich winter fishery. Slaughter at an unfavourable time was most often the result of a combination of sexual maturation and poor financial liquidity in the companies. Expectations of profitability driven growth in cod farming proved to be too optimistic. On top of the problems mentioned above, new challenges, out of the industry's control, led to a fall in prices. The two most important factors for the fall in cod prices were sharply increasing quotas for cod in the Barents Sea after 2007 and the financial crisis in the autumn of 2008. The financial crisis affected credit access to importers and hit Iceland hard. With increased supply, weakened demand and Icelandic players in a squeeze situation, prices of wild-caught cod fell sharply and the price of farmed cod followed.

The overall effect led to the cessation of cod farming as an industry when the last commercial cod breeders closed their businesses in 2013/14. Innovation Norway estimated that in the 10-year period from 2000 to 2009, approximately 3.5 billion NOK was invested in intensive cod farming. In relation to their involvement, the banks suffered heavy losses. It was also the case for Innovation Norway (estimated loss of NOK 110 million on loans) which was far less than the cod farming companies' loss. The owners of the aquaculture companies remained the biggest losers.[12,83]

6.4 | Access to suited marine areas

According to Henriksen et al[12] competition for areas in the coastal zone has intensified compared to previous attempts to establish cod farming. In the future growth of fish farming, cod and salmon/trout will compete for the same locations. However, some areas that are closed for salmon might be allowed for cod farms. Two conditions have the potential to limit access to locations for intensive farming of cod. The first is strict limits on the distance between fish farms based on infection protection.[84] In addition, the effects the Aquaculture Fund likely will have for allocation of areas between cod and salmon farming in the coastal zone.

Diseases can be transmitted between different species in fish farming. The Norwegian Food Safety Authority sets requirements for minimum distances between locations. Locations for cod farming must, for safety reasons, be placed at least 5 km from farms where other species are farmed if one of the farms is defined as large (over 3,600 tons MTB), and 2.5 km for smaller fish farms. The 5 km limit

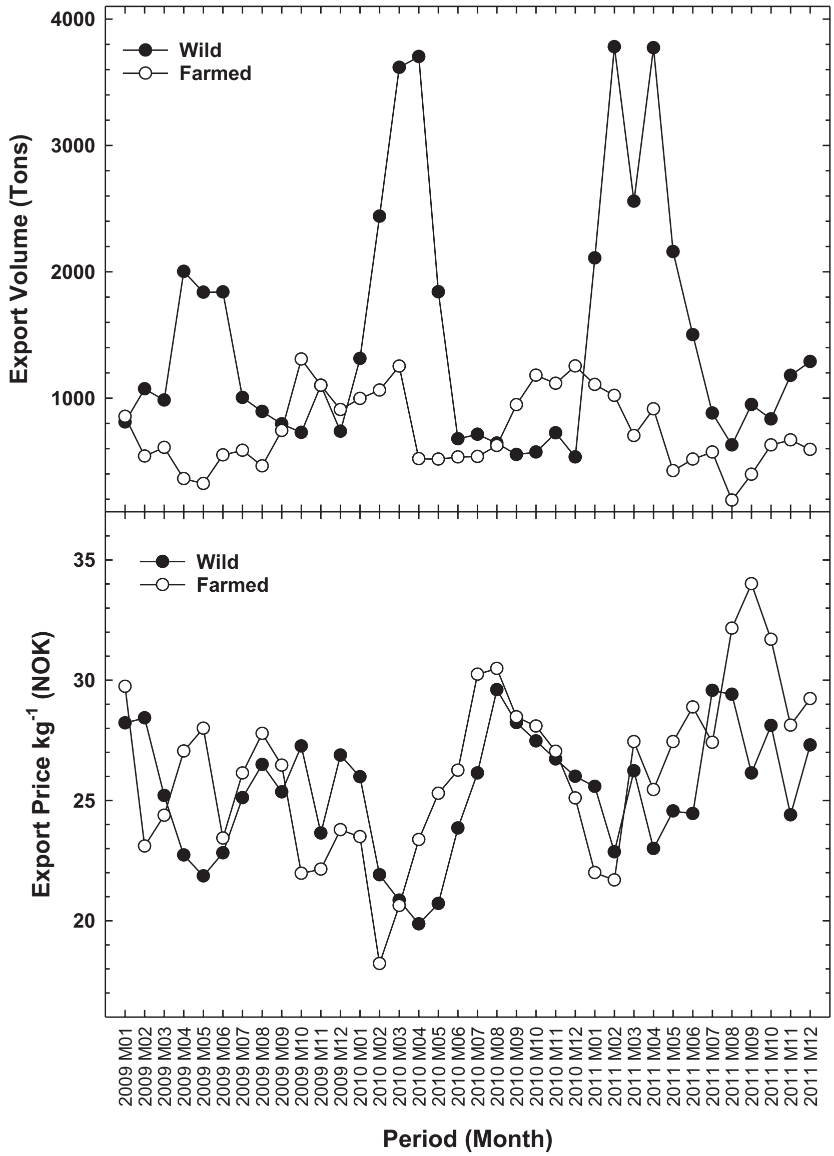

FIGURE 5 Export volume (ton) and price (NOK) for whole wild-caught and farmed cod in the period of 2009–2011

also applies to other activities that might impose a potential risk for spreading of diseases.[84] However, since 2014, polyculture of salmon and cleaner fish (lumpfish and wrasse) in the same cage has been already allowed. Thus, farming different fish species such as cod and salmonids might be allowed and the rules regarding the distances between the farms could be changed.

The Aquaculture Fund was established by the Parliament in 2015. As of 2016, 80% of the fees based on future growth in the aquaculture industry will be distributed through the Aquaculture Fund to the municipal sector. So far, the fund includes locations for salmon, trout and rainbow trout in seawater. Other species, including cod, are not included in the Fund's revenue base. The first payments from the Aquaculture Fund were paid out in 2017, and 60 million NOK were distributed. In 2018, the payments were 3.15 billion NOK. The revenues are so large that it will have to influence how municipalities and counties prioritize in the competition for areas in the coastal zone.

Separately, the requirements for distance between locations and that cod are not included in the basis for calculation of the Aquaculture Fund are likely to have the same potential effect; it limits access to locations in the coastal zone for cod farming. The willingness to prioritize cod farming areas is likely to be adversely affected by the prospect of losing revenues. Allocating areas to cod farming strongly rejects the possibility of alternative use of close by locations for salmon and rainbow trout. Future profitable cod farms, and the cod farming industry as an equal source of funding of the Aquaculture Fund, have the potential to make the industry competitive also for scarce and attractive locations.

7 | DISEASES IN FARMED ATLANTIC COD

In this review, we provide an overview of known and potential disease risks associated with intensive Atlantic cod aquaculture. The

TABLE 2 Overview and prevalence of the most important diseases in farmed cod during the period 2005–2013, related to active licences and number of fish transferred to sea cages

Year	No. active Licences	No. fish in sea cages (1000)	Samples analysed/No. localities	Francisellosis	Vibriosis	VNN	Atypical furunculosis	Comments
2005	–	8090	–	4	23	0	3	First francisellosis diagnosis. Vibriosis vaccine tested.
2006	213	11301	–	7	20	3	13	First VNN diagnosis.
2007	240	15620	240/80	8	25	6	9	
2008	250	21740	350/85	14	22	3	16	High fry mortality, intestinal prolapse and inflammation.
2009	207	10368	250/80	8	22	1	16	Huge loss due to francisellosis. Vaccine testing for vibriosis and atypical furunculosis.
2010	–	5920	80/40	3	10	0	5	Loss due to intestinal disorder.
2011	–	3556	50/25	3	x	0	x	
2012	84	2370	21/11	2	5	0	1	
2013	–	726	12/8	1	x	0	0	

Sources: Fish health reports 2005–2013, Norwegian Veterinary Institute and Directorate of fisheries.

focus is mainly on previously characterized diseases that have been known to pose threats to farmed cod. Although bacterial infections dominate, both viral and parasitic infections do occur in farmed cod, in addition to different types of disorders. Among these, intestinal disorders are the most numerous. In facilities without diseases, disorders may account for over half of the total mortalities.[85] Table 2 shows the overview and prevalence of the most important diseases in farmed Atlantic cod in Norway during the period 2005–2013, related to active licences and number of fish transferred to sea cages (Sources: Annual Fish Health reports published by Norwegian Veterinary Institute, 2005–2013 https://www.vetinst.no/en/reports-and-publications/reports and Directorate of Fisheries). Although diseases and disorders were present in hatcheries (larvae and juveniles) and could have caused losses in grow-out facilities (sea cages), these issues did not play a major role in the collapse of the cod farming in the late 2000s.

7.1 | Bacterial diseases

The intracellular bacterium *F. noatunensis*, subsp. *noatunensis*, causative agent of francisellosis,[86,87] is considered the most important disease problem in Norwegian cod farming and was one of the reasons why the industry collapsed around 2010. The disease caused major losses especially in large cod. No antibiotics are effective against *F. noatunensis*, and several experimental vaccines have also been tested without effect,[88] making it necessary with alternative vaccine strategies. When both preventive measures and treatments are lacking, it is important to find other methods to prevent disease progression. In this context, breeding for increased resistance to francisellosis should be explored further.

The first outbreaks of francisellosis in Norwegian farmed cod were registered in 2004. Francisellosis caused by *F. noatunensis* has only been detected in farmed and wild cod in the Nordic countries.[89–92] Diseased cod has a loss of appetite and is dark in colour. Small ulcers in the skin and mouth may occur, associated with nodules (granulomas) in the skin, but usually there are no external signs of the disease. Large amounts of yellow granulomas in the kidney and spleen are seen (Figure 6) and may also occur in other organs.[89,90,93,94] Mortality is primarily associated with high seawater temperatures[89,95,96]; thus, temperature-related stress and down-regulation of the immune system appear to be important triggering factors.[97,98] Other factors may also be important but are yet not fully understood. Fish with *F. noatunensis* infections often have atypical *A. salmonicida* infections simultaneously.[99] Even though mortality levels decrease during the winter period, the infection does not seem to disappear from the population. Once the bacterium is established in a facility, the number of infected fish will increase with time until a disease outbreak occurs, often the second summer at sea.[100] During a disease outbreak, large amounts of bacteria are released into the environment.[101] Farmed cod can be infected with waterborne *F. noatunensis* from the environment. The only known natural reservoir in the environment today is diseased wild cod or

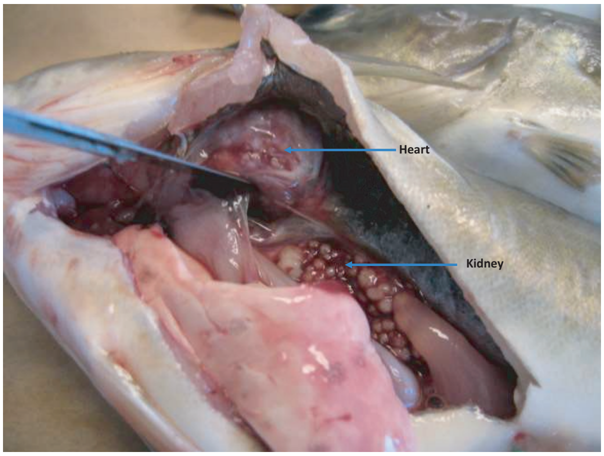

FIGURE 6 Photograph showing the severity of infection of *F. noatunensis* in an adult Atlantic cod

wild cod carrying the bacterium. *F. noatunensis* has been detected in historical samples from wild cod caught in the North Sea[102] and has thus been present before the development of modern cod aquaculture. *F. noatunensis* was detected in samples from all counties south of Sogn and Fjordane (61.5539° N, 6.3326° E) with 13% prevalence, and the enzootic area is southern Norway, the Swedish west coast and the North Sea down towards the English Canal.[91] It is unclear to what extent infection occurs in wild cod populations in Northern Norway. However, using real-time RT-PCR found infected cod was found in Nordland County, probably on their way to the spawning grounds.[103] The absence of disease outbreaks in Northern Norway may be due to lower seawater temperatures,[92] but it is important to note that temperatures in this region are often well within the tolerance of *F. noatunensis*. The higher temperatures in southern parts of Norway probably affect the cod immune system, resulting in increased susceptibility to diseases in general.

Farmed cod, wild cod and a variety of other fish species, brown crab and mussels can be carriers of the bacterium.[92] The bacterium has been detected from farmed salmon on one occasion in the immediate vicinity of a cod farm with francisellosis.[92] Horizontal infection (from fish to fish via the water) is well documented and appears to be the main route of infection. Vertical infection is a possibility, as fish with extensive granule formation and relatively much *F. noatunensis* in the tissues can still spawn. The bacterium has also been detected in egg batches and fry. It seems unlikely that vertical spread of *F. noatunensis* plays a role in nature, but this can still not be rejected in aquaculture where one infectious individual may be enough to infect a farm.[100]

No vaccines are available against francisellosis in cod. While infection models against *F. noatunensis* have been conducted recently, no conclusive models have been available yet.[104,105] Disease challenge experiments against francisellosis using formalin killed *F. noatunensis* subsp. *orientalis* (Fno) for immunization in tilapia (*Oreochromis niloticus*) showed improved survival and lower loads of bacteria in blood and internal organs.[106] However, Mertes et al using extracellular membrane vesicles (MV's) from *F. noatunensis* subsp. *noatunensis* (Fnn) and *Francisella orientalis* reported no protective immunity either in Atlantic cod or in tilapia.[107] NCBP is currently working on developing challenge models that will lead to work on developing vaccines.

Atypical furunculosis, caused by atypical *Areomonas* sp, is a serious problem in cod farming. Infections in cod can vary from limited outbreaks via chronic infections with high incidence of granulomas, to high, acute mortality. Age and stress of the fish due to handling and high temperature can affect the outcome.[108–110] Differences between bacterial strains can also play a role in disease development.[99] Atypical furunculosis has been reported in more than 20 farmed and 30 wild fish species worldwide,[108,111,112] and it is found in both wild and farmed Atlantic cod.[110,112] Atypical *A. salmonicida* strains are heterogeneous with respect to serological and biochemical characteristics.[112–114] In Norway, the disease in cod is caused by *A. salmonicida* subsp. achromogenes.[115] Isolates from different geographical areas have been studied over a long time period, and results indicated that infections with this bacterium are persistent.[116] Studies have shown that pathogen is contagious between different species.[117] Efforts to develop a vaccine for atypical furunculosis have been carried out when Atlantic cod farming was at its peak in Norway. However, since the decline in the cod farming activities and partly due to the heterogeneity, as mentioned above, currently no effective vaccines exist.

Vibriosis, caused by several serotypes of *Vibrio anguillarum*, is a significant disease problem in cod farming in Norway. The most frequent serotypes of *V. anguillarum* isolated from cod are O2b followed by O2a.[99] The bacterium is found both in the environment as free living and within the fish[118] and is primarily transmitted through water and can be transmitted for long distances.[84] Although the entry portal for *V. anguillarum* has been debated, either skin, gills or digestive tract of the fish could be the main portals of entry.[119] There are no records of direct transfer of this pathogen between wild and farmed cod. But wild fish and prey organisms act as reservoirs for different strains of *Vibrio* spp.[120,121] Vibrios are found in many marine organisms, and vibrios infects both wild and farmed animals, including most gadoids and salmonids.[120] Commercial cod aquaculture started only in the early 2000s, but this occurrence of vibrios in wild cod was documented well before the development of modern aquaculture[122] reported in Ref. [123]. The main clinical signs are haemorrhage around fins (fin rot), mouth and eye, and the intestine can also be swollen, and fluid filled.[123,124] Fish are also sluggish and dark-coloured and are found near the water surface.[125] To control this disease, good water quality of farmed animals and minimizing the stress to the fish is essential. Before the vaccines for vibrios are developed, antibiotic-medicated feed has been widely used control this disease in cod and other farmed fish.[126] But the development of antibiotic resistance and public outcry prompted the vaccine development to prevent the vibriosis disease outbreaks.[127] Results from vaccine development projects showed that the cod immune response is very specific and that dip vaccination of cod based on only one *V. anguillarum* serotype (eg O2a) does not yield protection against infection with other closely related serotypes (such as O2b), and vice versa. By contrast, a triple vaccine based on all three serotypes found in cod, O2a, O2b and atypical O2 (biotype II), offers very god protection against all three serotypes.[85,99] Currently, vaccine for vibriosis is available for many farmed marine fish species including Atlantic cod.[128]

7.2 | Viral pathogens

Viral nervous necrosis (VNN) or viral encephalopathy and retinopathy (VER) disease is caused by betanodavirus (NV) in many marine fish species globally,[129] including Atlantic cod.[130] Few reports of VNN outbreaks have been reported in farmed marine finfish species such as Atlantic cod,[130,131] Atlantic halibut[132] and turbot.[133] NV infection particularly affects the larval or juvenile stages of fish, in which mortality may be very high.[129] Diseased fish show general clinical signs of disease, such as loss of appetite and darkening of the skin.[130] In addition, the clinical signs relate to neurological distortion with abnormal swimming behaviour consisting of looping or spiral swimming with belly up and loss of coordination. Internally, the gastrointestinal tract is empty, and the swim bladder distended to various degrees.[130]

VNN has been detected in wild Atlantic cod as well as in farmed cod.[134,135] In the late 2000s at the height of the cod farming activities in Norway, this virus has been detected in many cod aquaculture facilities in Norway and Canada, although in many cases no clinical signs were found.[135] Because of no apparent clinical signs exhibited by the infected cod juveniles, they could act as carriers of the virus.[134] NV can survive in water environment that is used cod larva/juvenile rearing for an extended period which makes it very contagious.[136,137] Although the mode of transmission of nodavirus is not fully understood, there are indications that it can be transmitted both vertically (through the parents to progeny) and horizontally (from the rearing water).[133] No effective control measures are available for the nodavirus and disinfection of inlet water, and keeping virus-free broodstock and monitoring of wild-collected broodstock using a PCR test are recommended. Unfortunately, there are no vaccines for VNN is developed, and development of proper virological, molecular and in vitro techniques is required before any vaccine development. Thus, cod farming still could be vulnerable for this disease when more farming activities develops in coming years.

Viral haemorrhagic syndrome virus (VHSV) is included in this review, not because it has caused any disease outbreaks in farmed cod in Norway, but because it has been isolated from a high number of different wild freshwater and marine species throughout the Northern Hemisphere and because it is known to cause disease outbreaks in both wild and farmed fish species.[138,139] VHSV has been detected in many gadoids in the wild including Atlantic cod (summarized in Ref. [140]). In Norwegian waters, the prevalence of VHSV is extremely low.[141,142] Even in experimental infection studies, Atlantic cod could not be infected with viral isolated from wild fish and the fish could only be infected through injection[143,144] although an infection route from wild fish to farmed fish through contact may not be ruled out. Norway has a VHSV-free status in farmed fish since 1994 (https://www.vetinst.no/sykdom-og-agens/viral-hemoragisk-septikemi-vhs), and it is important to maintain this situation. As such, detection of the virus in farmed cod will have serious consequences for the farming industry.

7.3 | Parasites

Although wild Atlantic cod is host to more than 120 parasite species,[145,146] problems with parasite infections have so far been less in farmed cod. The most common parasites in hatchery-reared cod farmed in sea cages are the digenean *Cryptocotyle lingua*, causing black spot disease,[147,148] the monogenean *Gyrodactylus marinus* and the protozoans *Spironucleus torosa* and *Trichodina* spp.[148] Other parasites occurring frequently are the parasitic copepod *Cresseyus confusus*, the myxosporean *Zschokkella hildae* and the nematode *Hysterothylacium aduncum*.[148] Food-borne parasites such as nematodes and digeneans in hatchery-reared cod have been shown to be sparse compared to wild cod, and caligid copepods are rare,[148] demonstrating that these are most unlikely to become a health problem for farmed cod, while parasites with simple life cycles and pelagic transmission stages, such as monogeneans and trichodinids, may dominate the parasite fauna of farmed cod.[148] However, lice problems requiring treatment have occasionally been caused by *Caligus elongatus*, which does not normally infect the larger cod as larvae. Thus, massive infections must represent adult lice transferring from wild fish in the vicinity of the pens.[147] In northern Norway, *Caligus curtus* infects pen-reared cod as both juveniles and adult lice[147] heavy infections by *Ichthyobodo* spp. occasionally occur, but usually associated with other pathogens.[147]

7.4 | Production disorders and diseases without known causative agents

Different disorders have been reported in farmed Atlantic cod, some of which may cause reduced growth and mortality. Enteritis causes decreased appetite, ascites (abdominal fluid) or intestinal prolapse. The condition can be severe and lead to high mortality. The cause of the inflammation is unclear (Anon. 2009). A condition named sideline necrosis where skin is depleted in the side lines has been observed on some occasions. The cause is unknown, but a viral cause is suspected.[149] Cod ulcus syndrome (CUS) is observed in both wild and farmed cod. It is believed that a virus in the group Iridovirus plays a role in the development of the disease (reviewed in Ref. [150]). It has also been suggested that a virus-like VHSV may have been involved,[151] in addition to environmental factors.[152] In diseased fish, small blisters in the skin are found which can eventually develop into large wounds. CUS causes a chronic condition, and it is likely that the same fish can have several outbreaks. Mortality is not high, but the quality of the fish deteriorates. There is no treatment for this disease.[149] Egg bound syndrome (EBS) is a phenomenon that is recorded in the spawning period of female cod that does not release the eggs.[153] The fish gets swollen, red in the belly and develops wounds. EBS generally leads to death, and the mortality related to EBS could be up to 36% of the spawning mortality.[154] It is suggested that stress related to higher stocking density[154] or due to spending considerably more energy to increase the stomach water content to masticate the dry diet which could have reduced the access of water during the final maturation and hydration.[153] Fin rot is also observed. The fish gets a heavily distended belly because the peritoneum is filled with fully developed gonads (Figure 7a). The cause of the problem is not clear, but signs of bacterial infections in the gonads of spawning cod (*Vibrio* sp.) have been found.[149] Eye damage in cod is a problem and may be due to snapping of eyes, suboptimal farming conditions, infections with eye itch and cataracts related to suboptimal nutrition (Figure 7b).[155]

Volvulus (intestinal strangulation) is a condition where the intestine, as a result of rotation, is blocked for passage of feed. There is a partial or complete constipation that will be life-threatening if it is not abolished reasonably quickly. The disorder is relatively common in farmed cod.[85,99,115] The condition was first registered in 2004, and the cause is unknown. The affected fish are often in good condition and without other external damage besides a somewhat enlarged belly. In many cases, it may be difficult to distinguish volvulus from fish ready for spawning or early sexually matured. The intestine is strangled at one or more points, it swells, and the passage closes, blood supply stops, the tissue necrotizes, and the fish dies shortly after.[156] The disorder most often appears when feed rate and growth are high. Probably, the causal link is complex, and increased feed intake is a triggering factor. Other factors may be environmental and stress-related, inflammatory conditions and infections, parasitic conditions, anomalies, and more. There is also the possibility that the intensive feeding in fish farming poses a problem to Atlantic cod in general.[156]

FIGURE 7 (a) Egg bound syndrome (EBS) and cataract in Atlantic cod. Note the enlarged abdomen (a) which shows the problem of unreleased eggs and white membrane (b) in the eye

8 | ESTABLISHMENT OF NORWEGIAN SELECTIVE BREEDING PROGRAMME FOR COD

Sustainable aquaculture of new aquatic species calls for establishment of selective breeding programmes, where achieved improvements in economically important traits are permanent and cumulate over time.

Potential for genetic gain can be as high as 12% per generation.[157] Consequently, genetic improvement has the potential to increase the profitability of farming by reducing production cost or by increasing production output, or a combination of both.[158]

The NCBP started at Nofima's Centre for Marine aquaculture (CMA) in Tromsø in 2003. NCBP has two facilities, a land-based facility CMA in Kraknes (69.7629° N, 19.0466° E) and an experimental sea cage facility at Røsnes (69°48'00.0"N 19°16'00.1"E). The CMA has infrastructure and equipment for holding and rearing broodstock, hatchery for egg incubation, livefeed production system (Rotifers and *Artemia*), first-feeding tanks for larval rearing and on-growing tanks for juveniles. The Røsnes facility has sea cages to rear the juveniles to adulthood for two years (Figure 8). The objective of the National Cod Breeding Program (NCBP) was to create genetically representative breeding nucleus, adopt production and selection strategies to genetically improve the production of farmed cod in each generation. The selected material, when disseminated to the cod farmers, increases the profitability of the cod aquaculture industry. NCBP has had great importance as a knowledge base for the cod farmers because NCBP has faced and solved several production issues similar to those experience by commercial farmers. Implementation of a criterion to select good quality eggs in 2007 along with improvements in nutritional quality of livefeed and rearing protocols from 2006 onwards in NCBP has exemplified a recipe for production of good quality juveniles. The chronology of the NCBP fits between the start of the commercial cod farming activities in the 2000s and the re-emergence of current cod farming activities. Thus, in this section, we will discuss the NCBP and explain the selective breeding strategies within the NCBP to improve the growth and disease resistance of cod.

8.1 | Base population and genetic diversity

The prerequisite for a sustainable and long-term breeding programme is a wide genetic background of the base population. Three populations of cod in Norwegian waters, the resident north Norwegian Coastal Cod (north NCC), the resident south Norwegian Coastal Cod (south NCC) and the migratory northeast Atlantic Cod (NEAC) were used as the base population for the NCBP (Figure 9). All three populations spawn in the fjords and

FIGURE 8 National Cod Breeding Program (NCBP) land-based and sea cage facility. (a) Broodstock holding room—spawning/gamete striping. (b) Hatchery—egg incubation. (c) Rotifer production system. (d) First-feeding room—larval rearing. Insert showing the programmable robot feeders for live and dry feed for larvae and early juveniles. (e) Land-based on-growing. (f) Sea cage facility

coastal waters of Norway, but eggs from NEAC drift northwards and fish from this population grow up in the Barents Sea. Both north and south NCC stay in fjords and coastal waters all the life. These two populations of Atlantic cod have two variants of the pantophysin gene Pan I (Pan I^{AA} and Pan I^{BB}), which makes it possible to identify to which population they belong by pantophysin analysis.[159,160]

Genetic variation in Atlantic cod populations across the Norwegian coastline was secured in the base population for NCBP by including both stocks: NEAC and NCC. Since there are several subpopulations of NCC along the Norwegian coast, NCC broodfish from both the west coast part and the northern part of Norway, together with broodfish from the NEAC population, were brought into the breeding facility in Tromsø. Process of collecting wild broodfish was repeated three times in the years 2003–2005. The wild-caught broodfish was used to produce the first cod families without selection (the P-generation). In 2006, the first generation of selected cod (F1 generation) was produced by parents from the 2003 year-class. This was repeated in 2007 and 2008 with parents from the 2004 and 2005 year-classes, respectively. Thus, in 2006–2009 we started three independent breeding lines (except mating that are used for creating genetic links across lines). In 2013, these lines were merged into one population, and thereafter, a new generation is produced every third year (Table 3).

8.2 | Breeding strategy

The NCBP produces cod families with traceability to the pedigree and has so far used a traditional combination of family and individual selections based on phenotypic features. Families are produced according to the natural spawning cycle of cod in March-April by stripping gametes from selected, individually tagged ripe broodfish. Subsequently, eggs from two females and milt from two males are split in two and used to produce all four possible half-sib families. Each family is kept separately during incubation, start-feeding and weaning, until individual PIT (Passive Integrated Transponder; Sokymat, Switzerland) tagging at 180 days post hatch (dph) in September/October for breeding nucleus, test station(s) and experimental purposes. After tagging, fish are stocked together in larger (25 m^3) grow-out tanks. In January, 3–4 months after tagging, the breeding nucleus and the test station fish are transferred to the sea cage facilities for further growth under authentic farming conditions. The test stations act as a back-up for the breeding nucleus in case of any disaster at Røsnes (breeding nucleus sea cage facility) and,

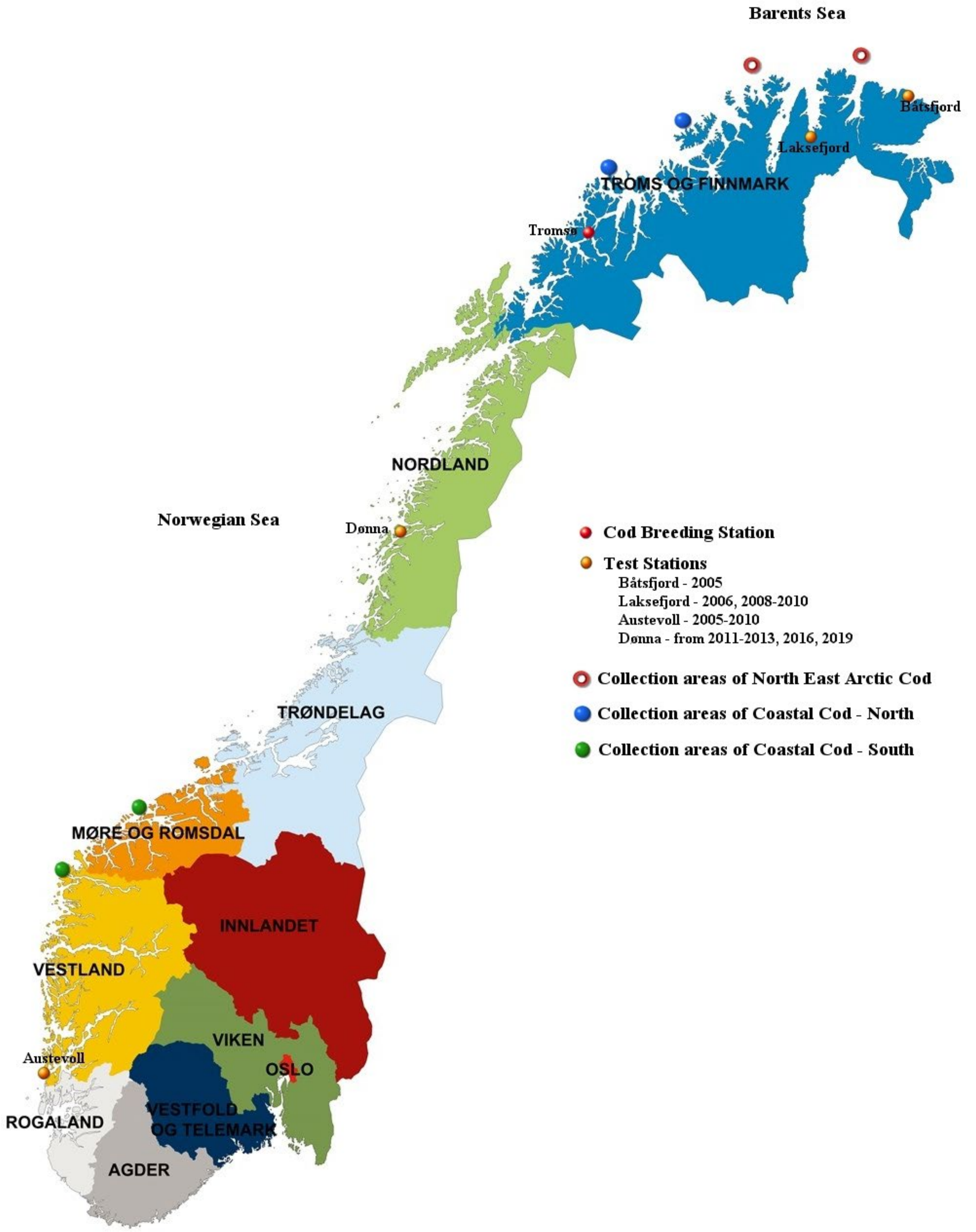

FIGURE 9 Map of Norwegian and Barents Sea showing the locations of the base cod populations used in NCBP and locations of Cod Breeding station in Kraknes near Tromsø and the test stations

TABLE 3 Overview of the production of number of cod families produced since the start of the NCBP

Year	Hatchery activity (d)	Number of families produced			Generation
		Hatchery	Start-feed	Tagging	
2003	69			40	P
2004	66	127	97	73	P
2005	60	169	155	84	P
2006	43	326	285	110	F1
2007[a]	30	425	222	191	F1
2008	36	485	252	197	F1
2009	35	451	217	202	F2
2010	29	510	232	194	F2
2011	23	331	121	104	F2/F3[b]
2012	22	279	137	120	F3
2013[c]	22	268	120	83	F3
2016	25	404	254	229	F4
2019	32	446	242	203	F5

[a]Indicates the year when the strict egg quality criteria were implemented.

[b]Indicates when two (F3)- and three (F2)-year-old brood stocks were used for family production.

[c]Indicates when the family production activities changed from every year to every third year.

additionally, makes it possible to study genotype-by-environmental interactions (Figure 9).

Performance of all breeding candidates relative to growth and deformities are registered at 2+ age, and the sex is determined with ultrasound. Figure 10 illustrates the steps involved in a classical selective breeding programme. After breeding value estimation, parents for the next generation are selected by optimizing the genetic gain in the breeding goal and the relatedness between the breeding candidates to avoid inbreeding. The selected fish is transported back to the breeding station to start a new production cycle.

8.3 | Traits of interest in NCBP

The genetic research of aquaculture cod has mainly concentrated on assessing the heritability and genetic architecture of growth and disease resistance. Additionally, early sexual maturation,[56,161] social interactions[162] and behavioural responsiveness[163] have been traits of interest. We are summarizing here only genetic studies directly applicable in cod aquaculture.

8.3.1 | Body weight and genotype-by-environment interactions

Fast growth, that is large body weight at the time of harvest, has been the main selection criterion in NCBP. Consequently, several studies have focused on estimation of the heritability of body weight traits across the production cycle: at tagging, 1+ of age, at 2 years, 2.5 years/harvest. Overall, moderate to high estimates of heritability have been reported for body weight at different stages of production,[56,162,164-167] with exception of Bangera et al[168] who estimated mainly low heritability for 2.5-year body weight at different geographical locations. Body weight measurements registered close together are genetically highly correlated, whereas more distant body weight measurements are less genetically correlated.[56,166]

Realization of genetic gain in economically important traits at different aquaculture locations is dependent on the consistency of the performance across different environmental conditions. If genotype-by-environment interaction (G × E) exists, genetic gain across environments will be inconsistent. From the strategic point of view, it is important to assess and quantify the degree of re-ranking of families in different environments. In the case of significant G × E, it might be necessary to establish specific breeding lines tailored to fit all production environments. Studies conducted on Atlantic cod have reported high genetic correlations, that is, low degree of re-ranking of families in body weight traits at different geographical locations.[56,168,169] This indicates insignificant G × E in farmed cod. This suggests that there is no need for separate breeding lines for body weight traits in Atlantic cod. Both the estimates of heritability and the lack of severe G × E are beneficial for sustainable selection for body weight in Atlantic cod, resulting in eggs and juveniles suitable for aquaculture along the whole Norwegian coast.

8.3.2 | Early sexual maturation

Several attempts have been made to estimate the genetic variation in early sexual maturation. Kolstad et al reported uneven frequencies of sexually mature fish at 2 years of age in three geographical locations and significant heritability for this trait (0.21±0.04). Attempts to assess genetic variation in early sexual maturation in

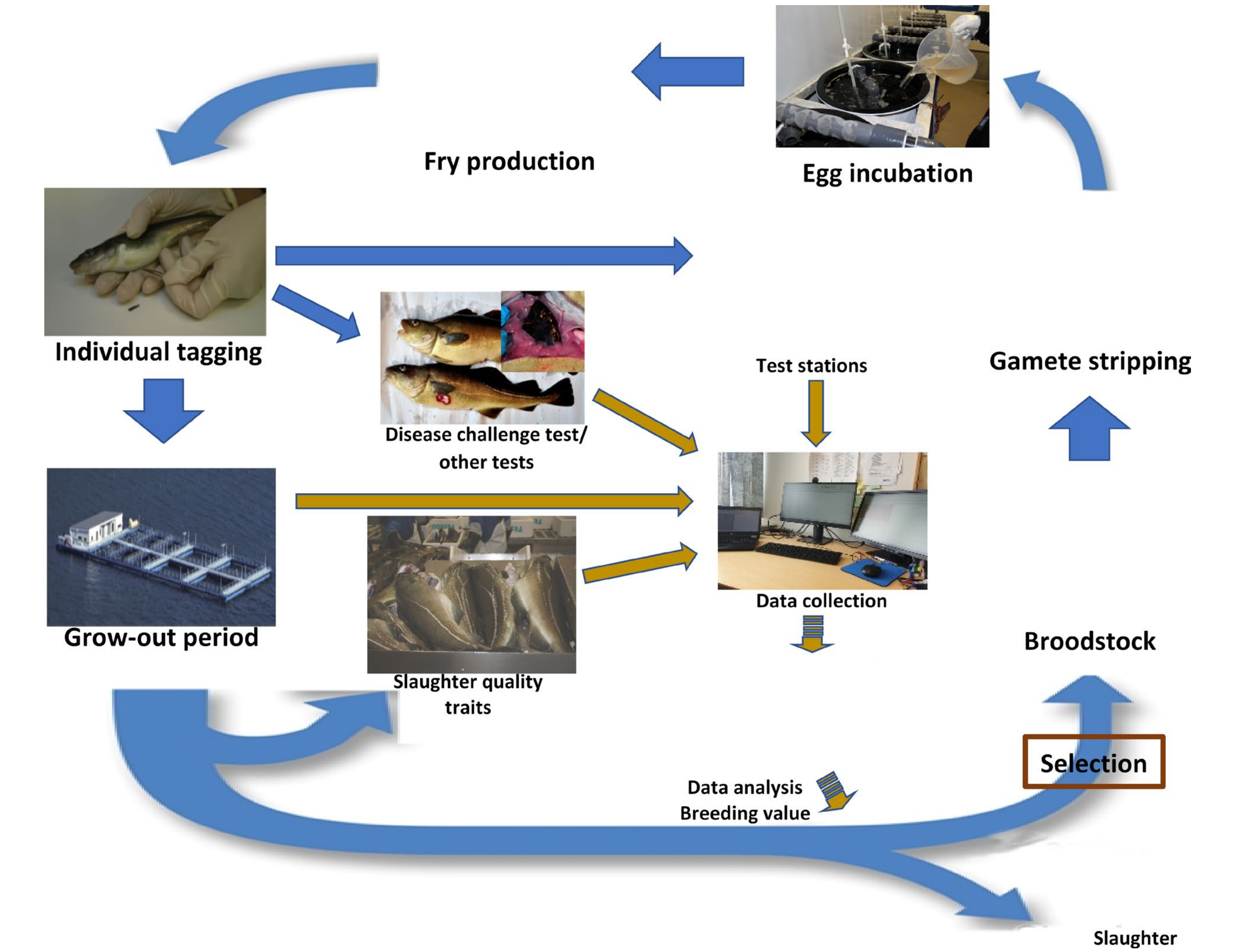

FIGURE 10 Illustration showing the main activities of classical family-based Atlantic cod breeding programme

TABLE 4 Least square means of body weight and gonadosomatic index (GSI) for each sex and maturation status of 2-year-old fish

Maturation score	Body weight		Gonadosomatic index	
	Male	Female	Males	Females
0	731^{Aa}	797^{Aa}	0.33^{Aa}	0.78^{Ba}
1	994^{Ab}	1279^{Bb}	7.01^{Ab}	17.5^{Bb}
3	969^{Abc}	1153^{Bb}	2.71^{Ac}	10.36^{Bc}
4	904^{Ac}	972^{Bc}	1.19^{Aa}	2.97^{Bd}
All	922^{A}	1024^{B}	–	–

Note: Within a row, means without a common uppercase superscript differ ($p < 0.05$). Within a column, means without a common lowercase superscript differ ($p < 0.05$).

NCBP genetic material have been performed.[161] Results showed 96% of immature individuals in one-year-old fish and 94% frequency of mature individuals in two-year-old fish (Table 4; Figure 11).[161] Such frequencies are not suitable for reliable estimation of genetic.[161] In 2018, a small sample of breeding candidates were scanned with ultrasound to register sex, sexual maturation, body weight and body length by at 2 years of age. Fish was again registered approximately six months later for body weight and length. The data were small and non-balanced but indicated that immature fish have a clear growth advantage between two (spring) and 2.5 years (autumn). Investment on the growth of gonads and subsequent long recovery period hinders early maturing fish to compensate the lost growth potential. Further efforts are made to optimize the experimental design to register the variation in early sexual maturation, to estimate the genetic parameters of the trait and to evaluate the need of including selection against early sexual maturation as a part of the breeding goal.

8.3.3 | Deformities

In the NCBP, deformities are registered when fish are weighted. A deformity registration system classifies the deformities in five main groups: axial deformity (eg neck bend), spinal deformity (eg fusion

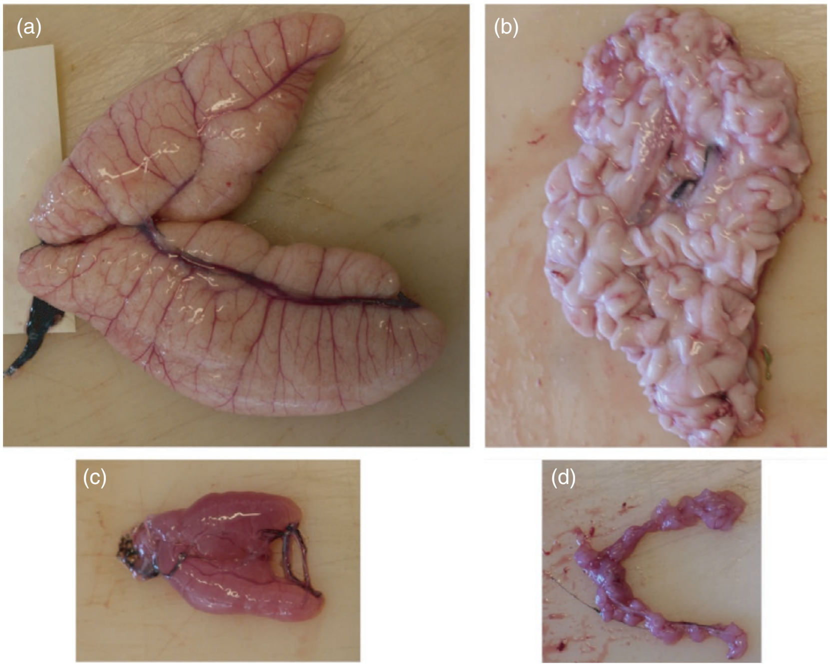

FIGURE 11 Matured ovary (a), matured testis (b), immature ovary (C) and immature testis (d) of 2-year-old Atlantic cod. More than 95% of the fish were at stage a or b while less than 5% were at stage c or d.

of vertebrae), head deformity (eg underbite), soft tissue deformity (eg liver hernia) and damage (eg wounds). At early stages of cod aquaculture, high frequencies of deformities were recorded throughout the production cycle. It was reported that spinal deformity frequencies ranged between 28 and 74% at different geographical locations.[165] Another study in NCBP reported 11.3% deformities in 1+ fish, whereas for 2+ fish, the frequency was almost fourfold but most of these deformities were mild.[166] The most likely reason for the discrepancy between the two frequencies is the difficulty to identify certain types of deformities in small fish. In the last cohort of selection candidates (year-class 2016), 12.4% of the individuals had one or more deformity. When considering the skeletal deformities alone, only 7.66% of the recorded fish had skeletal deformities and most of these deformities were very mild (80.82%). Kolstad et al estimated low-to-moderate heritability (0.18–0.38) for occurrence of spinal deformities at three different geographical locations.[165] There was indication that rapid growth was genetically connected with higher occurrence of spinal deformities ($r_g = 0.50 \pm 0.13$). Undoubtedly, the high frequency of deformities right after domestication has been a consequence of suboptimal production environment and/or feeding. Frequency and type of deformities are routinely recorded, and individuals with severe deformities are culled from the breeding nucleus.

8.3.4 | Disease resistance

Details of the pathogen, frequencies of the outbreaks and aetiology of the diseases are presented above in the 'Diseases in farmed Atlantic cod' section of this paper. Here, we are presenting genetic research conducted within NCBP in three diseases (vibriosis, viral nervous necrosis and francisellosis).

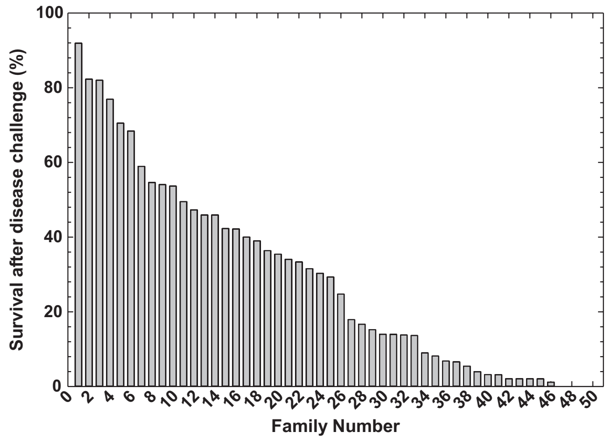

FIGURE 12 Family variation (Number of families = 50) in survival of cod juveniles after experimental VNN challenge in YC2007

Vibriosis, caused by several serotypes of *Vibrio anguillarum*, is a significant disease problem in cod farming in Norway and consequently was at focus in the early genetic work within the NCBP. Already the first generation, progeny (F0) of wild fish, was tested for resistance to this disease in a controlled challenge test.[170] The first challenge test showed significant between-family variation in survival after challenge and thus gave promising genetic improvements for vibriosis resistance.[166,170] These results were confirmed by another study[171] and challenge test results from the next year-class, and also, representing F0 generation showed low-to-moderate heritability (0.08–0.17). Later two studies[167,172] combined challenge test information from several year-classes and confirmed low-to-moderate heritability of vibriosis resistance (0.33). Vibriosis resistance was included in the breeding goal until a vaccine was developed to protect from this disease.[128] The last vibriosis challenge test was run for year-class 2009.

Viral nervous necrosis (VNN), caused by Betanodavirus, has been one of the major limiting factors in the culture of marine fish species all over the world.[123] The first challenge test with VNN was conducted using fish from year-class 2007 (F1 generation). These first results showed extremely high between-family variation after challenge, and consequently, the estimate of heritability was very high: 0.75±0.11 (underlying scale; Figure 12). Additionally, there were significant differences in survival between the strains (CC, NEAC). CC had a survival of 56% after the challenge test, whereas only 10% of NEAC survived. Hybrids between these strains had intermediate survival of 31%.[173] Bangera et al analysed VNN challenge data from two year-classes (2007, 2009) using different statistical approaches and confirmed very high heritability for resistance against VNN.[167,172] Baranski et al[174] used 110 polymorphic microsatellite markers in the search of quantitative trait loci (QTL) behind the high heritability. Five genome-wide significant QTL were detected, which explained 68% of the phenotypic variance for VNN resistance. Later Bangera et al[175] found numerous SNPs affecting the resistance but concluded that large effect loci are present, but that the high heritability is of polygenic nature. The most important genomic regions were left to be characterized, but there is potential for utilization of the detected SNP markers in marker assisted or genomic selection. VNN was not a 'problem' in Norwegian cod aquaculture in the 2000s or now and within-family marker-assisted selection (MAS) can allow selection for 'resistant' genotypes in the face of any future VNN outbreaks.

Only one study is available on genetic variation in disease resistance against francisellosis, caused by *F. noatunensis*, based on survival data from a field outbreak.[176] Bangera et al used three statistical models and low-to-moderate heritability (0.10–0.17) for resistance.[176] But NCBP is in the process of developing infection models followed by challenge tests to test the heritability.

8.3.5 | Molecular genetics

Genetic markers are used for population genetics, fisheries management and in selective breeding programmes in aquatic species worldwide. In NCBP, sets of polymorphic microsatellite markers were developed to be used for parental assignment for individuals originating from communal.[177-181] Microsatellites were also used for detection of QTL for VNN resistance.[174] SNP markers have also been identified and characterized.[182] In NCBP, Bangera et al[175] used 12K SNP array to assess the genetic architecture of VNN resistance. Recent developments in molecular technologies have enabled comparisons between individual complete genomes.[183] However, still there are only limited resources of high-throughput genotyping available for high-resolution genetic studies on Atlantic cod.

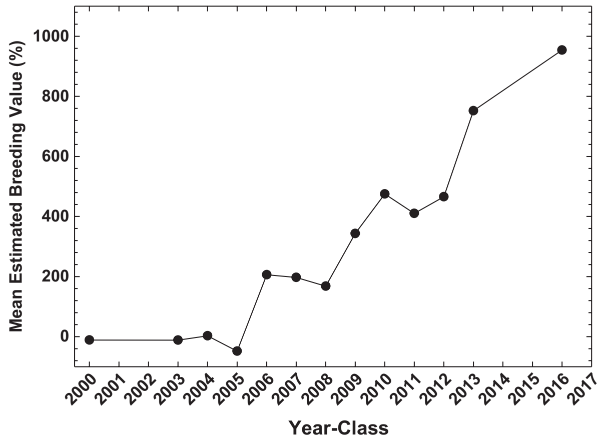

FIGURE 13 Mean estimated breeding value of cod of different year-classes from 2003 to 2017

Consequently, currently no genomic selection is utilized in selective breeding for Atlantic cod.

8.3.6 | Genetic diversity and genetic gain

Main breeding goal of the NCBP has been rapid growth until 2+ age. Selection for vibriosis resistance became unnecessary after development of effective vaccine against this disease. Collapse of the cod aquaculture industry prompted for moderate selection pressure for body weight and maintenance of genetic diversity; thus, no other traits have been included in the breeding goal so far. Benchmarking of year-class produced in 2016 showed that the breeding and mating strategies practiced in NCBP have been successful; there has been significant genetic gain in body weight at 2+, and this has not compromised the genetic diversity, expressed as low average inbreeding coefficient of 1.3% (Figure 13).

9 | IMPROVEMENTS IN DIFFERENT PRODUCTION CYCLES OF COD

In this chapter, we will describe the improvements made in broodstock husbandry, securing good quality gametes, egg incubation techniques, larval rearing protocols to improve growth, survival and quality of juveniles and live feed protocols.

9.1 | Broodstock diet

The development of specific broodstock diet is a neglected area of research not only for Atlantic cod but also for most marine finfish species because running proper broodstock diet experiments are costly.[184] With larval rearing protocols for Atlantic cod standardized, efforts are now directed towards nutrition of cod broodstock.[153,185-188] Traditionally, cod broodstock were fed with bait

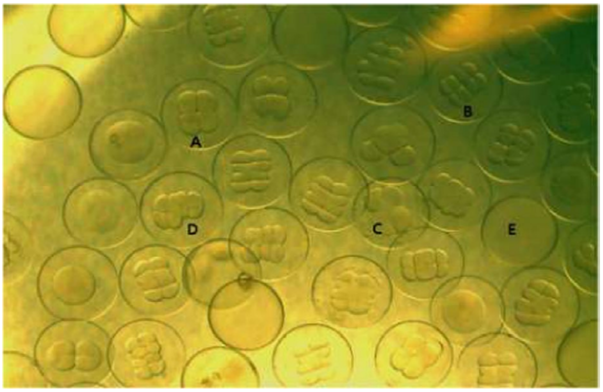

FIGURE 14 Normal cleavage and abnormal cleavage embryo of cod. (a) Normal 4-cell embryo. (b) Normal 8-cell embryo. (c) Abnormal 4-cell embryo. (d) Abnormal 8-cell embryo. (e) Unfertilized egg

fish[60]; however, the nutritional composition of trash fish is variable, difficult to transport and handle on farm and bring risks of disease transmission. Intermittent interest and development in cod farming activities did not allow enough opportunities to do R&D work on developing specific cod broodstock diets. However, recently attempts were made within NCBP to develop such diets which resulted in improvements in egg quality, post-spawning mortality and recovery.[153] With the current increasing interest in commercial production of cod, more attention is now directed in further development of a specific cod broodstock diet.

9.2 | Photomanipulated broodstock

Cod farming, as in any other fish farming, involves high capital and production costs. The natural spawning of cod is seasonal (spring), and thus, depending on natural seasonal spawning for juvenile production will leave the infrastructure unused for most of the year. This necessitates a year-round production of high-quality eggs. Using photomanipulations protocols, spawning periods can be shifted easily but the egg quality has been unsatisfactory.[189] Experiment carried out at NCBP has revealed that it is necessary to control both the photoperiod and the temperature to obtain good quality gametes.[61] Currently, NCBP is developing three photothermal manipulated broodstock and the results from the first production (3 months of advanced spawning) in 2021 in terms of gamete quality, larval performance and the juvenile quality are comparable with natural spawning production (Puvanendran et al *personal Communication*).

9.3 | Stripping of eggs

Frequent handling of mature fish stress and/or can injure them and as a batch spawner handing of broodstock is high during the spawning season. With the experience gained over the last two decades in the NCBP, better handling protocols are now in place for Atlantic cod broodstock. Using the current protocols, fish showing visible signs of readiness (bulged belly) are selected for stripping of eggs and they are checked within the tank by giving a small pressure on the lower abdomen. If a reliable quality and quantity of eggs are released, then they are transferred to the spawning/stripping table. On the stripping table, a wet towel is spread, and the fish is placed on the towel and the eye of the fish is covered to reduce the stress. Two experienced people handle the fish: one to hold the fish in place and the other do the stripping of eggs. When stripping of eggs, only a mild pressure is applied over the abdomen by moving the hand from anterior to posterior of the abdomen. Usually, the males are always ready to release the milt, so that stripping of males is done only after collecting good quality eggs. These protocols improved the welfare of the broodstock and reduced the spawning-related mortality.

9.4 | Egg and sperm quality

Egg quality is a paramount importance in the performance of subsequent life stages of cod. At the initial period of the cod breeding programme, all the eggs regardless of the quality were incubated (Figure 14) and the newly hatched larvae transferred to the first-feeding tanks. This practice was continued for four years from 2003 to 2006. However, families with lower fertilization rate and normal cleavage patterns (below 70–80%) resulted in lower hatching success and eventually lower larval survival and juvenile quality.[190] Lanes et al compared the transcriptomic activities in early embryos of wild and farmed origin of Atlantic cod and reported that several differentially expressed sequences involving metabolic pathways of fructose, fatty acid, glycerophospholipid and oxidative phosphorylation.[191] This indicates the importance of broodstock nutrition on maternal mRNA which in turn affects the egg quality and embryonic development. Thus, a better broodstock management plan needs to be developed through better husbandry protocols and nutrition.

Sperm quality is still a neglected area in cod farming practices. It is difficult to evaluate the sperm quality visually as it is done for eggs. For experimental evaluation of sperm kinetics of fish, motility objective assessment by computer-assisted sperm analysis (CASA) is used. However, quantifying the sperm density and motility has been standardized using a system comprising microscope equipped with a camera, time-date generator, monitor and video cassette recorder (for more details see 63,64,192). CASA system was expensive, however with the release of ImageJ® CASA plug-in made it inexpensive.[193] Thus, these standardization techniques of sperm quality could be easily used as an evaluation method of sperm quality in commercial hatcheries. NCBP is planning to implement this in the next family production cycle.

9.5 | Hatchery husbandry

Before 2007, the practice was to incubate all the eggs collected regardless of the quality of the eggs. Some attention has been given to fertilization rate, but checking the normal cleavage pattern has been neglected. Experience from NCBP suggested that these two parameters need to be monitored in improving larval survival and growth in the first-feeding stage. From 2003 to 2006, all the egg batches were incubated until hatch regardless of the quality. This non-standardized transfer of all egg batches to the larval rearing tanks resulted in high mortalities of larvae. Thus in 2007, lower threshold criteria for fertilization rate and normal cleavage pattern were set at 80%, and after 24 h post fertilization, both the egg quality parameters were examined. When any of the two or both the parameters were found to be below 80%, the egg batch was discarded. This practice of quality control of egg in the hatchery resulted in better survival of larvae in the start-feeding stage and led to proper management of resources and reaching the target of number of cod families that has been produced in a given production year (Table 3).

9.6 | Livefeed production

During the 2000s, rotifers were produced using a batch culture method and were fed with baker's yeast and live algae.[194] In this method, new culture tanks are started at low concentrations (50–60 rotifers/mL) and new water is added daily as the culture grows. After 4–5 days of culture, the density reaches 100–200 rotifer/ml and 30–40% of the rotifers are harvested to be used as food, while the remaining rotifers are served as starter culture for a new tank. This cycle repeats every 4–5 days. However, this batch culture method is labour intensive, and feed used, especially the yeast, promotes unwanted bacterial growth which often leads to crash of the culture. However, in the late 1990s and early 2000s, a continuous culture recirculation system was developed. This system consists of a culture tank (usually 1000 L) and connected to a biofilter system containing nitrifying bacteria, and a protein skimmer and the rotifers were fed with nonviable algae paste.[195,196] The rotifer concentration in this system reaches a maximum of 10,000 per mL and runs for several weeks at this level. This new system revolutionized the rotifer production for marine finfish larvae and is now successfully used in many hatcheries including at the National Cod Breeding programme facility.

9.7 | Start feeding

The standard larval rearing protocol has been modified from Brown et al[33] and for detailed current larval rearing protocols, see 36,153 Larvae are usually transferred to the first-feeding tanks (180-L circular tanks) at two dph. In NCBP, initially larvae were stocked at high density (150 larvae/L)[26]; however later, this was reduced to 75 larvae/L because no differences were observed in surviving number of larvae in high or low stocking densities (Puvanendran et al, *personal communication*). Water temperature is gradually increased from 5°C (temperature in the hatchery) to 10°C from 5 to 10 dph and kept at 10°C until 180 dph. A 24-h light is provided at an intensity of 300–600 lux. Algae (paste) are added to the tanks from 2 to 15 dph, and larvae are fed with enriched rotifers (enriched with Multigain®, PhosphoNorse®, Pavlova and Chlorella) from 2 to 24 dph (1.02–1.81 million rotifers per feeding & 7 feeding a day). A mixture of rotifer and enriched *Artemia* (enriched with Multigain®, MicroNorse® and PhosphoNorse®) are used as prey from 25 to 29 dph. From 30 to 37 dph, only *Artemia* is used as prey (0.88 million *Artemia* per feeding and 5 feedings a day). From 38 to 44 dph, a co-feeding strategy is implemented where dry feed is added to the tanks 1 h before *Artemia* feeding. Weaning onto dry feed (AgloNorse®) is done by gradually decreasing the amount and feeding frequency of *Artemia* and increasing the amount of dry feed. Weaning is started from 45 dph and completed at 56 dph through 5 steps.

In recent years, the importance of delivering these HUFAs in the form of phospholipids (PL) through livefeed has also been emphasized.[26,35,197,198] Furthermore, the presence of PL such as phosphatidylcholine (PC), phosphatidylinositol (PI) and phosphatidylethanolamine (PE) in cod larval natural prey (copepods) underlines the importance of these PL in cultured livefeed.[26] However, it is difficult to maintain the quantity and quality of these HUFAs in the cultured livefeed because both *Artemia* and rotifers catabolize these HUFAs which makes the chemical composition of the livefeed highly variable,[199,200] which often results in unpredictable growth, survival, and quality of the juveniles. Since livefeed production is expensive, and it has limited opportunities to improve its nutrition further, more of the current research focused on the formulated diets and were aiming to reduce the dependency on the livefeed.[32,201,202] Earlier attempts did not provide greater success due to poor acceptability of the feed by the larvae due to a low residence time in the water column, and relatively high nutrient leaching creating unfavourable hygienic conditions and microbial assemblages leading to higher larval mortality and poor quality juveniles. The convergence of new feed manufacturing technologies, an improved understanding of nutritional requirements of larvae and the advances in larval rearing technologies have resulted in some improvement in microparticulate diets. Most of the commercial production in early the 2000s used early weaning of cod larvae into micro-diets, but this has compromised the quality of the juveniles. Recent research at the CMA in Tromsø showed that early weaned larvae loose out to late weaned larvae in slaughter weight at least by 20% (Puvanendran et al, *personal communication*). Tactical use of *Artemia* along with co-feeding strategies of formulated diets, however, has resulted in better growth and survival of larvae and better quality juveniles.[36] All these improvements that were made within the NCBP have been implemented in the current larval rearing protocols which has improved the survival and quality of the larvae and juveniles.

9.8 | Larval and early juvenile husbandry

Cod larvae are fed several times a day during the live feeding, weaning and post-weaning stages.[36] These high feeding frequencies increase the organic loading in the tank due to uneaten feed and faeces and create an unbalanced microbiota diversity in the tanks.[203] This necessitates control of the larval rearing tank environment by removal of the organic waste, and this can be done by using a combination of proper water exchange and regular cleaning.[40] While increasing water exchange improves the tank environment and elevates the growth in cod larvae,[40] higher than optimal water velocities can impair the behaviour and affect the homogenized distribution of cod larvae in the tanks (Puvanendran et al, *personal communication*). Further, frequent cleaning of the tanks can disturb the microbiota community.[204] Through coordinated research and observations in the last few years, cod larval feeding frequencies, feed densities and water velocities were optimized and optimal schedules for tank cleaning have been developed (Puvanendran et al, *personal communication*).

9.9 | Juvenile quality and behaviour

Currently, there is no major commercial production of cod juveniles in the Atlantic region, and thus, no information from a commercial scale production is available on the quality of farmed cod juveniles. However, recent research indicates that the severe skeletal deformities (scoliosis, lordosis and kyphosis) in farmed cod have been significantly reduced to below 1% and the mild deformities (mainly jaw and head deformities) to below 10–15%.[36] This reduction in deformities in cod has been attributed to improvements in broodstock management, livefeed, formulated feed and possibly to selective breeding of cod.

In the 2000s, cannibalism among cod juveniles was very high and many cannibalistic juveniles could be seen with another juvenile in their mouth. Currently, the cannibalistic behaviour has almost disappeared among cod juveniles and this reduction could be attributed to domestication through selective breeding and improvement in feeding and nutrition. Further, it was shown that farmed cod has divergent geometric morphology compared to the wild cod and have smaller fins, head, eyes and jaw and larger body depth.[205] Similar observations have also been reported by other studies.[206] Cannibalistic cod generally have larger heads and jaws which enable them to cannibalize even same size fish,[207] and any reduction in the size of these two morphological traits would have reduced their ability to become cannibals. Reduction in body size variations among the same cohorts would have further reduced the cannibalistic behaviour. In both above studies,[205,206] the farmed cod was from F_0 generation and just one generation gap created such a vast difference in the morphometrics which shows the plasticity of these traits under different environmental conditions.[208] The NCBP has produced 5th-generation cod in 2019, and it is not surprising to see the disappearance of cannibalism among the cod juveniles.

10 | CAGE PRODUCTION

Unlike production in land facilities, production in open cages provides many challenges both physically/technologically and biologically. In land facilities, no severe weather issues are encountered but in cage facilities inclement conditions are common and resulting in damages to cage structures and nets. This will result in escaping of fish. Feeding practices and feed need to meet the feeding behaviour of fish which changes with the changing weather patterns. Further the light conditions and temperature varies, and both environmental variables are known to affect the sexual maturation in fish. So, measures to deal with the early sexual maturation are a priority in sea cages. We will discuss the measures to reduce escape, improving the feed and feeding, mitigation of early sexual maturation in cod in sea cages in the following sections.

10.1 | Feed and feeding practices

Since the collapse of the cod farming operations in the late 2000s, no major sea cage farming operations of Atlantic cod have been undertaken until now. Norcod AS is planning to stock 1.6 million cod juveniles in sea cages in 2020 (Rune Eriksen, CEO, Norcod AS Per. Comm.). The Atlantic salmon feeding practices have been upgraded to high-tech operations which include automated demand feeding aided by video monitoring of the feeding behaviour of the fish.[209] This demand feeding system has been used in the NCBP sea cages since 2003. This high-tech feeding can be used in cod sea cages with some modifications after careful analysis of the initial operation, and this will reduce the feed cost in sea cage operations.

At present, there is no specialized cod feed for the sea cage operations. At the sea cages, cod are fed with the same feed year-round. Studies have shown that varying seasonal temperature and photoperiod affect the feeding motivation of Atlantic salmon.[210,211] Seasonal changes in temperature affect the enzyme secretions in fish, and lower water temperatures negatively affect the digestion of the feed.[212] In temperate regions, temperature greatly varies throughout the year and the digestion, absorption and metabolism will vary season to season.[213] Hemre and Sandnes[213] showed the importance of feeding Atlantic salmon a diet adjusted to each season to achieve similar growth throughout the year by adjusting the contents of protein, lipid and antioxidants in the feed. Currently, no such seasonally adjusted diet for cod is available. New feed R&D studies should be undertaken to further improve performance of the juvenile cod in sea cages.

10.2 | Escapes

Mayer et al[214] showed that the first captive generation of farmed Atlantic cod has developed a smaller brain compared to wild fish. Although they did not study the detailed changes in brain morphology, studies from salmonids showed that farmed Arctic charr had smaller brain and consequently smaller telencephalon which led to reduction in exploratory behaviour and sedentary feeding behaviour.[215] Uglem et al[206] reported that the length of upper and lower laws of famed and wild cod from Frøya (63.9705° N, 8.8887°

E) and Ytterøya (63.7821° N, 11.0671° E) was significantly different. Farmed Frøya cod had lower and upper jaw lengths of 2.94 and 3.26 cm while wild Frøya cod had 3.36 and 3.64 cm, respectively. Similar significant differences have also been reported for the Ytterøya cod. Such smaller jaws in farmed cod would have reduced the ability of biting the net and consequently reduced the escape of farmed cod. In the above study, these morphological changes were observed in the first generation of cod.[206] Since NCBP has now produced 5th-generation cod, the morphological changes (reduction of jaw size) could be even more pronounced. Further, the observations at the NCBP sea cage sites indicate changes in behaviour of adult cod such as swimming in circles and away from the nets and no incidents of net biting (Puvanendran et al, *personal communication*), which shows the reduction in exploratory behaviour.

Escaped cod interacting with wild cod and reproducing is also discussed by several studies.[75,216] While the possibilities of such reproductive interaction cannot be ruled out, the expression of secondary sexual characteristics in farmed cod has been modified compared to the wild counterparts.[217] Varne et al[218] studied potential genetic introgression of farmed cod escapees and net pen spawning in Trondheimsfjord, Norway, and found no clear genetic footprint in the local wild population. They could not find any larvae of farmed origin in plankton samples and related the lack of genetic footprint to fitness and survival of net pen spawned larvae and adult escapees. Changes in drumming muscle mass and reduction in the size of the pelvic fins of farmed cod make them less competitive in a courtship behaviour with the wild cod. The morphological divergence in farmed cod is rapid which could affect their competitiveness in terms of reproduction and survival capabilities.[206] Further, there are clear differences in morphology, physiology and behaviour between farmed and wild cod in terms of anti-predator behaviour and feeding strategies.[219] They suggested that these differences between farmed and wild cod will make the farmed cod less competitive if they are to be released intentionally or escape to the wild.

Further, technological improvements have been made in sea cage fabrication (better nets and barges) which can withstand extreme weather.[220-222] Since 2016, smaller sea cage farming operations of cod have been undertaken in Norway, and although in smaller scale, no escapes are reported.

10.3 | Sexual maturation

A variety of biotic and abiotic environmental cues, but mainly food availability, photoperiod and temperature, control the timing of sexual maturation.[223] Further, timing of sexual maturation is also linked to growth and metabolic status.[224] While attaining puberty is a natural phenomenon, under fish farming conditions some fish species such as Atlantic cod, seabass and salmon enter the maturation status earlier before attaining a minimum preferred slaughtering weight which is 3 kg for cod. Early maturation before slaughtering leads to decreased growth performance, feed conversion and flesh quality in cod.[225] Further, sexual maturation and spawning in fish tend to increase the susceptibility to infectious diseases through reduced immune parameters[226,227] and an unattractive appearance to the consumer and resulting in a lower commercial value. Because of these negative effects, husbandry practises in aquaculture aim at avoiding early sexual maturation before harvest. In the following sections, we will discuss possible measure that could be taken to mitigate the early sexual maturation in cod. It should be noted that no farming efforts were taken since the late 2000s, not many studies have been undertaken in controlling sexual maturation in cod.

10.3.1 | Using light and/or feeding manipulations

Photoperiod manipulation is used by fish farmers to control gonadal maturation in farmed fish species.[71] Farmed Atlantic cod reach puberty at the age of two plus years, and, as in other farmed fishes, this early maturation is a major problem in cod farming due to negative effects on growth, production time, survival and fish welfare.[13] Due to these negative effects, researchers and farmers were exploring ways to delay or inhibit early maturation through manipulating environmental parameters (photoperiod, temperature), feeding practices (ration, frequency) and nutrition .[70,72,223,225,228-230] These continuous light regimes are successful in controlling early maturation of farmed cod in indoor tanks[70,228,229] but similar results could not be achieved in sea cages and even strong CL treatment often only delays puberty by 4–6 months, perhaps due to the interference of strong ambient light cycle in sea cages.[231] However, Kolbeinshavn et al[232] showed that farmed cod reared under artificial light in sea cages had 33% higher weight (approx. 3 vs 4 kg) compared to fish reared in natural light in Iceland. The use of continuous light in sea cages at different stages could delay the sexual maturation by 6 or 12 months and results in increased body weight and condition at harvest compared to fish that were kept in either continuous or natural light regimes.[233] Thus, tactical use of continuous light in sea cages can offer better results in terms of growth and delaying sexual maturation. It is suggested that subsurface feeding regimes at deep in the sea cages would prevent the need to ascent to surface water (when fed on the surface)[231] and the cod would experience more consistent light regime which could minimize the effects of external ambient light on maturation. Spectral quality of the lightening system could also be an issue for the failure of arresting early maturation, and it should match the natural light spectrum.[234]

Atlantic cod is dependent on the energy reserves, especially the lipid reserves in the liver, for sexual maturation.[235] Farmed cod with larger liver, which seems to be related to dietary lipid levels,[236] can easily invest in gonadal development which could lead to early maturation.[237] Based on this idea, tactics involving periods of starvation,[72,230] exercise by subjecting the cod to combination of different current speeds and photoperiod[73] and a combination of continuous light and varying protein and lipid composition of feed were tried, but all resulted in limited or no success.[73]

While using CL in controlling the early sexual maturation could have some positive effects (better growth and delayed sexual maturation), it could have negative effects on the welfare of the cod.[238] Subjecting Atlantic cod, Atlantic salmon and European sea bass to continuous light for a short period (3–25 days) resulted in significantly increased cortisol levels and the retinal damage. Studies on the physiological implications[229] and kisspeptin and gonadotropin genes involvement in sexual maturation[239] when using CL did not give any clear indications of the mechanisms involved. Thus, additional knowledge about how photoperiod modulates puberty entry and completion and the endocrine mechanisms controlling these events and the welfare implications are therefore needed for refinement of such techniques for use in sea cage farming.

Since the collapse of cod farming in the late 2000s, no attempts were undertaken to farm cod in sea cages. Thus, no attempts have been undertaken to control the sexual maturation using light or feeding practices. With resurging cod farming attempts now, the farming industry has taken efforts to control early sexual maturation using submerged LED lights in sea cages.

10.3.2 | Sterility

The production of sterile (triploid or gonad-less) fish has been considered an option for reproductive control and genetic containment in farmed aquatic species to meet both industrial (improved post-pubertal somatic growth, survival and quality) and environmental (no genetic interaction with wild fish) criteria.[240] To date, the production of triploids is recognized as the most practical, economical and effective method for large-scale production of sterile fish[241] while production of gonad-less fish using molecular techniques such as CRISPR gene editing and gene knockdown is developing.[242]

Triploidy suppresses the gonadal development and allows the triploid fishes to invest the metabolic energy and nutritional resources into somatic growth rather than directing it to the development of sexual characteristics and reproduction. Thus, triploid fish may grow faster and convert food more efficiently than diploids. Attempts have been made in cod to induce triploidy by applying cold/heat shock[243] or hydrostatic pressure shock[244–246] at an appropriate time to retain the second polar body within the egg. In cod, the hydrostatic pressure treatment of eggs to induce triploidy usually results in a higher survival and less deformities at hatching if compared with other methods.[247] Despite the possible positive effects due to suppressed gonadal maturation, the triploid induction in Atlantic cod did not always result in better growth and triploid fish have significantly more skeletal deformities (head and jaw) than the diploid siblings.[246,248–250] Trippel et al reported comparable growth of triploid Atlantic cod growth with diploid fish over a 4-year study,[251] suggesting that diploid fish invest heavily on reproduction while triploid fish did not invest in reproduction. While gonadal development in female cod is suppressed, male cod develop testis.[246,252,253] Thus, an all-female production approach could be an alternative solution to avoid sexual maturation.

10.3.3 | Genetic selection

In fish, early sexual maturation reduces the growth and product quality and leads to welfare issues. While light manipulations and triploidization provide short-term solutions to early sexual maturation, a long-term strategy of selecting against early maturation should be employed in cod breeding programme, especially for males who mature in the second year.[254] QTLs for controlling sexual maturation have been found for both males and female Atlantic salmon[255] and also in rainbow trout.[256] For cod, attempts have been made to identify the genetic variation in early maturation, however, failed to produce reliable heritability estimation.[161] Genetic analysis of early sexual maturation performed in NCBP has been described above. With the Atlantic cod genome has been annotated,[257] this marker-assisted selection technology will prove useful to find molecular techniques that will delay the sexual maturation in Atlantic cod.

11 | NORWEGIAN COD FARMING INDUSTRY DEVELOPMENT FROM 1990 TO 2000S

In the 1990s, approximately 400 cod farming licences were distributed along the Norwegian coast and most of these licences were used for capture-based aquaculture rather than stocking intensively reared cod juveniles.[258] However, the number of licences decreased to 118 in 1999.[259] During the late 1990s, scientific research on intensive cod larval rearing was initiated in many North Atlantic countries but it was at its early stages.[33] With reduced cod quota in the late 1990s and optimism from salmon farming success triggered interest in commercial cod farming in the early 2000s. In the mid-1990s, researchers and private companies in Norway began to work on biological solutions and methodology for larval rearing of marine cold-water species, such as halibut, turbot and cod. This R&D work, however, focused mainly on medium-sized mesocosm systems (ponds) to enhance natural plankton blooms to provide sufficient food of high quality for the early life stages of cod. Due to the unstable and variable production of juvenile number from these systems, in the mid- to late 1990s, private Norwegian companies and research institutions shifted their focus on developing protocols for intensified production techniques.[260] The cod hatchery technology at this time was a concept that was used in Mediterranean hatchery technology used for seabass and seabream.[261] These new and developing technologies were at the R&D stage when the cod farming started in the early 2000s. While research institutes mainly focused on development of larval rearing protocols and mass juvenile production, private companies adapted modified technologies borrowed from salmon sea cage farming. The perceived belief of adapting salmon farming infrastructure and technologies into cod farming proved to be not entirely true. Farmers who adapted such technologies soon realized that cod is a distinct species in many ways such as feeding, robustness and diseases at various life stages. Thus, without proper scientific background on cod biology in intensive rearing systems, farmers have started mass commercial production of cod. The growth of cod farming peaked between 2002 and 2008 with cod juvenile production increased more than 60 per cent a year. It was reported that 16 commercial hatcheries which produced four million cod juveniles in 2003[13] and it was expanded to 26 in 2007 (Table 5). At its peak in 2008, there were 26 commercial hatcheries and 533 cage farming licences, but the industry had completely disappeared from Norway in 2014.[262] Major reason for this failure has be discussed above and below of this chapter.

In the early 2000s, the cod farming industry collected the gametes from mass communal spawning in tanks from few wild-collected adults and the quality of the gametes was not closely monitored.[260] This led to the production of inferior quality of embryos and larvae. Further, the use of batch culturing method used for rotifer production in the early 2000s led to unstable rotifer systems and inferior nutritional quality of rotifers was offered to the larvae. Due to the instability in livefeed production and high labour cost to produce rotifer and *Artemia*, cod commercial hatcheries wanted to reduce the dependency on cultured livefeed. For this reason, they have chosen to wean the cod larvae early onto dry diets which led to high mortality (maybe the larvae are incapable of digesting the dry diet at that early stage, water quality issues created by the uneaten dry diet, etc.), increased cannibalism (inherent property of cod enhanced by increased size variation by early weaning) and higher incidences of deformities due to malnutrition.[260] When such inferior quality juveniles were transferred to sea cages, they encountered mass losses up to 50%.

TABLE 5 Commercial cod hatcheries producing cod juveniles in Norway in 2007. Production capacity (in million) is given when data is available

County	Hatchery	Production capacity
Finnmark[b]	Sponfish	
	Trollfish	
Tromsø[b]	Norfra	
	NCBP[a]	
Norland	Lofilab	0.5
	Codfarmers	
	Fjord marin	
	Sponfish	
	Helgelandtorsk	
	Vikholmen	
Møre and Romsdal	Fjordlaks	
	Branco	
	Villa cod	
	Holstad marine	
	Profunda	5
	Aquaforsk genetic centre[a]	
Trøndelag	Skei marin	
	Fosen aquacenter	
	Trodenskjold cod	
Sogn and Fjordane[b]	Nærøysund	
	HMY	5
	Bremar	
Hordaland[b]/Rogaland	Cod culture Norway (CCN)	5
	Sagafjord	1
	Grieg	
	Marine Harvest	
	Marine Farms	

[a]Denotes research institutions.

[b]Denotes county divisions in 2007.

12 | CURRENT STATUS OF THE NORWEGIAN COD FARMING INDUSTRY

Currently, cod farming is active only in Norway. There are approximately 7–8 companies involved in cod farming since 2018. While few of them are new to the cod farming, experienced cod farmers are also involved (Table 6). HMY was established in 2002 and active during the early 2000 cod farming activities and have produced millions of cod juveniles. Operations ceased in the late 2000s but kept a tailor-made 'breeding programme' since 2003. The company claims to have 6th-generation cod now and will produce their 7th-generation cod in 2021. Their facility has a capacity to produce ten million 2–3 g cod juveniles per year. They plan to build a new facility which they claim to have a capacity of producing 25 million cod juveniles of 1 g in 2022. Others have the plan to produce their own juveniles but are currently buying juveniles from either NCBP or HMY or both.

Norcod is the current big player and has stocked 1.8 million fish in sea cages in 2019. Norcod is now listed in Merkur Market and secured 250 Million NOK in investments, and their market value has risen 50% since the listing in Merkur Market.[263] This shows a positive trend and a belief in cod farming. So far almost one billion NOK from private investors has been invested in cod farming in 2020. The positive results from NorCod operations so far (better harvest weight, less than 5% loos at sea, lower deformities, investor trust, etc.) will also attract farmers from other North Atlantic countries such as Scotland, Iceland, Faroe Island and Canada. They expected to harvest 6500 tons in 2021 and plans to increase it to 25,000 tons in 2025.[264] Norcod not only operates commercial sea-based cod farming but also is involved in the entire value chain through co-operation with key players. They claim that this whole value chain approach will bring the cod farming into a success. Currently, a national network for cod farming has been established with different stakeholders (cod farmers, R&D actors, feed companies and industrial actors, government agencies and research institutes) and the steering group is led by Nofima.

Unlike in the early 2000s, gametes are now produced using the selectively bred broodstock (multipliers), and as explained above,

TABLE 6 The current commercial companies actively involved in cod farming in Norway and their main facilities and activities

Company	Sea cage	Juvenile Grow-out	Juvenile production	Hatchery
Gadus Holding AS	Yes (2021)	Yes	Yes (2021)	Yes
Arctic cod AS	Later	Yes	Yes (2021)	Yes
Kime Akvakultur AS	Yes (2022)	No	No	No
CIT Holding AS	Yes (2021)	No	No	No
HMY AS	No	Yes	Yes (2021)	Yes
NorCod AS	Yes (2021)	No[a]	Yes	No[a]
Statt Torsk AS	Yes (2021)	No[a]	Yes	No[a]

[a]Denotes that these companies get these services through Arctic cod AS and HMY AS.

both NCBP and HMY have the domesticated broodstock and are capable of supplying required number of embryos to the cod industry year-around. This improved the quality of the embryo and the larvae. Further, NCBP has great success of juvenile production using late weaning and has recommended the cod hatcheries to use these techniques.

13 | STATUS OF COD FARMING TODAY

With the renewed interest in cod farming in Norway, we will discuss the current status of cod farming regarding production-related issues, market vulnerability, political environment and the investment opportunities.

13.1 | Production

Currently, the farmed cod juveniles have improved in all measurable parameters such as better growth, survival and disease resistance. The quality of the cod juveniles is much superior in growth rates, pleasing external appearances (lower deformities, good external colouration, external morphology) compared to the juveniles produced in the early 2000s owing to the domesticated healthy cod from NCBP. Otterå et al[265] showed that farmed cod had 48–67% higher weight compared to the wild counterparts within two generations. Further, the weight of the cod after being in sea cages for 20 months has reached four kg (32 months from hatching) and the loss in sea cage is less than 5–10% which is a great improvement from more than 50% loss in the 2000s.[266] Through the selective breeding of cod over five generations, the researchers have increased their knowledge of the biology of cod and fish that are suited for captive breeding and sea cage life were selected. The use of submerged LED lights has been employed by Norcod in their sea cages recently to delay early sexual maturation, and the results so far are encouraging compared to the sea cages without the LED lights.

Apart from the HOG flesh, cod liver (oil), gonads and tongue (delicacy) can also fetch higher price in the market. However, the quality of the oil from farmed cod depends on the chemical composition of the liver which depends on the fatty acid composition of the feed for cod.[267] Since the cod farming did not take off very well even in the 2000s, the marketability of these products needs to be developed after conducting more biochemical analysis and marketing studies.

13.2 | Role of NCBP

As discussed earlier, contribution of NCBP was vital for the current surge in interest on cod farming in Norway. Domesticated cod broodstock through five generations has produced good quality offspring and contributed to increased growth and disease resistance. As mentioned in the NCBP chapter, currently, we are working on early sexual maturation and in the coming years, NCBP will include other traits such as fillet quality. The willingness of the Norwegian Government to support the cod breeding programme will give confidence to the developing cod industry.

13.3 | Current market and future forecast

Currently, the COVID-19 pandemic has caused massive economic disruptions and precipitated a dramatic slowdown in global economy.[268] For seafood, COVID-19 has led to a drop in demand and prices and disrupted logistics and production in both fisheries and aquaculture.[269,270] COVID-19 has also affected the market for cod. Although export of fresh whole cod from Norway has slightly increased in 2020, the price has dropped compared to 2019.[271,272] There has also been a shift from fresh to frozen products in line with the overall food trend observed since the onset of the COVID-19 pandemic. Consumers now prefer frozen and pre-packaged products.[273] Furthermore, the International Council for the Exploration of the Sea (ICES) has recommended a 20% increase in the total allowable catch (TAC) for Atlantic cod for 2021. An increase in TAC in 2012–2013 by 30% also lead to a significant decrease in cod prices.

The current market situation for farmed cod is very similar to the period 2009–2011. There are massive economic disruptions in the global economy because of COVID-19, and the TAC for Atlantic cod has been increased. It is thus very likely that the price of wild cod could drop in 2021. If that happens, this would be the 3rd time the price of wild cod faces a significant drop since 2008, either because of increase in TAC, global economic disruptions, or both. This illustrates that it is reasonable to expect that the price of wild cod would fluctuate in the future. As the price of farmed cod has been shown to be dependent on the price of wild cod, the price for farmed cod could also decrease in 2021.

One possible way to achieve a higher price for farmed cod is to differentiate farmed from wild cod. This will require a significant investment in marketing and development of new products and sales channels for farmed cod. If farmed cod is sold in the same manner as during the last period of cod farming, the price of wild cod will, to a large extent, dictate willingness to pay for farmed cod, and thus, it could influence the profitability of cod farming.

13.4 | Current political environment

At the turn of the millennium, there were political ambitions to build an industry with the potential to be a strong contributor to securing employment and settlement in coastal Norway. Such ambitions no longer exist, and there is a growing public scepticism of aquaculture that also includes cod. Nevertheless, since the establishment of the breeding programme, the government has continued to fund it. This has been supported by Parliament. There have been no signals that the state funding of the programme will be stopped. However, there are no signals from the state to provide extraordinary instruments to stimulate private actors to invest in the industry. Any new growth in cod farming will therefore have to be based on sustained profitability.

13.5 | Capital investment

After the millennium banks regarded the risk too great to finance cod farming, however, it was possible to raise venture capital. Our impression is that while the banks still (in 2020) are sceptical, and therefore, reluctant when it comes to new involvement, it is more likely to raise venture capital. An article in the press[274] and conversations with informants in the financial industry shows that it has been possible to finance cod farming and that there is registered a substantial growth in investing in the industry. Future access to capital from both banks and the venture market will depend on whether the industry can be run profitably. Financial players and investors will have expectations of competitive profitability and return on their investments.

14 | SUMMARY

Commercial farming of the most important North Atlantic fish species Atlantic cod has been tried in the early 2000s in Norway and other North Atlantic countries but the efforts failed to succeed due to three major reasons: 1. not understanding the biology of the cod in captive conditions, 2. recovery of wild cod stocks in the late 2000s which brought the market price down and 3. the economic meltdown in Europe in the late 2000s. Although the cod farming dwindled in all the countries in the North Atlantic region, the Norwegian government continued to fund the NCBP that was started in 2003. Research carried out within the NCBP on cod biology and selective breeding for better growth and disease resistance have resulted in better quality juveniles. Most of the biological knowledge gaps which were instrumental for the failure of the early 2000s cod farming was closed. NCBP has produced the 5th-generation domesticated stock in 2019. The domestication has reduced the aggression in the tanks among the juveniles which eliminated cannibalism. Further, the occurrence of deformities in juveniles is reduced to less than 10% and most of these deformities are mild. Domestication has also reduced the net biting behaviour, and thus, the escape/loss in the sea cages is less than 5%. Further unlike the early 2000s, this time the approach is cautious and only a few but seasoned farmers are involved. Investors have faith in cod farming this time, and companies have successfully secured the faith of the investors. While there are many positives now compared to the 2000s, there are some pitfalls too. Early maturation before slaughtering is a problem which needs to be addressed either by selective breeding (long process) or photomanipulations (quick returns). The use of modern LED light in sea cages is already showing positive results on delaying the first maturation until slaughtering. Vaccine development and development of other preventive measures against the most important diseases are needed to be developed further for a robust and successful industry. Although the market prices for fresh cod have been high in 2020, it is very likely it will drop in 2021 because of the economic disruptions following the COVID-19 pandemic and the increased TAC of wild cod. Based on historical data, the price of wild and farmed cod will vary depending on the global economy, the global catch of wild cod and the production of farmed cod. Thus, the farmed cod should be differentiated from wild by major investments in marketing and product development to achieve a good market price. However, lessons learned in the early 2000s attempt and the cautious approach of the companies involved this time would provide a greater opportunity for profitability for future cod farming. Thus, even with the above-mentioned pitfalls, cod farming could be in a better position than it was in the early 2000s to succeed.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Velmurugu Puvanendran https://orcid.org/0000-0002-4416-7000

Anne Kettunen https://orcid.org/0000-0002-1217-7079

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