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REVIEW

REVIEWS IN Aquaculture

Ecological interactions between farmed Atlantic salmon and wild Atlantic cod populations in Norway: A review of risk sources and knowledge gaps

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Abstract

Aquaculture provides an important and expanding source of protein rich and healthy food to the world. However, to minimize environmental harm from aquaculture, interactions with wild fish communities need to be thoroughly assessed. Here, we characterize the existing knowledge pertaining to such interactions, exemplified with Atlantic salmon (*Salmo salar*) farming in open net pens along the Norwegian coast and potential consequences for wild Atlantic cod (*Gadus morhua*) populations. Importantly, the wild cod fishery also provides a protein rich, high quality food source with high economic value. We identify seven risk sources that may affect behaviour, physiology, and survival in wild cod. Of particular importance is the large amount of waste feed that causes wild fish to aggregate around farms, thereby altering a multitude of ecological interactions including predation and disease transmission. Moreover, altered food quality in pellets may alter physiological processes and cause mortality to vulnerable life-stages in wild cod. More research is needed on mechanisms and thresholds for harm. As the most important cod fisheries are found in northern Norway, where climate change also is rapid, we expect stronger and potentially more harmful interactions between fish farming and wild cod fisheries as aquaculture continues to expand. We hope that our analysis will inspire further research, on farmed salmon and wild cod interactions, but also on aquaculture and wild fish interactions in general. Such research is fundamental for the development of management systems that can reduce the impact of aquaculture on fisheries and the environment.

KEYWORDS

aquaculture and wild fish interactions, Atlantic salmon, knowledge strength, risk sources, wild Atlantic cod fisheries

1 | INTRODUCTION

About one fifth of the world's wild fish stocks are considered overexploited, and with the increasing global demand for aquatic food products, fisheries are unable to keep up.[1] Managing harvested fish stocks are fundamentally challenging. As technological advances have improved the efficiency of the fisheries, often combined with destructive alterations of habitats and ecosystems (e.g. from trawling),[2] the risk of reducing or depleting fish stocks has increased dramatically.[3] This, in combination with impacts from ongoing climate change and other anthropogenic factors, means that many wild fish stocks are threatened by multiple stressors.[4,5] In response to the diminished return from fisheries there has been an unprecedented increase in the farming of aquatic organisms over the past decades, and currently approximately 50% of global aquatic food consumption comes from aquaculture.[1] While large-scale aquaculture provides a valuable alternative to wild fisheries in providing protein-rich and healthy food to the world, it may also represent an additional stressor to wild fish populations in areas where farming overlap with important habitats.[6,7]

In Norway, farming of Atlantic salmon (*Salmo salar*) dominates the aquaculture industry, representing the largest salmon aquaculture industry in the world with a sale of 1,552,000 tons in 2022, worth around 8500 million Euro.[8] The farming of Atlantic salmon is mainly done in open net pens, meaning that the fish have continuous access to well oxygenated water. At the same time, toxic substances (lice treatment, antifouling chemicals, etc.), feed, organic production waste and pathogens can be spread directly into the environment. The impacts of salmon farming on wild anadromous salmonids are well documented, including negative effects of the parasitic salmon louse on salmonid fish species,[9–13] and genetic introgression from escaped farmed Atlantic salmon into wild Atlantic salmon populations.[14–16] However, the effects of salmon aquaculture on wild marine fish, such as the Atlantic cod (*Gadus morhua*), are not well understood. This lack of knowledge is particularly problematic given the political aim of a fivefold increase in aquaculture production of Atlantic salmon in Norway by 2050.[17]

At the management level, decisions must be based on the best available scientific knowledge, but also uncertainty and gaps in existing knowledge.[18] Moreover, stakeholders like politicians and managers of aquaculture and fisheries need to work towards a mutual understanding of what risk factors exist. This may be facilitated by a new risk assessment methodology developed for marine aquaculture and guided by risk science. In this method, stakeholders with different value perceptions are brought together to reach a common understanding of the main risk drivers and the uncertainties related to critical factors in the system.[18] The method uses the latest thinking in risk science, with special emphasis on knowledge characterization, arguably fundamental for risk assessment and management processes.

Of the marine fishes' present along the Norwegian coast, Atlantic cod is of special importance as the coastal cod fishery have secured the livelihood for coastal communities for millennia.[19] Along the Norwegian coast the Atlantic cod is found in fjords, bays and in open coastal waters. The Atlantic cod in Norwegian waters is classified into two offshore stocks—the Northeast Arctic cod (from now on NEA cod) and the North Sea cod. In addition, there is a coastal component of the Atlantic cod, the Norwegian coastal cod, that has a more stationary stock complex inhabiting the fjords and the outer coastal waters, but also with a migratory component using the offshore coastal banks.[20,21] The NEA cod fishery represents the largest cod fishery in the world, with records of historical catches from year 1520, with landings of about 85,000 tons,[22] and with 376,000 tons caught in 2021, worth around 700 million Euro. The Norwegian coastal cod is recently divided into three management units: (1) south of 62° N, (2) between 62° and 67° N and (3) north of 67° N. However, genetic studies indicate that there could be several overlapping biological populations isolated by distance.[23,24] While the North Sea cod spawns offshore in the North Sea,[25] NEA cod spawns on the coast of Norway north of 62° N,[23,26] primarily in the Lofoten archipelago or further north. The Norwegian coastal cod spawns in fjords, bays, and around skerries all along the Norwegian coast.[27–30]

The highest catches of Atlantic cod in Norwegian waters are north of 62° N, where both Norwegian coastal cod and NEA cod are present. These ecotypes differ in life-history, movement ecology, and genetic population structure.[21,30,31] The NEA cod grows and feeds offshore in the Barents Sea and performs long-distance spawning migrations up to 1200 km to the coast of northern- and mid-Norway.[26] The eggs, larvae, and young juveniles drift in the coastal current back to the Barents Sea.[26,32,33] However, both yearlings (0-group) and older juveniles have been found in the autumn in the fjords of Northern Norway.[31,34] The Norwegian coastal cod spawns in fjords and coastal bays, where it may also complete its full life cycle.[20,27,35] Compared to NEA cod, the stronger local residency of Norwegian coastal cod in fjords and coastal areas[31] implicate that habitat overlap with salmon farming can occur year-round.[36] This is of a particular concern since the Norwegian coastal cod stock complex is already severely reduced, most likely due to a fishery conducted above long-term sustainability levels.[37,38]

Here, we exemplify the potential risk to wild fish populations from aquaculture by discussing and analysing the interactions between wild Atlantic cod and farmed Atlantic salmon along the Norwegian coast. We provide an in-depth knowledge characterization related to a selected set of identified risk sources in salmon farming that may harm wild Atlantic cod populations. We believe this may be a steppingstone for improved risk-adapted management decisions related to the interactions between farmed Atlantic salmon and wild Atlantic cod populations. Moreover, this approach can be adapted to fit similar interactions between aquaculture and wild fish of other species and may guide the future development of marine food production systems to reduce or minimize their negative impact on the environment.

2 | BRIEF OVERVIEW OF THE MAIN INTERACTIONS BETWEEN WILD MARINE FISH AND FARMED ATLANTIC SALMON

The activities related to Atlantic salmon aquaculture are interconnected with the surrounding ecosystem (Figure 1). Farming Atlantic

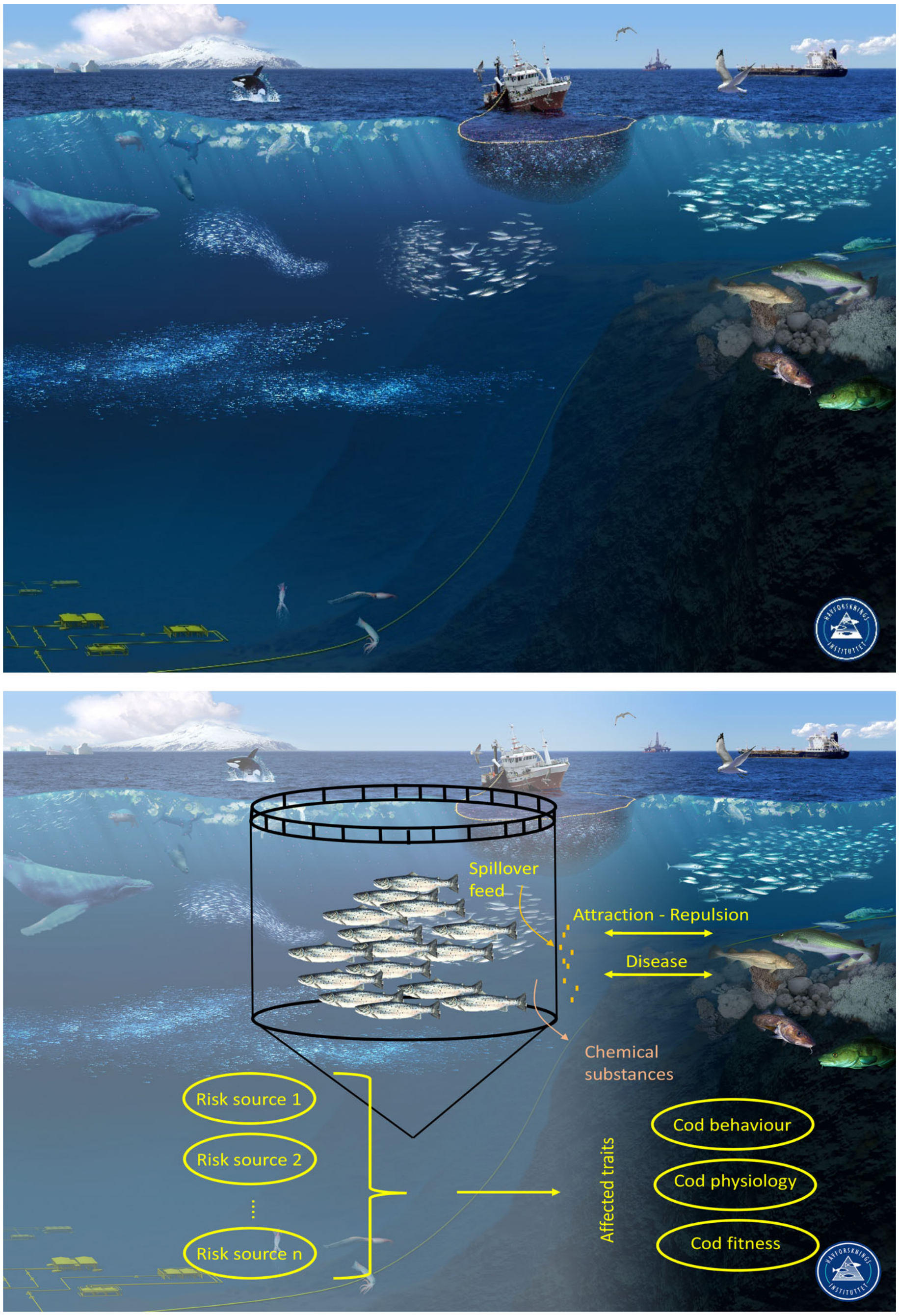

FIGURE 1 Impact of salmon farming on wild Atlantic cod. Illustration of a natural Norwegian coastal marine ecosystem with cod and other organisms in the food-web (upper); and how a salmon farm adds interactions and risk sources that may affect different traits like behaviour, physiology, and fitness in the wild Atlantic cod population (lower). Background illustration by Arild Sæther/Institute of Marine Research.

salmon in Norway is predominantly using open net pens. Hence, excess feed, waste products from the fish, and chemical substances including medicines, lice treatments, and antifouling agents, will leak into the surrounding waters and interact with the ecological community in the vicinity of the farm. In addition, potentially disease-causing pathogens may also be transferred between farmed and wild fish, especially since wild fish aggregate around salmon farms.[39]

Open net pens may offer opportunities for wild fish, for example, the significant amounts of waste feed that becomes available,[40] but may also cause harmful effects from malnutrition, toxicity, or disease. Substances emitted from salmon farms may therefore both attract and repel wild fish to active farms. Effects from interactions between farms and wild fish may both be direct (e.g. spill-over feed, exposure to toxic chemicals, and pathogens) and indirect (e.g. changes in abundance for species that wild fish prey on, or changes in the ecosystem that modify food-web interactions). Moreover, effects may be positive (e.g. alternative feeding opportunities) or negative (e.g. reduced food quality) for the wild fish. For fish species with ontogenetic niche shifts, for example, Atlantic cod, effects of aquaculture are also likely to be more pronounced for certain life-stages.

3 | IDENTIFYING KEY RISK SOURCES

In the following, we briefly describe what we have identified as the main risk sources from salmon farming and their causal effects on wild populations of Atlantic cod. We categorize these risk sources based on which traits that may be affected; (i) changes in behaviour, (ii) changes in physiology and (iii) changes in survival (fitness). Often, different risk sources may interact, and a single risk source could also affect several traits (Figure 2).

3.1 | Risk sources related to changes in behaviour

The causal triggers for behavioural changes in wild Atlantic cod caused by salmon farming, are related to activities at or near the farm. This may comprise the presence of the physical structure of the farm (working as a fish attraction devise, FAD), the different activities producing noise, changes in trophic resource availability, especially due to the spill-over of waste feed, and the emission of chemical or biological substances affecting fish olfaction. The behavioural responses of the Atlantic cod to this complex interplay of factors may involve repulsion from, or attraction to salmon farms, both of which have ecological consequences.

3.1.1 | Risk source 1: Atlantic cod attracted by salmon farms

Spill-over feed is available year-round near salmon farms and attract wild fish including cod. Other smaller wild fish may be prey for cod. Also, the physical structures of farms, including use of artificial light to prevent maturation in salmon, ropes, chains, and moorings may represent attractive habitat elements for cod and other fish species. Artificial light and physical structures may also concentrate or attract plankton and planktivorous fish, which again serves as food for larger piscivores. Organic enrichment of the sea floor under and in the vicinity of the farms may alter and boost bottom-dwelling and benthic invertebrates, again making food for certain fish species more accessible. The cascade of events described above may cause significant alterations in natural coastal ecosystems, depending on the extension of the impacts and the hydrodynamics of the surrounding waters.

3.1.2 | Risk source 2: Atlantic cod repelled by salmon farms

Activities on and near farms involve the use of boats and other heavy-duty machinery that may produce noise, smell (e.g. from leaking oil or other chemicals), and artificial light. Moreover, large amounts of salmon are moved around for delousing or slaughtering. These factors may scare and repel wild fish from salmon farms.

3.2 | Risk sources related to changes in physiology

Physiological effects, such as altered biochemical composition, metabolism, or reproduction in wild Atlantic cod, are primarily discussed in relation to altered food quality and quantity near salmon farms. Emission of toxic chemicals, or indirect effects on important species in the food-web that the cod interacts with, may also cause physiological effects in wild Atlantic cod.

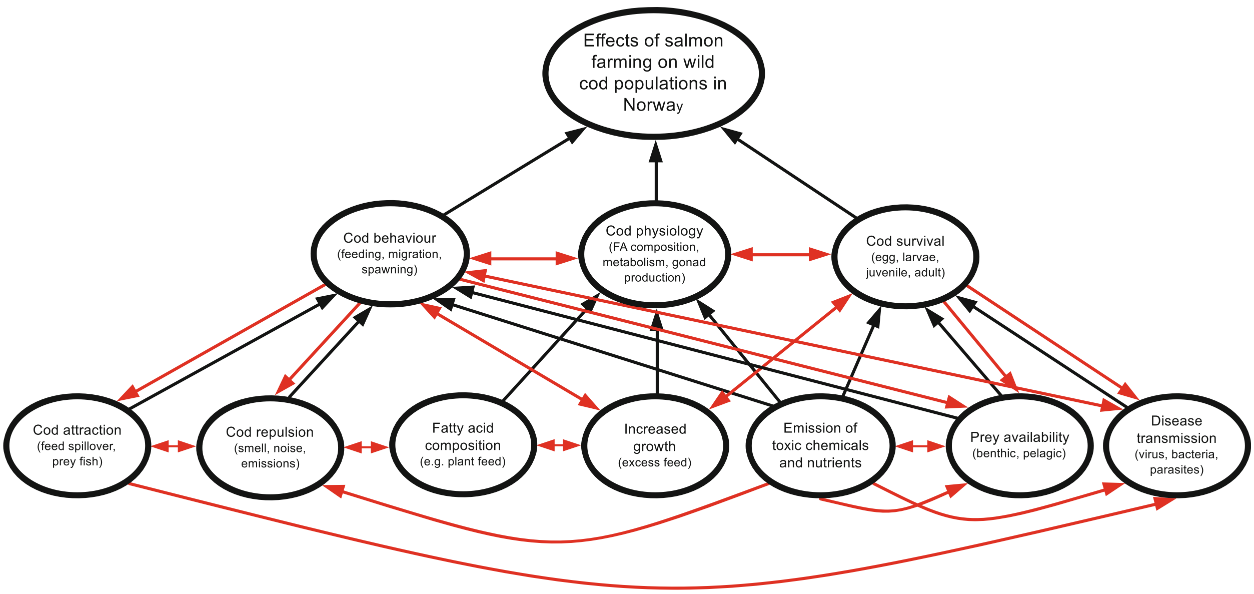

FIGURE 2 Simplified causal-risk diagram (black arrows) with seven identified risk sources (bottom level nodes) affecting three different trait types (middle), which result in overall risk of impact on wild Atlantic cod populations in Norway (top node). More realistic links, interactions and feedback between nodes and levels are added by the red arrows, as discussed in Section 4.

3.2.1 | Risk source 3: Altered fatty acid composition from plant feed

Fish feed is at present primarily produced by terrestrial ingredients that deviate consistently in fatty acid composition compared to feed organisms in the marine food webs. The terrestrial fatty acids propagate into muscle tissue and gonads, but the extent to which this will affect reproductive processes in adult fish (e.g. maturation and production of gametes) or viability of the more sensitive early life-stages (e.g. eggs yolk-sac larvae, juveniles) is largely unknown.

3.2.2 | Risk source 4: Increased growth from excess feed

The increased amounts of feed present around fish farms represent a resource for wild fish. This easily accessible food can be utilized for rapid growth of liver, gonads, and body tissue, thereby increasing condition and fecundity, and shifting age of maturity to younger ages.

3.3 | Risk sources related to changes in survival (fitness)

Reduced survival may be caused directly by emission of toxic chemicals, or indirectly through reductions in natural food items (e.g. zooplankton, shrimps, or shellfish that can be harmed by anti-sea-lice drugs), or transmission of diseases from the high density of fish in aquaculture or by increased contact from aggregations of wild fish around salmon farms.

3.3.1 | Risk source 5: Emission of toxic chemicals and nutrients

Salmon farms emit toxic drugs and chemicals used for delousing and other treatments. This also includes exposures to components or metals from antifouling protection of net pens. Emissions can be a result of routine operations or accidental. Nutrients in the form of N and P are also emitted and may result in altered local food-webs.

3.3.2 | Risk source 6: Alteration in availability of prey species

Emissions of toxic chemicals linked to salmon farms can affect the ecological communities in the nearby environment, causing changes in the availability of natural food resources for Atlantic cod.

3.3.3 | Risk source 7: Disease transmission

High density of individuals held together in a limited space, such as Atlantic salmon in farms, increases the risk for local disease outbreaks and transmissions. Moreover, aggregation of wild fish near the farm increases the contact rate between farmed and wild fish, thus increasing the risk of disease transmission, either from farmed to wild, or from wild to farmed fish.

4 | IN-DEPTH CHARACTERIZATION OF RISK SOURCES

In this section, we discuss the present scientific knowledge for each of the seven risk sources identified in the previous section. We also highlight areas of particularly important knowledge gaps and outline research hypotheses that should be investigated to fill these gaps.

4.1 | Risk source 1: Atlantic cod attracted to salmon farms

Several mechanisms may attract fish and other wildlife to fish farms. Physical structures, such as moorings and cages provide shelter for small fish and habitats for organisms, which in turn may attract larger predatory fish. Hence, fish farms can act as fish aggregation devices (FADs).[41] A substantial amount of feed pellets is lost from Norwegian salmon farms, with an estimated 3%–5% of the pellets passing through the open net pens uneaten.[42] Since the annual feed sale is 1.98 million tonnes in the Norwegian salmonid farming industry,[43] about 60,000–100,000 tonnes of salmon feed may be lost to the marine environment yearly. In addition, significant amounts of undigested faecal material are also emitted to the nearby environment.

The most abundant fish taxa aggregating around the Mediterranean and Norwegian fish farms had all consumed substantial amounts of the pellets fed to the farmed stock.[44,45] Such pellet feeding can have an effect at a regional scale. For instance, fisheries landings may increase due to consumption of feed waste.[46] Hence, one of the main reasons for wild fish being attracted to salmon farms, is the trophic subsidy provided by waste feed. Direct support for this mechanism comes from studies showing that the number of wild fish aggregating around fish farms is related to the feed intensity at the farm.[36,47] It is also shown that feeding times can be correlated to wild fish aggregation responses.[48]

The increase of other natural resources could enhance the aggregation of predatory fish around fish farms. For instance, larger mature Atlantic cod may feed on saithe (*Pollachius virens*) aggregating around fish farms.[49] Also, artificial light is often used at salmon farms to inhibit salmon maturation and thereby to increase somatic growth.[50] Pelagic invertebrates, such as the krill, are typically attracted to light[51,52] and zooplankton abundance can therefore be elevated around fish farms,[53] in turn attracting larger fish predators.[54] Direct and indirect effects of artificial light in marine ecosystems are reviewed by Marangoni.[55]

A meta-analysis of environmental impacts of aquaculture found elevated abundance of wildlife, mostly fish, surrounding aquaculture farms.[56] In Norway, saithe often dominate around cages in fish farms, but also other species have been reported to aggregate under salmon farms in Norway, including the Atlantic mackerel (*Scomber scombrus*), Atlantic cod and haddock (*Melanogrammus aeglefinus*). These species were reported to comprise, respectively, 92%, 3.5%, 2.4% and 1.8% of all aggregated fish under salmon fish farms.[39,57] In a recent study, Meier et al.[58] documented that 13% (in 2018) and 20% (in 2019) of the mature Atlantic cod caught at spawning grounds around Smøla (Norway) had specialized its diet to waste pellets from nearby salmon farms.

If a significant number of fish from the local population aggregate around fish farms, it may work as an ecological trap. An ecological trap is a situation where the population prefers a low-quality habitat ultimately leading to a population decline.[59] For example, Callier et al.[60] suggested that wild fish accumulating around fish farms are more susceptible to capture by fishing. On the other hand, farms might also act as marine protected areas due to decreased availability of the wild fish to local fishermen.[61] Dempster et al.[62] argue that prohibiting fishing around coastal aquaculture sites worldwide would protect tens of thousands of tons of adult spawning stock of wild fish that would otherwise have been exposed to fishing. In particular, a ban on fishing within 100 m of aquaculture facilities could be effective in protecting a relevant part of the adult Atlantic cod stocks aggregated around aquaculture facilities.[57] However, fish farms may also increase the predation pressure by attracting predators to the area, which again may lead to changes in the behaviour and distribution of potential prey fish. One example is that large numbers of fish in the farms can act as a food source for protected predators such as dolphins, seals, sea lions, and birds.[63] Top predators can become accustomed to the easy prey and may start to hunt wild fish in the surrounding area as well, such as *Pomatomus saltatrix*[64] or *Thunnus thynnus*.[65]

4.1.1 | Knowledge strength and gaps

It is well documented that wild fish, including Atlantic cod, can aggregate at aquaculture facilities. However, relatively little is known about the consequences of this aggregation behaviour for natural mortality, fishing mortality, and population productivity. There is also a need to better understand the changes in pelagic and benthic invertebrate communities that may serve as food for Atlantic cod around aquaculture facilities.

4.2 | Risk source 2: Cod repelled by salmon farms

In some circumstances wild fish, including Atlantic cod, may be repelled by salmon farms. Since the inception of the Norwegian aquaculture industry, local fishers have repeatedly claimed that the salmon farms along the coastline of Norway have altered the behaviour of Atlantic cod. Their perception is that cod will tend to avoid fjords with salmon farms, causing the abandonment of historically important spawning grounds.[66]

Fishermen's traditional ecological knowledge has been studied through interviews and social science methods,[67] and Maurstad et al.[66] concluded that fishermen indeed can make reliable observations of cod behaviour in aquaculture intensive areas. Reasons for why Atlantic cod is repelled by areas with aquaculture may involve pollution from toxic chemicals or other waste products, or noise. Fish have evolved olfactory responsiveness to a wide range of odorous substances (water-borne steroids, prostaglandins and their metabolites), known as pheromones.[68] These are detected with great sensitivity and specificity by the olfactory organs and influence reproductive behaviour and physiology in several taxa.[69] Hence, odorants from farmed salmon may affect behaviour in wild fish, but this is largely unknown.

Repeated experimental studies in the laboratory, where wild coastal cod were given a choice between remaining in or avoiding tanks containing water from salmon farms, found that wild-caught Atlantic cod typically avoid staying in tanks with a very small proportion (2.5 ‰) water from salmon farms.[70] The repellent mechanism in this case was odour, not changes in water quality, as cod with blocked olfactory epithel (anosmic) did not respond to the same odour. Follow-up experiments showed that fish caught near or under fish farms also avoid water from salmon farms, but to a lesser extent than non-exposed Atlantic cod. Exposure to odours from conspecifics resulted in a similar behavioural change in wild Atlantic cod, thus it may seem like the observed behavioural responses are not related to a specific odour, but general components that accumulate in the water with high density of fish. The migration pattern of coastal cod with blocked olfactory system has also been investigated under natural conditions, in a large-scale telemetry study.[71] Atlantic cod was caught in a farm intensive fjord with spawning areas, and the olfactory system was blocked in half of the fish. Fish from both groups released in the innermost part of the fjord were not deterred by the aquaculture facilities and stayed there for the duration of the field study, while all fish released in the outermost part of the fjord left the fjord within a week. Hence, the results were inconclusive, no evidence were found to support that migrating Atlantic cod avoids fjords with salmon farms. However, due to the difference in life history between stationary coastal cod and migrating NEA cod, the stationary Atlantic cod may get accustomed to the odours surrounding fish farms. A more recent telemetry study found substantially higher residency of Atlantic cod at spawning sites compared to nearby farmed sites, and no indication of less residence at spawning grounds close to salmon farming operations compared to spawning grounds further from any farming operations. Therefore, the authors concluded that there is little support for the hypothesis that salmon farms disrupt spawning dynamics on nearby spawning grounds.[72] Notwithstanding this, some Atlantic cod clearly showed long-term attraction to the salmon farms.[36]

Sound is used for communication between fishes, mating behaviour, the detection of prey and predators, orientation, habitat selection and migration.[73] Machinery and routine operations in salmon farming includes vessels, feeders, power washers, etc., generate noise that can disturb these ecological processes in wild fish. The behavioural responses of marine animals to anthropogenic sounds may include escape reactions,[60,74] avoidance or changes in swimming behaviour.[75] Atlantic cod can be conditioned to move towards a defined feeding arena as a response to a sound signal,[76,77] and wild fish, especially saithe, are also observed to be attracted to the sound of feeding in salmon farms. This response can be utilized in fisheries,[78] and does not seem to be very species-specific. Other effects of environmental noise have been reported, including barotrauma,[79] which may cause significant increase of stress-related blood parameters.[80]

Atlantic cod communicate by "grunts" during reproductive behaviour, aggression, or escape behaviour.[81] Female cod prefer mates with bigger bodies and long fins, but mating success is also correlated to sound production.[82] Cod exposed to long term noise have been reported to have a lower fertilization rate, up to 40% reduction, compared to non-exposed fish, but also fish exposed to short-term noise showed an increase of blood cortisol.[83] Hence, noise-generating aquaculture activities can scare fish off, initiate stress responses, disturb natural communication and ultimately reduce the fitness of the fish. However, there is also the option of fish being attracted to the facility due to the sound produced by the feeding system, after learning that certain sounds mean food.

4.2.1 | Knowledge strength and gaps

Repulsion of cod from fjords with salmon farms is described by local fishers and documented in scientific articles. However, as repulsion is a long-term effect that likely can be influenced by many causal factors, effects may need many years or decades to materialize. Therefore, cod repulsion from salmon farms is difficult to analyse and test as a regular scientific hypothesis. More studies should be performed on the chemical and biological cues on olfactory capacity of Atlantic cod, as well as effects of marine noise.

4.3 | Risk source 3: Altered fatty acid composition from plant feed

The added nutrient load to the environment surrounding fish farms may have a physiological impact on the wild fish aggregating at these sites. Both the amount of feed spillover eaten by wild fish, and the altered quality of that feed (e.g. the fatty acid composition) must be considered for potential changes in wild cod physiology. Clearly, the combination of a high proportion of the food intake that comes from aquaculture spillover, and that this feed contains a high proportion of terrestrial fatty acid, will increase the likelihood of changes in wild fish physiology.

The salmon feed used in Norwegian aquaculture has changed over the last decades, with an increase in feed sources from a terrestrial origin, and a corresponding decrease of high-cost marine proteins and oils. The change to a diet with predominant terrestrial ingredients has decreased the digestibility of the feed and increased the faecal discharge from salmon farms.[43,84]

The amount of marine ingredients in salmon feed has decreased from 90% in 1990 to 25% in 2016 having been replaced with plant-based ingredients that has increased to make up 73.1% of the ingredients in fish pellets presently.[43,84] This change in the salmon feed composition alters the fatty acid (FA) profile in the feed because marine oils are replaced with plant oils, like rapeseed oil. The rapeseed oil has high levels of terrestrial FAs such as oleic acid (18:1n-9), linoleic acid, (18:2n-6), and α-linolenic acid, (18:3n-3), and this represent typically 44%, 15% and 8% of total FAs, respectively. In comparison, these FAs typically contribute to; 12%, 2.5% and 1.5% of the total FAs in fish oils.[85]

Cod that feeds on a lipid-rich diet gets a pronounced increase in liver size as cod store fat in the liver.[86] According to Jobling[87] the large livers of cod feeding on formulated feeds may originate from an overload of intestinal digestive capacity, along with increased fat synthesis and deposition due to changes in rates of nutrients supply. In addition, the liver FA composition will change rapidly reflecting the FA profile of the diet.[88–93]

Wild fish consuming spillover feed from fish farms are shifting their diet from a natural diet containing marine highly polyunsaturated omega-3 fatty acids to a diet with terrestrial omega-6 fatty acids.[44,94] Fatty acid changes have been noted in several species such as saithe,[44,95] horse mackerel (*Trachurus mediterraneus*),[96] bogue (*Boops boops*),[97] mugilid (*Liza aurata*) and sparid (*Oblada melanura*)[98] as well as in cod.[44,58]

Meier et al.[58] showed that for wild cod eating salmon pellets the terrestrial FAs (18:1n-9, 18:2n-6 and 18:3n-3) contributed more than 50% of the total FAs in the liver compared to wild cod eating marine prey where these levels were below 20%. Similarly, salmon-pellet-eating cod had 27% and 26% of terrestrial FAs in the lipids of the ovary and testis, respectively. For cod feeding on marine food the terrestrial FAs contributed with 7% in the ovary and 15% in the testis. Although cod may tolerate a diet based on plant proteins and oils without negative impacts on the growth and health of the fish,[99] it is unclear whether feed sources of non-marine origin have negative consequences for reproduction.[100] It has been demonstrated that farmed cod fed capelin, herring or squid may have fecundities 2–4 times that of their wild counterparts,[101] probably reflecting the increased access of energy for vitellogenesis and gonadal growth in farmed fish.[102] Similarly, cod fed a formulated diet also show almost a doubling in relative fecundity compared to wild cod.[103,104] However, an optimal broodstock diet through gametogenesis is important for optimal egg and sperm quality.[105,106] Studies have shown that fecundity and larval survival are positively correlated with long-chain polyunsaturated FAs (LC-PUFA; C_{20-22}).[107–110] Moreover, optimum levels of docosahexaenoic acid (22:6n-3, DHA) and arachidonic acid (20:4n-6, ARA), as well as the ratio between ARA and other LC-PUFAs such as eicosapentaenoic acid (20:5n-3, EPA) are also important. These essential compounds are important structural components in phospholipids (PL) during gonadal development, in addition to being involved in physiological processes such as steroidogenesis and as precursors for prostaglandin synthesis. The LC-PUFA (DHA, EPA, and ARA) are considered as essential FAs for cold-water marine fish since they cannot be biosynthesized in sufficient quantities to support normal development and play important roles in multiple physiological and biochemical processes.[111] Eicosapentaenoic acid and arachidonic acid are relevant precursors of prostaglandins in marine fish and play a predominant role in immune regulation. Ganga et al.[112] showed that increased inclusion of vegetable oils in the diet or gilthead seabream (*Sparus aurata*) might profoundly affect the fatty acid composition of plasma and leukocytes, especially highly unsaturated fatty acids, and consequently, the production of PGE3, which can be a major prostaglandin in plasma. Alteration in the amount and type of prostaglandins produced can be at least partially responsible for the changes in the immune system and health parameters of fish fed diets with high inclusion of vegetable oils. Shift from marine oils (rich in w3 fatty acids) to plant oils (higher in w6 fatty acids) in the diet of commercially reared Atlantic cod could have adverse effects on the whole organism through the increase in the production of prostaglandins belonging to those derived from w6 fatty acids.[113] Therefore, a similar effect can be expected in wild cod that substitute their natural diet with a salmon farm diet.

Cod associated with fish farms is usually found with less food pellets in their stomachs than saithe, ranging from 6% to 30% depending on fish size.[44,49,114] This suggests that cod is less dependent on waste feed and is most likely attracted to marine fish farms due to large aggregations of prey fish.

Disparities of fatty acid composition have been shown in farm associated fish versus non-associated fish, both in gonads and in muscle, at several trophic levels.[100] Predators attracted by smaller prey fish will therefore also be affected by waste feed even though predators are not consuming the pellets themselves. Gonzalez-Silvera[100] also found histological differences in the gonads between farm associated fish and the control group, which reflected an accelerated development of oocytes in farm associated Round sardinella (*Sardinella aurita*).

Of the Atlantic cod present in Norwegian waters, the more stationary life history of the coastal cod makes this ecotype more dependent on local conditions than the migratory NEA cod, and hence more vulnerable since it is exposed to farm feed (and other discharges) over much longer time periods. The depleted state of the Norwegian costal cod makes it even more important to thoroughly evaluate the impact of farming on these local cod stocks.

4.3.1 | Knowledge strength and gaps

The magnitude and consequences of the shift from natural prey to waste feed for wild fish is not well understood. Consumption of pelleted food by wild fish, may alter reproductive physiology, potentially decreasing the quality and survival of eggs and cod early life-stages. However, the threshold levels of salmon feed (amount, duration and timing) consumed by wild cod before it affects the quality of eggs, sperm or other life-stages are not known and require new experimental data to be identified.

4.4 | Risk source 4: Increased growth from excess feed

The consumption of waste feed and prey fish around salmon farms, by cod and other gadoids may also represent increased food availability, leading to increases in the body and liver conditions of the fish. Fernandez-Jover et al.[44] reported 2–3 times greater liver, that is, hepatosomatic index (HSI) for farm-associated cod than cod not associated with farms and Skog et al.[95] reported greater HSI in farm associated saithe than those captured in the reference area 10 km away. Dempster et al.[49] found significantly higher HSI, condition index and gonad index (GSI) for cod caught around fish farms. However, a partly contradictory result among cod aged 2–4 years is also shown.[115] Meier et al.[58] found that wild mature cod caught at a spawning ground near salmon farms had a lipid composition suggesting that they were feeding intensively on salmon pellets and had much larger and fatty livers (2–3 times) compared with cod that are feeding on marine prey. However, in the latter study no large differences in gonad size between the salmon-pellets eating cod and marine feeders were found. In sum, this indicate that fish farming may increase the liver size and energy condition of the wild fish aggregating and feeding around fish farms. However, the observation of mature cod at the spawning ground Smøla indicate that the liver energy content was well above what is needed for oocyte production and other metabolic requirements, and that the high liver lipid content found in cod feeding on salmon waste pellets do not necessarily lead to greatly enhanced reproductive success.

It has been reported that wild fish associated with farms were on average 1.7 times heavier than non-associated fish and that farm associated fish went through a dietary shift, to either pellets or taxonomic changes of the gut content.[56] Cod that include feed from salmon farming in their diet may alter their life-history with earlier sexual maturation, as increased liver size is associated with sexual maturation in younger cod.[116] As in other fish, maturation in cod takes place when the fish reaches a particular age and size, but also a minimum energy reserve in the form of lipids are assumed to be necessary to proceed with the maturation process.[117] The main energy store in Atlantic cod is in the liver, and cod associated with fish farms typically have higher GSI and HSI because of the trophic addition of spillover feed from fish farms.[57,118] The extra feed translates into higher reproductive potential.[119,120]

Female cod withdraw lipids from the liver to supply energy to the gonads during the spawning period, which results in better fed fish producing more eggs and having higher fecundity than poorly fed fish.[121] It has been suggested that the total energy content can influence the age at maturation in cod,[122] which implies that the trophic subsidy from waste feed in the fjord ecosystem can promote earlier maturation in cod associated with fish farms. Maturing earlier might decrease the size of the adult fish because of the trade-off between somatic growth and reproduction.[123,124] There is a positive correlation between the size of adult fish and fecundity, which consequently can have repercussions on population biomass and fishing yields.[125] The energy status during yolk deposition, which occurs 3–4 months before spawning, is significant for the fecundity of female cod. If the energy status during this period is too low the cod might skip spawning altogether.[102,126]

Whether feed from fish farms affects maturity and fecundity in wild Atlantic coastal cod is unknown. A study conducted by Barrett et al.[127] investigated reproductive fitness of cod in areas with high and low farming density and found no differences in egg production, viability, fertilization or hatching success. However, this study reported smaller sized eggs in farm associated cod which eventually can lead to lower fitness and survival during larval development. As mentioned earlier, farm associated fish tend to have a higher condition factor which was not the case in the Barrett et al. study, indicating that the trophic subsidy from fish farms did not increase the general fitness of the studied cod population.

The female nutritional status during yolk deposition is crucial for the egg quality in cod, with yolk deposition beginning between September and November.[121] The energy status and nutritional composition of the female during early vitellogenesis is imperative for final fecundity. Skjæraasen et al.[102] found that energy reserves during early vitellogenesis was highly influential on potential egg production, and total lipid energy has been associated with population recruitment.[120,128]

4.4.1 | Knowledge strength and gaps

For any assessment of cod fitness in the wild, new studies need to test the effects of both quantity and quality of available food/feed. High growth rates may not be linked to high fitness if, for instance, the fatty acid composition of the food cannot support critical early life development. More evidence about the nutritional, physiological and ecological effects of antinutrients on cod from wasted feed from salmon need to be obtained through experimental studies of single and mixtures of relevant compounds.

Risk sources related to reduced survival

Reduced survival in cod may be caused by emission of drugs, medical substances and toxic chemicals. These may harm wild cod at different life-stages and lead to increased mortality rates. Increased mortality may also come indirectly if emissions of toxic substances reduce natural food items (such as zooplankton, shrimps or shellfish that can be harmed by anti-sea-lice drugs), which may be crucial for a certain life-stage of the cod. Finally, reduced survival may be related to increased disease transmission between farmed and wild fish or within the wild fish due to aggregation around farms.

4.5 | Risk source 5: Emission of toxic chemicals and antinutritional factors

4.5.1 | Anti-lice drugs

Chemical treatments have been one of the most common ways to control lice in farmed salmonids.[129] There are several types of chemicals that are used, including organophosphates, pyrethroids, and ivermectins. These chemicals are typically applied to the fish either through immersion or by adding them to the feed. These chemical treatments reduce the amount of the parasitic salmon louse but will also lead to release of these substances into the nearby environment. This may cause both direct and indirect effects and responses in the food-web with potential consequences for the Atlantic cod.

4.5.2 | Antifouling

Cleaning the fouling of a salmon farm involves removing any organisms, such as algae, barnacles, mussels, and other marine growth, that have attached to nets, ropes, and other structures on the farm. These organisms can cause a variety of problems, including significant reductions in water flow and flushing time with consequences for availability of oxygen and accumulation of waste products.[130] There are several types of biocides that are commonly used in salmon farms for antifouling and copper is one of the primary ingredients. It is effective against a wide range of fouling organisms and is relatively inexpensive. Copper can be applied as a coating on the nets or can be released in a controlled manner from copper-containing materials such as wires or mesh. Zinc is another common biocide used in salmon farming. It works by releasing zinc ions into the water, which are toxic to fouling organisms. Zinc is often used in combination with copper to increase effectiveness. Organotin compounds or stannanes were previously used as biocides in salmon farming, but their use has been restricted or banned in many countries due to their toxicity. Additionally, chlorine is sometimes used as a biocide as well as hydrogen peroxide. Most salmon farmers undertake regular in situ net cleaning using specialized high-pressure washing rigs. Generally, the material removed from the net during cleaning is discharged into the surrounding environment. This activity represents environmental risks because the deposition of organic material and antifouling biocides affecting benthic communities around farms.[131]

4.5.3 | Heavy metals

Mercury is one of the most concerning heavy metals found in fish feed, as it can cause neurological and developmental damage in humans and animals. Mercury enters the environment from various sources, such as industrial pollution and natural sources, and can accumulate in fish, particularly in predatory fish at the top of the food chain. In fjords in southern Norway, mercury pollution from industry correlates with poor recruitment in local populations of coastal cod, suggesting that this pollution has caused a reduction in the reproductive potential of the spawning fish.[5] Fish oil and fish meal are often derived from wild-caught fish, which can be contaminated with mercury and other heavy metals from industrial pollutants in the ocean. DeBruyn et al.[132] found elevated levels of mercury in demersal rockfishes near salmon farms in coastal British Columbia, Canada, attributable to a combination of higher rockfish trophic position and higher mercury levels in prey near farms. However, Bustnes et al.[133] did not support the notion that salmon farms in general increase the concentrations of potentially harmful elements in wild fish, and the distribution of Hg and other elements in cod and saithe in Norwegian coastal waters may be more influenced by habitat use, diet, geochemical conditions, and water chemistry.

4.5.4 | Persistent organic pollutants in feed

Historically, salmon pellets have been made with lipid from fat pelagic fish. The fish feed had therefore relatively high levels of persistent organic pollutants (POPs) and fish farms have therefore been considered as point sources of POPs in the marine environment in Norway.[118] A survey conducted in 2007 showed that fish eating under salmon farms had much higher levels of POPs compared with fish from a reference area (Cod 50% and Saithe 20% higher).[118] However, salmon feed has changed in content and plant lipids, which have a reduced level of POPs, have replaced marine ingredients.[134] This has reversed the situation; wild salmon have been shown to have higher levels of POPs compared to farmed salmon.[135] However, the new plant-based ingredients may have residues of pesticides used in terrestrial agriculture,[136–138] and transported feed may be treated with other potentially harmful chemicals, such as the feed antioxidant, ethoxyquin, which may accumulate in wild fish.[139] Ethoxyquin may also alter the planktonic microbial metabolism with ecosystem consequences, including higher nitrogen availability and loss of diversity.[140]

Dioxins (PCDD/PCDF) and polychlorinated biphenyls (PCBs) are other groups of undesirable POPs that can accumulate in the environment and food chains, particularly in fatty tissues of fish. Fish oil and fish meal are often derived from wild-caught fish, which can be contaminated with dioxins and PCBs from industrial pollutants in the ocean.[141] Vegetable oils, again, are generally considered safer. However, vegetable oils can be contaminated with dioxins and PCBs, during the production process, particularly if the plants were grown using pesticides.[142] Therefore, it is important to monitor the levels of dioxins and PCBs in cod tissues to evaluate the potential impact from salmon feed.

4.5.5 | Antinutritional factors

In addition to lipids, changes in the source of protein from fish to terrestrial vegetable sources can have detrimental effects on cod health. Not only does the use of high levels of plant proteins increase the potential for inducing nutritional specification issues, like essential amino acid limitations, but most plant protein resources also contain a variety of biologically active antinutritional factors.[143] These come from the plants need to protect themselves from grazing. Many plants produce different types of antinutritional factors (e.g. saponins, lectins, protease inhibitors that can reduce nutrient utilization or food uptake, leading to impaired gastrointestinal functions and metabolic performance). The influence of these antinutritional factors on fish can be considerable and varied. Possible harmful effects of antinutritional factors include reduced palatability, less efficient nutrient utilization, alteration of nutrient balances of the diets, inhibition of growth, intestinal dysfunction, immune modulation, altered gut microbiota, goitrogenesis, pancreatic hypertrophy, hypoglycemia, or liver and kidney malfunction.[144,145] It has been shown to cause enteritis in Atlantic salmon[146,147] and may also cause similar effects in cod.[148] Thus, the negative impact of ingesting plant-based feed seen in salmon may also cause problems to wild fish.

Most of the research conducted with alternative protein sources for marine fish has focused on the use of proteins from the same plant origin as the alternative lipids. However, these sources are often deficient in one or more essential amino acid(s) and may contain antinutritional factors which can reduce palatability, protein utilization and growth.[149] Protease inhibitors, phytates, antigenic compounds and alkaloids, at levels usually present in fish feed from a plant-derived origin are unlikely to affect fish growth. Other antinutritional substances, however, such as glucosinolates, saponins and tannins among others could have negative effects.[149]

4.5.6 | Knowledge strength and gaps

The effects of emissions of toxic chemicals from salmon farms on wild fish that aggregate in the nearby ecosystem is not well known, except in part for the deposition of copper. Indirect effects on cod, via the food-web (e.g. benthic trophic natural resources), is even less studied. Therefore, effects of antinutritional factors must be evaluated in wild fish, including Atlantic cod.

4.6 | Risk source 6: Alteration in availability of natural prey species

The effects of organic discharges from salmon farms include changes in infauna community composition, but also filter-feeders such as zooplankton will consume suspended matter.[150] Juvenile cod feed on zooplankton, such as copepods, before progressing into bigger crustaceans such as deep-sea prawns (*Pandalus borealis*). Larger cod, both benthic and pelagic, feed on smaller fish such as capelin (*Mallotus villosus*).[151,152] However, the feeding ecology differs between regions and is often dependent on local conditions such as prey availability. In a study using citizen science, Enoksen and Reiss[153] found significant differences in feeding ecology between connected fjords.

The feed subsidy from salmon farms can induce trophic changes to the surrounding ecological communities along multiple pathways. For example, aggregations of sea urchins can drive ecosystem regime shifts towards barren states,[37] while densities and growth rates of juvenile cod are typically higher in vegetated habitats.[25,154] Different stages of cod will be affected differently as they undergo ontogenetic niche shifts. Larger sized cod typically feeds on organisms from higher levels in the food web, more connected to the benthic part of the ecosystem[155] and may accumulate compositional elements coming from aquaculture (bioaccumulation/biomagnification).

4.6.1 | Knowledge strength and gaps

Food-web and ecosystem alterations due to nearby salmon farms are in general not well known. Further research should emphasize key prey species for Atlantic cod at all relevant life-stages along their ontogenetic development.

4.7 | Risk source 7: Disease transmission (virus, bacteria and parasites)

The potential of disease transmission from farmed to wild fish depends on a variety of factors, including the scale of the disease outbreak, that is, number of sick fish that shed pathogens into the environment and the concentration of shed pathogens, the survival of the pathogen in the environment, the virulence of the pathogen, and the susceptibility of the wild fish.

Wild unvaccinated fish in proximity to fish farms with an ongoing outbreak of disease may be exposed to pathogens. If susceptible, such exposure may cause different scenarios depending on the host-pathogen interaction. The host-pathogen interaction will depend on the animal's general health status and the virulence of the pathogens: (i) The host may successfully clear itself of the pathogen; (ii) the host may survive the infection and become a carrier and (iii) the pathogen successfully colonizes the host, which develops disease and eventually dies.[156]

Disease is more easily spread and transmitted in high density populations. Such circumstances may also increase virulence in pathogens.[157]

Some pathogens can infect a variety of species and easily adapt to new host species, while others are more host specific. Examples of pathogens regarded as host specific to salmonids are infectious salmon anaemia virus (ISAV) and salmon lice (*Lepeophtheirus salmonis*).[158,159] Pathogens that are not as species specific are bacterial infections like furunculosis (caused by species of *Aeromonas salmonicida*), vibriosis (caused by various serotypes of *Vibrio anguillarum*), bacterial ulcers (caused by *Moritella viscosa* and *Tenacibaculum* spp.) and parasitic infections like amoebic gill disease (AGD, *Paramoeba perurans*) and sea lice (*Caligus elongatus*).[159–163] Most of the pathogens listed above are known for infecting Atlantic cod and both vibriosis and furunculosis are well known disease problems in farming of Atlantic cod.

Effective vaccines have been essential for the successful development of the fish farming industry.[164] At the present, there is still a need for improving the vaccines available to farmed Atlantic cod. Atlantic salmon are protected through vaccination against several diseases such as vibriosis and furunculosis, thus these bacterial infections are limited in today's salmon farming. That said, there is a general increase in bacterial infections in Norwegian salmon farming and ulcers have become a major welfare problem.[165] There is also a debate and lack of knowledge surrounding the possibility of vaccinated fish serving as vectors that shed pathogens to the environment. This so called "vaccine leakage" may also drive the evolution towards a more virulent pathogen with the potential of a more severe effect on unvaccinated hosts.[166,167] In addition to the 'traditional' pathways for disease transmission, movements of both wild fish and farm escapees also need to be considered as vectors for disease propagation.[168] The review of Johansen et al.[169] describe the potential disease interaction and pathogens exchanges between wild and farmed fish.

4.7.1 | Knowledge strength and gaps

Little is known about the baseline of various pathogens in wild fish populations. The susceptibility to pathogens may also depend on the general health status, and it is also thought to be variable between life stages. Thus, pathogens may affect the host differently depending on life stage. In addition, knowledge is scarce about the actual challenge dose and exposure time needed for fish to get infected. Increased knowledge of all these matters is essential to understand the possible consequences and how disease transmission between farmed and wild fish occur. The potential effects on altered disease resistance in wild cod if it feeds on salmon feed is also not known.

5 | GENERATION OF NEW RISK HYPOTHESES FROM IDENTIFIED KNOWLEDGE GAPS

Importantly, one single risk source *may cause several effects on the receiving species or community*. Hence, several risk hypotheses may need to be formulated for a single risk source. For example, feed spillover from salmon farming may lead to a number of effects in the wild cod population. These effects can be written as testable hypotheses: Feed spillover causes attraction of wild cod to salmon farms (H_1); increased feeding opportunities for wild fish (H_2); altered food quality for wild fish due to terrestrial feed ingredients (e.g. fatty acid profile) (H_3); and altered residues of toxicologically relevant chemicals in the cod (e.g. marine food ingredients with higher levels of dioxins and PCBs being replaced by terrestrial ingredients with agricultural pesticides) (H_4). A similar network of hypotheses can be generated for all identified risk sources we have identified. Table 1 summarizes the elements for hypotheses building for the risk source "feed spillover".

6 | SUMMARY, RESEARCH RECOMMENDATIONS AND MANAGEMENT MITIGATION STRATEGIES

Each of the about 1200 salmon net pen farms that span the Norwegian coastline constitutes a highly productive food system that is open to the natural environment. Hence, any associated discharges such as waste feed, faeces and therapeutant, delouse or antifouling chemicals freely interact with the local benthic and pelagic environment. For actively swimming wild fish, impact may extend to a larger area (e.g. a

TABLE 1 Example of how one risk source (feed spillover) from salmon farming may cause different effects, response types, and consequences for wild cod populations. We also indicate the knowledge strength for each of the fields of knowledge.

Risk source	Effect	Response type	Consequence(s)	Knowledge strength
Feed spillover	Attraction of wild cod to salmon farms	Behaviour Mortality	Fish abandoning natural habitats/spawning grounds. Altered fishing mortality (trap or protection)	High on attraction, weak on consequences
Feed spillover	Increased feeding opportunities	Physiology Fitness	Increased growth/fecundity Altered fitness depending on food quality, see below	High on increased feeding/growth/fecundity low on fitness effects
Feed spillover	Altered food quality (e.g. terrestrial fatty acids and antinutritional factors)	Physiology Fitness	Reduced survival of egg/sperm/juvenile cod (mismatch with offspring needs)	Moderate on fatty acid profiles and antinutritional factors, low on effects and fitness consequences
Feed spillover	Altered toxicological residues in fish	Physiology Toxicity Fitness	Altered profile of toxic chemicals (depending on marine vs. terrestrial feed ingredients)	Moderate on residues from feed ingredients, low on effects on wild fish

fjord-level) due to attraction or repulsion of fish from farms. In general, the volumes of excess feed from aquaculture net pens are considerable, and the scientific literature confirms that wild fish aggregate around fish farms. Such alteration in the distribution of wild fish may have serious consequences for interacting coastal ecological communities as well as for local fishermen.

It is well documented that cod eat waste feed and predate on other fish that have eaten waste feed. This feed is currently based on a terrestrial diet with deviating fatty acid composition compared to what is naturally available in marine systems. These terrestrial fatty acids are transferred to liver, ovaries, testis, and muscle in the fish. However, we lack information on how an altered fatty acid composition will affect the quality of sperm, eggs and thereafter the survival of the different ontogenetic life-stages of cod. As such, there is a clear need for studies directed towards the effects of a suboptimal fatty acid composition on cod using a dose–response approach with different feed types.

Another key risk source that stems from the use of open net pens, is spread of pathogens (virus, bacteria and parasites) that have multiple potential hosts. Well known pathogens such as furunculosis, vibriosis, francisellosis, amoebic gill disease and sea lice represents a risk for wild cod populations. The risk of transfer between species is exacerbated among species that aggregate around active farms, and thermal stress due to climate warming may increase pathology in cod.[170] Wild fish also take feed and natural prey off the seabed, where such pathogens can reside, thereby increasing risk of ingestion. The sediments may also serve as a reservoir for pathogens.[171,172] More research needs to be conducted into these potential heterospecific transfer mechanisms to properly assess the parthenogenic risks to wild species. Nevertheless, well founded biosecurity measures together with effective and protective vaccines are essential to minimize outbreaks of disease and by that the risk of disease transmission to wild fish.

We also recommend that the complex, multi-factorial and multi-consequential attraction versus repulsion of cod issue is evaluated in field studies. Using acoustic telemetry to track fish caught near and far from farms and with release sites at different locations, one may disentangle movement behaviour and fate depending on the previous experiences of the fish.[173]

For mitigation strategies, we highlight that four out of the seven identified risk sources would be largely solved by using closed farming systems. The excess feed would not enter the environment and hence avoid behavioural attraction in the wild cod as well as the physiological effects of altered fatty acid composition and altered growth. Moreover, the disease interaction between farmed and wild fish would be strongly limited or eliminated, depending on the waste-water treatment system being used. That leaves the potential repulsion of wild fish from activities around farms, caused by emission of toxic chemicals and/or nutrients. The ability to control the release of nutrients, and perhaps also toxic chemicals, would also be largely improved in closed farming systems. Another mitigation strategy is to move salmon farms offshore. This would reduce the interaction with the coastal ecosystem, including the coastal cod and the spawning areas for the NEA cod. Open ocean farming may also be combined with closed or semi-closed farming systems.

7 | CONCLUSION

With the increasing scale of aquaculture production, for Atlantic salmon, but also for other species including Atlantic cod, there is growing concern for concurrent negative environmental effects. Most of the future growth in the production of Norwegian farmed Atlantic salmon is expected to happen in the northernmost parts of the Norwegian coast, where the combination of previously unused areas and low temperatures offer favourable conditions for industrial aquacultural development. At the same time, these areas are near pristine environments and support the world's richest fishery for migratory wild NEA cod, in addition to the more resident and vulnerable coastal cod. We need to manage our marine ecosystems based on existing scientific knowledge. We argue that the seven risk factors we have identified is a good starting point for further research and to mitigate negative effects of salmon farming on wild cod populations and their coastal ecosystem. Although not emphasized in this article, the pronounced climate change (mainly warming) in the Northern Atlantic represents a variable and uncertain factor that can affect all life-history stages of the Atlantic cod.[174,175] The effect of climate change on cod stocks has already been described, so in a situation of multiple stressors the consequences on the stocks may be exacerbated.[174] Hence, climate effects also need to be considered in future risk analysis. By combining the frontline scientific knowledge with continuous monitoring and risk assessment, adjustment of aquaculture practices can be done in response to changing conditions and new information on the impact on wild fish populations, such as the NEA cod and the coastal cod populations. This allows for flexibility and learning over time, improving our ability to reduce the environmental risks associated with salmon farming.

AUTHOR CONTRIBUTIONS

Thomas Bøhn: Conceptualization; writing – original draft; investigation; visualization; writing – review and editing. **John F. Strøm:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Pablo Sanchez-Jerez:** Writing – review and editing; writing – original draft; investigation. **Nigel B. Keeley:** Writing – original draft; writing – review and editing; investigation. **Torild Johansen:** Writing – review and editing; investigation; writing – original draft; funding acquisition. **Karl Ø. Gjelland:** Investigation; writing – review and editing; writing – original draft. **Nina Sandlund:** Writing – original draft; investigation; writing – review and editing. **Bjørn-S. Sæther:** Investigation; writing – review and editing; writing – original draft; funding acquisition. **Ingeborg Sætra:** Investigation; writing – review and editing; writing – original draft. **Esben M. Olsen:** Investigation; writing – review and editing; writing – original draft; funding acquisition. **Jon E. Skjæraasen:** Investigation; writing – review and editing; writing – original draft; funding acquisition. **Sonnich Meier:** Investigation; writing – review and editing; writing – original draft. **Terje van der Meeren:** Investigation; writing – original draft; writing – review and editing. **Pål A. Bjørn:** Conceptualization; funding acquisition; writing – review and editing; writing – original draft; investigation.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest.

DATA AVAILABILITY STATEMENT

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

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