










REVIEW

REVIEWS IN Aquaculture

An aquaculture risk model to understand the causes and consequences of Atlantic Salmon mass mortality events: A review

Zaman Sajid^{1,2}  | A. Kurt Gamperl³ | Christopher C. Parrish³ |
 Stefanie M. Colombo⁴  | Javier Santander³ | Charles Mather⁵ | Barbara Neis⁶ |
 Ingunn Marie Holmen⁷ | Ramón Filgueira⁸  | Cynthia H. McKenzie⁹ |
 Lissandra Souto Cavalli¹⁰  | Mohamed Jeebhay¹¹ | Wenzhao Gao⁶ |
 María Andréa López Gómez⁶  | Cory Ochs¹² | Sarah Lehnert¹³ |
 Cyr Couturier¹⁴ | Christine Knott¹⁵ | João F. Romero¹⁶  |
 Albert Caballero-Solares³  | Allan Cembella¹⁷ | Harry M. Murray¹³ |
 Ian A. Fleming³  | Joel Finnis⁵ | Mark D. Fast¹⁸ | Mark Wells¹⁹ |
 Gerald G. Singh²⁰ 

¹Ocean Frontier Institute, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada

²Mary Kay O'Connor Process Safety Center, Artie McFerrin Department of Chemical Engineering, Texas A&M University, College Station, Texas, USA

³Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada

⁴Department of Animal Science and Aquaculture, Faculty of Agriculture, Dalhousie University, Truro, Nova Scotia, Canada

⁵Department of Geography, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada

⁶Ocean Frontier Institute and Department of Sociology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada

⁷SINTEF Ocean, Department of Fisheries and New Bimarine Industry, Trondheim, Norway

⁸Marine Affairs Program, Dalhousie University, Halifax, Nova Scotia, Canada

⁹Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St. John's, Newfoundland and Labrador, Canada

¹⁰Department of Agricultural Diagnosis and Research, Secretaria de Agricultura, Porto Alegre, Rio Grande do Sul, Brazil

¹¹Occupational Medicine Division and Centre for Environmental & Occupational Health Research, University of Cape Town, Cape Town, South Africa

¹²Community Health and Humanities and Ocean Frontier Institute, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada

¹³Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St. John's, Newfoundland and Labrador, Canada

¹⁴School of Fisheries, Fisheries and Marine Institute, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada

¹⁵Department of Women's Studies, San Diego State University, San Diego, California, USA

¹⁶Centre for Veterinary Epidemiological Research, Atlantic Veterinary College, University of Prince Edward Island, Charlottetown, Prince Edward Island, Canada

¹⁷Helmholtz Centre for Polar and Marine Research, Alfred Wegener Institute, Bremerhaven, Germany

¹⁸Department of Pathology and Microbiology, AVC-UPEI, Charlottetown, Prince Edward Island, Canada

¹⁹School of Marine Sciences, University of Maine, Orono, Maine, USA

²⁰School of Environmental Studies, University of Victoria, Victoria, British Columbia, Canada

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *Reviews in Aquaculture* published by John Wiley & Sons Australia, Ltd.

Correspondence

Zaman Sajid, Ocean Frontier Institute,
Memorial University, St. John's, NL A1B 3X9,
Canada.

Email: zaman.sajid@mun.ca; zaman.sajid@tamu.edu

Funding information

Government of Newfoundland and Labrador's
Department of Industry, Energy and
Technology, Canada, Grant/Award Number:
20210487; Ocean Frontier Institute, Memorial
University of Newfoundland, Canada;
EarthLab, University of Washington; Texas
A&M University, USA

Abstract

Mass mortality events (MMEs) are defined as the death of large numbers of fish over a short period of time. These events can result in catastrophic losses to the Atlantic salmon aquaculture industry and the local economy. However, they are challenging to understand because of their relative infrequency and the high number of potential factors involved. As a result, the causes and consequences of MMEs in Atlantic salmon aquaculture are not well understood. In this study, we developed a structural network of causal risk factors for MMEs for aquaculture and the communities that depend on Atlantic salmon aquaculture. Using the Interpretive Structural Modeling (ISM) technique, we analysed the causes of Atlantic salmon mass mortalities due to environmental (abiotic), biological (biotic) and nutritional risk factors. The consequences of MMEs were also assessed for the occupational health and safety of aquaculture workers and their implications for the livelihoods of local communities. This structural network deepens our understanding of MMEs and points to management actions and interventions that can help mitigate mass mortalities. MMEs are typically not the result of a single risk factor but are caused by the systematic interaction of risk factors related to the environment, fish diseases, feeding/nutrition and cage-site management. Results also indicate that considerations of health and safety risk, through pre- and post-event risk assessments, may help to minimize workplace injuries and eliminate potential risks of human fatalities. Company and government-assisted socio-economic measures could help mitigate post-mass mortality impacts. Appropriate and timely management actions may help reduce MMEs at Atlantic salmon cage sites and minimize the physical and social vulnerabilities of workers and local communities.

KEYWORDS

aquaculture, aquaculture system designing, environmental stressors, mass mortality event (MME), risk assessment, salmon disease

1 | INTRODUCTION

In 2022, the Food and Agriculture Organization (FAO) of the United Nations estimated that global seafood production in 2020 was 178 million metric tonnes (MMT) with an estimated total sale value of \$406 billion US; of which \$265 billion US (88 MMT of fish production) came from aquaculture.¹ Thus, animal aquaculture accounted for nearly 49% of total seafood production globally in 2020. The growth of the industry and its sustainability are seen as critical to future seafood (food) security, given that the projected demand for seafood may increase by 44 MMT by 2050 (up to a 50% increase compared to the current production level),² and because commercial seafood fishery landings have plateaued. Expanded production can also reduce global seafood trade deficits in some countries, create local employment opportunities, and enhance community prosperity in often isolated rural regions.³ One of the possible constraints on expanded aquaculture production is an increase in the frequency and magnitude of large-scale farmed fish mass mortality events (MMEs) in many jurisdictions, as shown in Supporting Information: Table 1. Such events threaten the sector's sustainability.^{4–7}

Any given MME can vary in magnitude from a few thousand to over a million organisms.⁸ MMEs are defined differently in different jurisdictions and by various authors, who stress diverse aspects of their causes and effects. For example, Fey and colleagues define MMEs as 'catastrophic demographic events that can affect all life stages of an animal and have the potential to eliminate a substantial portion of a marine population in a short period'.⁹ Another study defines MMEs as 'large environmental perturbations that produce sudden major reductions in population size'.¹⁰ Another work on die-offs defines an MME as 'a decrease of 50% or more of a population in one year'.¹¹ Finally, Kibria defines an MME as the sudden death of a large number of fish over a short period in a defined area.⁸ In this study, we adopt an MME definition specifically related to aquaculture operations: an event that results in the loss of a considerable proportion of a farmed marine population over a period of days to weeks.

In the world's leading Atlantic salmon-producing countries, including Norway, Chile, the United Kingdom (UK) and Canada, recorded mass die-offs of salmon are of concern to industry and regulators.^{12,13} For example, in 2019, the Norwegian aquaculture industry lost 59.3 million farmed salmon,⁷ of which 52.8 million salmon died in MMEs.¹⁴

In 2016, nearly 12% of Chilean salmon production (more than 40,000 MT) was lost due to harmful algal blooms (HABs), resulting in an economic loss of more than \$800 million US.¹⁵ In 2020 in the UK, the Scottish aquaculture industry lost 27,000 MT of salmon due to MMEs—a production loss almost four times higher than the loss in 2010.^{6,16} At Scottish sea farms, post-smolt mass mortality due to MMEs is estimated to be approximately 14.5%.¹⁷ Finally, in 2020, Mowi Canada East experienced an MME at their farm sites on the south coast of Newfoundland, where an estimated 450,000 Atlantic salmon died due to high sustained water temperatures, in combination with hypoxia and the effects of sea lice and corresponding treatment interventions.¹⁸ These MMEs are also common for other salmonid species, such as coho salmon and trout. For example, on 2 January 2024, an MME in Chile caused the loss of approximately 3800 MT of Atlantic and coho salmon.¹⁹ On 20 November 2023, a similar MME resulted in the loss of ~500 MT of coho salmon and rainbow trout. The common cause for both MMEs was HABs.²⁰

There have been several lab-based studies on the effects of one or a combination of two factors (e.g., temperature, hypoxia, a combination of hypoxia and temperature, or a combined effect of temperature and sea lice) that contribute to the risk of salmon MMEs (e.g., see reference 21). Further, a study recently explored the correlation between 65 different causes of salmon mortality through linear models,²² and another detailed the putative determinants of 'baseline mortality' among Norwegian populations of farmed Atlantic salmon.¹³ However, these analyses often consider limited risk factors (and limited interactions between risk factors), and thus, describe a simplified view of the causes of salmon mortalities at sea farms. They do not consider the complex interaction of causes of MMEs and appropriate management tools to mitigate them (i.e., see fig. 7 in reference 13). A more holistic understanding that considers the simultaneous impacts of multiple stressors on salmon health/welfare and mass mortality is needed if the industry is to adapt to factors such as climate change and the complex and interrelated causes of MMEs (e.g., see reference 23). This can only be achieved when we understand the roles and interrelationships among the various causes of MMEs (i.e., the complexity of their relationships).

MMEs can pose serious economic, social, health and environmental issues for all stakeholders, including organisms, companies, workers and local communities. The company experiencing an MME suffers the loss of its biological assets and can even face suspension of its aquaculture licences.²⁴ One of the major environmental concerns after the occurrence of an MME is the removal and disposal of dead fish. These operations can also expose workers to occupational health and safety (OHS) risks, including injuries, illness/diseases and loss of life.^{25,26} Existing research has identified significant policy gaps related to aquaculture OHS surveillance, reporting and regulation in many contexts, making understanding OHS outcomes difficult.²⁷ MMEs can also significantly affect workers' livelihoods and community resilience through short-term and potentially long-term loss of employment in this sector.²⁸

Understanding the factors contributing to MMEs can improve intervention and anticipatory mitigation strategies, protect fish health and welfare, and prevent baseline mortalities and MMEs. Before conducting targeted research to aid in farm management, it is important

that we understand the causal processes that contribute to MME risk and delineate the impacts of MMEs. To address this research gap, we developed a comprehensive system model that considers the interactions between various risk factors that lead to Atlantic salmon MMEs and their subsequent consequences. This work involved creating a process system model for the Atlantic salmon aquaculture industry based on established expert-elicitation techniques for model building. The resulting risk model was achieved by combining five subsystems of aquaculture risk. Each subsystem provides a visual representation of how factors interact and allows for identifying strategies to mitigate the risk of MMEs.

2 | RESEARCH METHODOLOGY

This study developed an interactive model that assessed the causes and consequences of Atlantic salmon MMEs. We considered five interactive subsystems of aquaculture production to model risk factors for aquaculture MMEs: environmental risk (biotic and abiotic), fish pathogen and disease risks, nutrition risk, risks from and to aquaculture OHS, and risks from and to workers' livelihood. The first three risk categories are known to affect fish health and welfare and, thus, cause mortality, whereas the latter two risk categories (aquaculture OHS and workers' livelihood) affect workplace safety and the socio-economic security of workers and their communities due to MMEs. Each risk category was further classified into risk factors that were directly or indirectly linked to mass mortality.

We first worked with expert teams, knowledgeable in each aquaculture subsystem, to understand risk factors within each subsystem. Then, we brought all groups together to model risk across the entire aquaculture production system. A two-day international workshop on Atlantic salmon aquaculture mass die-offs was held to collect data for model building. Participants attended the workshop virtually (the workshop structure is outlined below). In this study, expert teams for each category were formed in various ways. Some experts were identified from a literature search of peer-reviewed articles using the keyword 'aquaculture mass mortality'. These individuals then identified experts who were asked to nominate researchers who have published peer-reviewed articles on Atlantic salmon MMEs and related risk factors. This snowball-sampling approach to identifying experts has been used in the literature (e.g., see reference 29). Experts also included researchers working on aquaculture at the host institution (Memorial University of Newfoundland, Canada). The goal was to develop a diversified team, working on different aspects of MMEs as comprehensively as possible. The workshop participants were senior and junior researchers, departmental leaders, and university professors from American, Canadian, Brazilian, German, Norwegian and South African institutions. While many participants were from Canadian institutions, many had experience researching aquaculture across countries. Importantly, every subsystem team had researchers with expertise across country contexts. For example, while many team leads within each subsystem were based at Canadian institutions, they had research experience in Canada, Norway, Chile and the UK, among other locations. This geographical breadth of research experience was

a pre-requisite for selecting team leads and a consideration for the make-up within teams. Most experts were interested in contributing further and became co-authors in this work. All experts have extensive research and development experience studying the causes and impacts of Atlantic salmon MMEs and publishing their research in peer-reviewed journals.

The research methodology for this study consisted of three phases. In the first stage, each team of researchers produced reports on risk factors within their subsystems. Three groups studied environmental stressors (biological and abiotic), Atlantic salmon pathogens and disease, and risks related to feeding/nutrition that could lead to

MMEs. Two other teams looked at the contextual risk factors that make MMEs more consequential for OHS and communities and increase their vulnerability.

In the second phase, a modified multi-criteria decision-making technique, called Interpretive Structural Modeling (ISM), was applied to develop mutual relationships among risk factors.^{30,31} This exercise was conducted on Day 1 of the workshop. In the third phase, a modified Delphi technique was applied to modify graphical networks developed from the ISM. This exercise was conducted on Day 2 of the workshop, and subsequent follow-ups with each team were conducted. The research methodology for this study is shown in Figure 1,

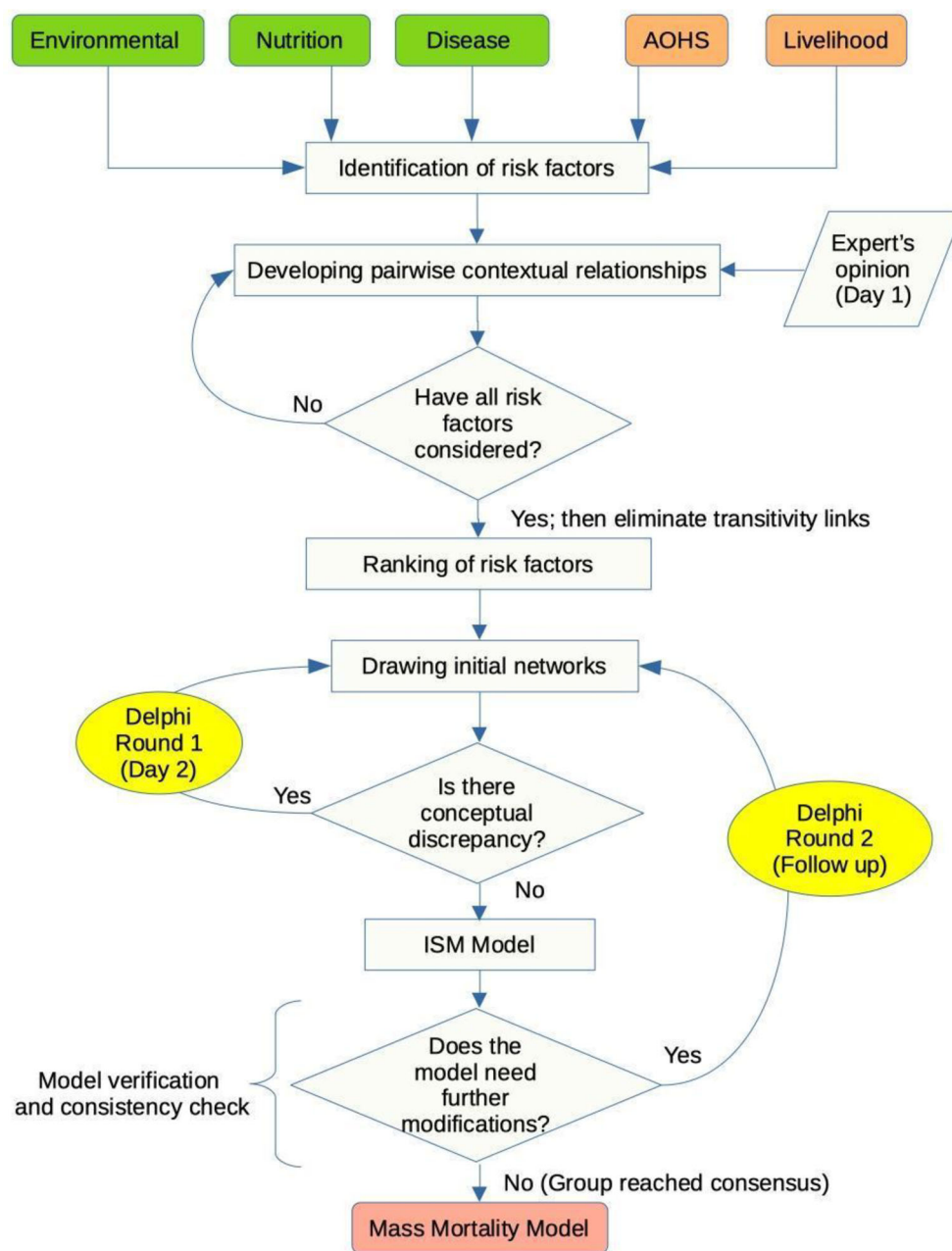


FIGURE 1 The methodological framework for mass mortality risk assessment used in this study. Green risk factors indicate the causes of MMEs, and orange risk factors show the consequences of MMEs. ISM stands for Interpretive Structural Modeling approach. This methodology was applied to the five subsystems individually. MME stands for mass mortality event.

and details are provided in the Supporting Information (see *Phases Involved in the ISM Technique*). On Day 2 of the workshop, experts identified more causes or risks leading to MMEs. In addition to these, they also identified risk mitigation approaches/strategies. Experts were also asked to identify whether an association existed between each pair of risk factors. Their responses were 'yes' if a correlation existed and 'no' if no relationship between the two risk factors could be identified. For example, experts responded 'yes' when asked if the 'aggregation of fishes in sea cages' (i.e., crowding) affects 'low oxygen levels in water (hypoxia)'. This way, experts identified pairwise correlations for each risk factor. Using this information on each pairwise correlation between risk factors, we developed causal structures and put them into directional causal chains. This approach has been extensively used in other fields of study.^{32,33}

Further details and the ISM steps utilized are provided in the Supporting Information. We also addressed different kinds of potential biases in collecting experts' data. For example, we addressed overconfidence bias by having group deliberations; experts were encouraged to challenge each other. We also protected against individual voices dominating input by having each individual submit their input without oversight by other experts.³⁴

3 | RESULTS AND DISCUSSION

The Appendix shows the list of risk categories and corresponding risk factors analysed in this study. The causal networks suggest that some risk factors directly contribute to MMEs, while others will only result in large-scale mortality if other risk factors are present. Examples of some direct risk factors are very high water temperature (>21–22°C), HABs, cage damage, low water oxygen levels (hypoxia, <60%–70% air saturation), freezing temperatures (winter kill/chill) and possibly winter syndrome (fatty liver disease), viral and bacterial pathogens (e.g., infectious salmon anaemia [ISA] virus, *Vibrio anguillarum*), sea lice, amoebic gill disease and the effect that climate change may have on these factors. Other risk factors influence direct risk factors, and/or indirectly contribute to MMEs. Examples of indirect risk factors, that influence MMEs through mediating variables or that cumulatively combine with other risk factors, are weather and climate, extreme and harsh ocean storms, jellyfish causing gill damage, jellyfish-associated reductions in cage water flow, increased runoff and nutrients, ocean acidification, weather events, low ocean salinity (salinity less than 20 PSU), and the aggregation of fishes (crowding) in sea-cages. There are also risk factors that are more distally related to MMEs and influence direct and indirect risk factors. These include seasonal exposure to environmental risk factors, high ocean salinity (salinity more than 20 PSU), and low protein to high lipid diets. It is acknowledged that not all risk factors occur in every salmon-producing area. For example, 'super chill' is a real challenge in Atlantic Canada, but this problem is insignificant in the UK, Norway, and Chile. Hence, the causes of MMEs are generalized here, and country- or region-specific risks should be identified based on the area of analysis. The causal models also suggest mitigation pathways and the common risk factors across

models. For example, feeding regime, sea lice treatment, net cleaning, and use of vaccination are common mitigation pathways across causal networks. The results also identified management actions across models that can contribute to or mitigate risk. For example, a management decision to increase stocking densities can be a catalyst for an MME, and a decision to upgrade cage-site infrastructure (nets, moorings, etc.) can mitigate MMEs. It is worth mentioning that not all the risk factors must be present for an MME to occur, and not all consequences co-occur. Further details are discussed in the sections below.

An aquaculture risk model developed through this study is available at <https://public.flourish.studio/visualisation/17695194/>. Results are presented and discussed in the order of environmental stressors, disease, salmon nutrition, aquaculture OHS and workers' livelihoods.

3.1 | Environmental stressors (abiotic and biotic) model

We identified and compiled potential abiotic and biotic environmental factors that could lead to MMEs, connected these factors to assess risk, and identified management decisions that could prevent or worsen MMEs at Atlantic salmon farms. There are many environmental challenges to open-pen salmon aquaculture, and while the industry's capacity to monitor (and anticipate) such changes is increasing, companies often have limited ability to control them or mitigate their potential effects. Given restrictions on the length of this review, the text focuses on the impacts of temperature and hypoxia on salmon mortalities, and their interaction with other risk factors. However, there are several other factors that can directly or indirectly result in MMEs (as detailed in Figure 2). For example, HABs are also a major (direct) challenge to salmon aquaculture. They can lead to major MMEs, as they can kill fish via various toxins, damaging their gills and causing hypoxic conditions.^{35–37} In addition, several emerging anthropogenic pressures are affecting the natural, biological, chemical, and physical drivers of HABs (including climate change-related changes in salinity, temperature and ocean acidification). Thus, MMEs due to HABs may increase in the future.

3.1.1 | Temperature

Warm temperatures

One of the greatest challenges to Atlantic salmon culture in sea cages is high water temperatures, given that climate change is increasing average ocean temperatures and the frequency and severity of heat waves.^{38–41} For example, there have been recent reports of high summer temperatures negatively affecting the production of sea-caged salmon in Tasmania,⁴² and 2.9 million salmon died in Newfoundland (Canada) in the summer of 2019.⁴³ However, it is very unlikely that temperatures of <21–22°C alone lead to salmon MMEs,²¹ and such events will only be seen when combined

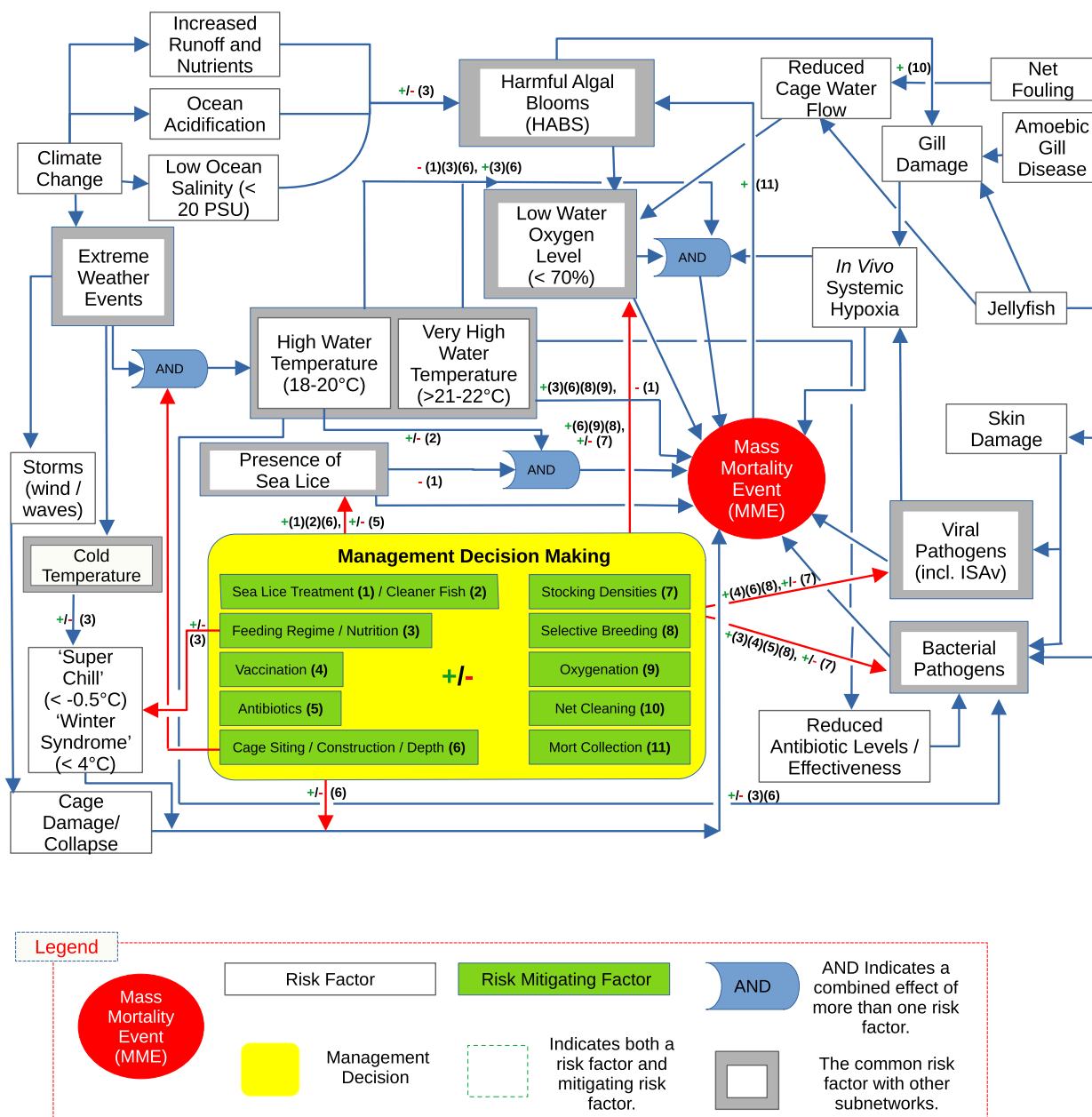


FIGURE 2 The environmental model. The environmental (abiotic) and biological factors that can directly cause and/or contribute to MMEs at Atlantic salmon cage-sites (if other interacting factors are present), and how industry decisions and management protocols can mitigate/reduce (+ effect) or increase (– effect) mortalities. In this figure, mitigation is shown as a (+) sign, while in subsequent figures, it is indicated as a green arrow. In some instances, impacts due to industry decisions and management are marked as red arrows, and the effect of the action taken is indicated. Where it was not possible to draw arrows from management actions so as to not further complicate the figure, numbers in ‘()’ alone correspond to the various strategies/actions taken. Blue-directed lines indicate the connections between risk factors. The yellow box indicates management strategies that can/may reduce (+) and/or increase (–) cage-site losses. The complexity of this figure precludes some effects/interactions from being shown. For example, cold temperatures are known to suppress the immune function of fish, and this increases their susceptibility to certain bacterial diseases. MME, mass mortality event.

with other stressors. For example, salmon can tolerate high temperatures (short-term up to $\sim 26^{\circ}\text{C}$; long-term up to $\sim 22^{\circ}\text{C}$) even when combined with moderate hypoxia ($\geq 60\%$ – 70% air saturation),^{21,44,45} but more severe hypoxia (e.g., that associated with HABS and other factors; see below) or in combination with high temperatures, can lead to large-scale mortalities. Sea lice infestation can increase the susceptibility of salmon to mortalities at high temperatures.⁴⁶ For

example, the combination of a severe lice infestation, chemical delousing and higher water temperature (~ 18 – 19°C for several weeks) was credited with the loss of fish in the Newfoundland heat wave of 2019.⁴³ In addition, high temperatures may increase the abundance and/or virulence of certain pathogens⁴⁷ and reduce post-treatment levels of antibiotics,⁴⁸ and thus, their effectiveness against bacterial pathogens.

The industry has limited capacity to influence cage site water temperatures, and even if salmon are provided with deeper nets (and thus access to potentially cooler waters), recent data indicates that the salmon will not necessarily avail of these cooler waters.⁴⁹ To avoid/reduce the incidence of mortalities at high temperatures, cage-site managers can select sites that are less likely to encounter this environmental challenge and ensure their nets have been cleaned (increasing water flow through the cage) or provide their cages with supplemental oxygen. Further, they could develop specific diets for high temperatures (as done in Tasmania; Optiline HT, Skretting) or select fish/broodstock that are more tolerant of high temperatures. Work on genetic markers of high-temperature tolerance in Atlantic salmon has begun on the east coast of Canada (e.g., references 44,45). Nonetheless, it is clear that environmental risk factors rarely lead to MMEs in isolation and should be understood in a system setting. High temperatures, particularly, enhance MME risk when combined with other factors. Even management decisions that are intended to address other stressors can add to MME risk during high-temperature events. For example, delousing treatments (which raise metabolic demands) can lead to MMEs during high temperatures and can even lead to large-scale mortalities at temperatures considered optimal without these treatments.^{50,51} The impacts of chemical delousing are usually restricted to crowding: mechanical delousing involves flushing the salmon with water jets and/or brushing, or using negative pressure and turbulence combined with flushing; and thermal delousing involves submerging the fish in a chamber with 28–34°C water for 20–30 s. These latter two delousing methods also entail crowding, pumping, and straining the fish, and this may lead to stress (and increased metabolic demands), a risk of hypoxia and mechanical injuries (see reference 52 for references).

Cold temperatures

The severity and frequency of winter storms are also expected to increase due to climate change,^{53–55} as are polar air outbreaks (southerly transport of extremely cold air^{56,57}); however, it remains unclear whether either will become a greater or lesser concern.⁵⁸ Nonetheless, ‘cold shock’ events caused large-scale losses of salmon at sea cages in Atlantic Canada in 2014, 2015, 2019, and 2020.⁵⁹ It is possible that the fish died when water temperatures dropped below the freezing point of their blood/tissues (–0.7°C to –0.8°C⁶⁰), which caused ice crystals to form. However, this is not the only potential cause of winter mortality in Atlantic salmon. In 2020, farmers in Iceland reported that cool sea temperatures caused salmon to move to the bottom of the sea cages, and that wounds caused by rubbing against the netting eventually led to the fish's death.⁶¹ However, recent studies^{62,63} have pointed to another cause. This research suggests that, like sea bream,⁶⁴ Atlantic salmon can develop ‘winter syndrome’—a condition associated with fatty liver disease and opportunistic infections that cause head and dermal ulcers. ‘Super chill’ can be lessened (but not completely prevented) by ensuring that fish stay in the deeper regions of the cage, and it has been suggested that functional diets can be developed to minimize the incidence of ‘winter syndrome’ and its associated aetiology.⁶²

3.1.2 | Hypoxia

Another serious environmental challenge to Atlantic salmon aquaculture is severe hypoxia (<60%–70% air saturation, depending on temperature). It can be caused by the upwelling of oxygen-poor water from deeper regions,⁶⁵ HABs⁶⁶ and net fouling (incl. jellyfish swarms which reduce water flow through the cages). Further, it can be exacerbated if the cage has a high stocking density or the fish are crowding within particular regions of the cage (e.g., see reference 67), and directly or indirectly (i.e., by contributing to the severity of HABs) made worse by the accumulation of large numbers of mortalities in cages (i.e., by contributing to the severity of HABs). However, if other factors are at play, fish may succumb to hypoxia at higher oxygen levels. For example, in the disease model (explained in the next section), the infectious salmon anaemia virus (ISAV) reduces the number of red cells in the fish's blood (i.e., causes anaemia). This leads to reduced blood oxygen-carrying capacity. In addition, certain algae,⁶⁶ jellyfish tentacles (nematocysts) (see references 68 and 69) and amoebic gill disease⁷⁰ can damage the gills and limit the ability of the salmon to take oxygen up from the seawater. Both of these effects result in ‘systemic hypoxia’ and limit the fish's capacity to deal with high temperatures, moderate environmental hypoxia, and/or other stressors present in the cage-site environment. Management practices that can prevent hypoxia in salmon sea cages include regular net cleaning and the collection of mortalities, siting farms in areas not prone to upwelling or HAB events and with good water currents/flushing, moving sites if HABs have been detected/identified, and aeration or oxygenation of the water within the cages through compressed air or oxygen. Supplemental air or oxygen can be added via various technologies during hypoxia and/or warm surface water temperatures.

Finally, significant interactions between biotic and abiotic environmental impacts and various factors may amplify the potential for MMEs at Atlantic salmon cage sites. For example, tentacles/nematocytes often break off when jellyfish impinge against the cage's netting, which can damage the salmon's skin (i.e., provide a route for bacterial infection). Certain jellyfish species are also vectors for the bacterium *Tenacibaculum*, which leads to gill lesions and skin ulcerations, which can magnify the mortalities associated with jellyfish blooms.⁷¹

3.2 | Infectious diseases and pathogens model

As in any intensive animal food-producing sector, the Atlantic salmon industry has experienced disease outbreaks that affect fish welfare and challenge the industry's sustainability and profitability. Parasites, pathogenic bacteria, and viruses are natural components of ecological systems and drivers of population dynamics that have the capacity to reshape ecosystems, alter services, biomass production and succession, and overall ecosystem stability. Under normal circumstances, diseases are an episodic component of marine ecosystems where hosts and pathogens co-exist in homeostasis.⁷² However, severe disease

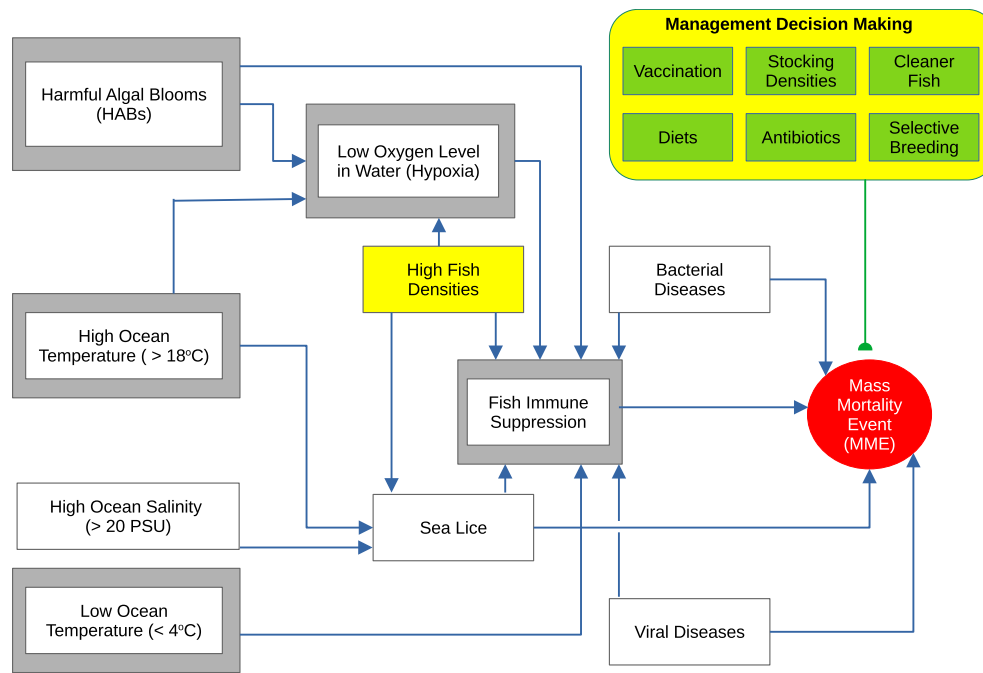


FIGURE 3 The disease model. The legend for Figure 2 also applies to this figure. The green line towards MME indicates the influence of management and mitigating risk factors on MMEs. MME, mass mortality event.

outbreaks can result from issues with the host (e.g., stress and immune suppression), pathogens (e.g., the introduction of a new pathogen, pathogen resistance to antibiotics and vaccines), or environmental conditions (e.g., pollutants, low temperatures that immune suppress the host).⁷³ For instance, Figure 3 shows that high water temperatures increase sea lice (e.g., *Lepeophtheirus salmonis*) development and the presence of the infective stage,^{74–77} increase bacterial transmission⁷⁸ and viral burst,⁷⁹ but surprisingly do not negatively affect the salmon's immune response.⁸⁰ Cold temperatures can also favour the growth of marine psychotrophic bacterial pathogens and viruses (e.g., *Moritella viscosa*, ISAV)^{81–84} and/or suppress the fish's (host's) immune system.^{62,85,86} Finally, the disease model in Figure 3 shows that water salinity, high temperatures and fish stocking densities contribute to increased sea lice abundance^{46,86} and disease transmission,⁸⁷ exacerbating the impacts of sea lice.

Figure 3 also shows several intervention points where disease management tools and strategies can be applied to mitigate the risk of MMEs at Atlantic salmon sites. These include adjusting/optimizing stocking densities; the use of cleaner fish to control sea lice infestations; using vaccines to mitigate the effects of infectious diseases; selective breeding or the use of genetically modified fish resistant to infectious diseases; and, as a last resort, the utilization of antimicrobials and chemotherapeutants. For instance, infestations of ectoparasitic sea lice are one of the most severe threats to cultured salmonids in the Northern⁸⁸ and Southern hemispheres.⁸⁹ Sea lice feed on salmonid tissues, leading to skin erosion, osmoregulatory failure, immunosuppression, and increased disease susceptibility, and require expensive control regimes to prevent mortalities.⁹⁰ Over the years, the Atlantic salmon industry has used several methods to combat sea

lice infestations.⁹¹ Chemotherapeutic treatment was the dominant sea lice control method for decades until the emergence of resistance in sea lice⁹² and increasing negative public opinion about the impacts of anti-lice drugs on the ecological equilibrium, particularly among crustacean populations. In addition, as we noted in the previous section, such interventions can also contribute to MMEs under certain conditions. Mechanical abrasion and thermal treatment are used as physical delousing methods, but adversely affect salmon health and welfare.⁵⁰

The Atlantic salmon industry has adopted Integrated Pest Management (IPM) strategies, in which multiple non-medicinal methods are used (e.g., net barriers/skirts, ultrasound, lice traps and feeding through snorkels).⁹³ Further, lice control using cleaner fish has been very successful in North Atlantic salmon farms.⁹⁴ Cleaner fish are considered an eco-friendly (green) alternative to other methods of sea lice control and a solution to lice infestation from both economic and ecological points of view. However, it is acknowledged that there are potential animal welfare issues with the use of cleaner fish. This concern is more prominent, especially in cases where wild species are being utilized for this purpose. Given these animal welfare issues, there may be a need to move to alternative green control measures for pest management. The mutually beneficial cleaner fish-salmonid association reduces the parasite burden on salmonids while providing a food source for the cleaner fish. In salmonid aquaculture, different wrasse species (e.g., the ballen wrasse [*Labrus bergylta*] and goldsinny wrasse [*Ctenolabrus rupestris*] and lumpfish [*Cyclopterus lumpus*]) are currently being used.^{95–97} Wrasse consume more parasites than lumpfish, but they reduce their activity at cool temperatures and eventually enter a hypometabolic winter dormant state (torpor) at

water temperatures below 5°C.⁹⁸ Lumpfish can effectively delouse at, or even below, 5°C,^{97,99} but they do not perform well at temperatures above 18°C.^{97,99,100} Nonetheless, the lumpfish has proven to be very effective in removing sea lice from Atlantic salmon¹⁰⁰ and has been domesticated and industrialized in the North Atlantic region.^{101–103} Cleaner fish use has become a prevalent practice in the last 10 years, eliminating the utilization of chemotherapeutants and reducing fish stress/immune suppression.

Vaccines are a critical health component in all intensive animal food-producing sectors, and their use has significant economic implications for these industries. However, here again, viewing management interventions holistically and as a part of Atlantic salmon aquaculture can reveal when interventions may be less effective than anticipated or even have negative consequences. Despite the success of fish immunization in the finfish aquaculture sector, microbial and viral infectious disease outbreaks are still having major impacts on this industry. Issues like the lack of vaccine efficacy in the host species or against local pathogens, the emergence of new pathogen variants, coinfections and environmental conditions that prevent vaccine efficacy due to immunosuppression^{104,105} can lead to MMEs. Verification of the efficacy of commercial vaccines against local pathogens is critical to deciding which vaccine formulation should be used at a specific site or within a particular region. Several recent disease outbreaks can be linked to climate change, including heat waves during the summer and cold temperature events during winter,^{63,106} perhaps associated with unknown or novel host-pathogen interactions. Isolation and characterization of potential new pathogens from farmed fish is a practice that is not widely conducted, but can provide critical information for strains that should be incorporated into customized autogenous vaccines.

Selective breeding for traits such as faster growth, flesh colour and resistance to infectious diseases is a common practice for farm animals, including finfish.¹⁰⁷ For instance, salmonids resistant to pests and pathogenic bacteria and viruses have been selected for, and used in, the industry.^{108–110} However, in many cases, the array of genes and molecular mechanisms that determine resistance are not known. The Atlantic salmon has only recently been domesticated. Although broodstock selection has been successful in some instances, climate change might/will require that other attributes be selected, such as increased thermal tolerance and disease resistance. Gene editing (i.e., CRISPR/Cas9)¹¹¹ is another potential tool to prevent MMEs. However, this technology must be technically viable, effective at scale, and socially and regulatorily accepted to become a global industrial option.

A recent study showed that the Atlantic salmon industry had the least antimicrobial use across the farmed fish species.¹¹² Comparatively low antimicrobial application rates in some countries, like Canada,¹¹² could reflect improved husbandry and management conditions, including high vaccination coverage and specific pathogen-free broodstocks. Ideally, antimicrobials should be restricted to use in hatcheries and high-value animals, like breeders. They should be avoided in open net pens to limit the development of antimicrobial resistance and/or the probability of MMEs. Also, as technologies/

tools for vaccines and selective breeding improve, antibiotic use is expected to be further reduced. For instance, several countries have experienced dramatic reductions in antimicrobial use rates since the introduction of vaccination and improved management and husbandry programs.^{113,114} Future strategies should aim to strengthen aquaculture production and prevent MMEs without pharmaceutical interventions by the utilization of technologies such as bacteriophage therapy, pre and probiotics, the development of state-of-the-art vaccines (e.g., mRNA, live attenuated and live recombinant vaccines) and fish genome editing technologies.

3.3 | Salmon nutrition model

The relationship between Atlantic salmon diet and nutrition, and MMEs, includes several indirect factors (Figure 4), and this suggests that salmon aquaculture depends on carefully managing feed composition and feeding regimes. In the context of MMEs, the main risk factors regarding salmon nutrition (as shown in Figure 4) are low protein/high lipid diets, high lipid (cholesterol or total fat) levels in the salmon's liver, starvation and increased feed consumption at high temperatures. Studies investigating a sudden increase in mortality in seemingly healthy salmon at 5°C have reported that changes in the dietary protein: lipid ratio may cause/increase mortality. Moribund Atlantic salmon from an MME had significantly higher lipid content in the liver and altered liver fatty acid composition.¹¹⁵ Diets low in protein and high in total fat can lead to fat accumulation in the liver, ultimately leading to MMEs, particularly when other factors stress fish. For example, while salmon grow optimally on a diet containing 55% protein and 24% lipid, today's salmon feeds typically contain ~35%–45% protein and ~25%–30% lipid.¹¹⁶ While the salmon's requirement for lipid is generally not this high, these latter diets allow lipid to be used as the primary energy source while dietary protein can be primarily used for tissue growth; a term called protein-sparing.¹¹⁶ This is also an efficient and economical strategy in feed formulation, since protein is typically the most expensive ingredient. Previous studies indicate that diets with higher protein and lower lipid levels may be beneficial in preventing mortality related to thermal stress in salmon.¹¹⁵ In addition, high-lipid diets can lead to lipid accumulation in the viscera, particularly in the liver and heart,^{117,118} and this has specifically been associated with feeding diets high in plant lipids.^{117,119} One of the reasons for this may be that plant oils do not contain phospholipids, such as phosphatidylcholine. Choline has been shown to reduce lipid malabsorption syndrome, which leads to excessive lipid accumulation.^{120,121} Adding phospholipids, particularly phosphatidylcholine or dietary choline, may help prevent MMEs related to temperature stress because of lower organ lipid accumulation. Betaine, which has roles in cellular function, is a naturally occurring choline derivative that may also be added to the diet and is also a well-known feed attractant to fish.¹²² This latter characteristic would encourage feeding.

Drastic temperature changes are stressful for fish, and cessation of feeding often indicates that a mortality event can occur if environmental conditions do not improve. However, the literature lacks

agreement on whether starvation or feeding prior to these events helps to alleviate mortality. Starvation in healthy salmon has been shown to reduce mortality.¹¹⁵ However, this may depend on the duration of feed deprivation. Stressful environmental conditions, such as an increase in temperature or extremely high temperatures, induce the release of corticotropin-releasing factor (CRF) and cortisol, inhibiting feeding in fish.¹²³ In a study that held fish at high temperatures of 22.9°C, Atlantic salmon cohorts experienced a temperature-induced cessation of voluntary feed intake for 2 months.⁴² The study demonstrated a significant negative linear relationship between feed intake and temperature, and a complete cessation of feeding in all fish as temperatures rose above 21.5°C. In another study, an incremental temperature increase (i.e., 1°C per week) resulted in a ~10% increase in the feed conversion ratio.²¹ The decrease in feed consumption was likely related to a direct effect of temperature on appetite. Feeding continuity (encouraging feeding when cessation of feeding would typically occur) and consistently low cortisol levels may help prevent mass mortality. It is possible that when salmon stop feeding due to stress from high temperature and hypoxia, the release of hormones like CRF and cortisol prevents feeding, putting fish at risk for mortality. Encouraging feeding may help alleviate stress and subsequent mortality, without increasing the risk of HABs.

Many risk factors shown in Figure 4 can be mitigated using functional diets that can help to enhance the innate immune system's response to stressors, including temperature and hypoxia. For example, several studies have demonstrated that functional feed additives,

such as pre and probiotics, can activate the innate immune system of aquatic animals by enhancing the growth of commensal microbiota.¹²⁴ Antioxidants may also have a role in preventing mortality during stressful events. Feeds with higher antioxidant levels (e.g., astaxanthin or vitamin E) that are fed prior to a temperature event may enhance survival. Modulating the dietary fatty acid composition may also positively affect salmon health when they are threatened with thermal stress. Finally, moderate inclusion of arachidonic acid (20:4 ω 6) and vitamin E in Atlantic salmon feeds has been shown to improve some indicators of non-specific immunity, such as respiratory burst,¹²⁵ and may help them deal with temperature stress.

Overall, MMEs can be mitigated or reduced in severity by modifying nutrients and using functional diets for Atlantic salmon. This may include feeding diets with a higher-than-normal protein/lipid ratio and including higher-than-normal dietary phospholipid amounts, particularly of phosphatidylcholine, which will help reduce lipid accumulation in the viscera, especially the liver. During the summer/early fall months when some MMEs are likely to occur, this may include improving/increasing feed consumption during high-temperature events by modulating cortisol through dietary means; for example, dietary inclusion of higher-than-normal arachidonic acid levels, higher astaxanthin and vitamin E for antioxidant capacity and improved immune response. A large body of evidence has accumulated, showing that nutrition strongly influences fish immunity. For example, the dietary replacement of marine ingredients (i.e., fish meal and fish oil) by terrestrial alternatives (e.g., vegetable oils) has been reported to cause

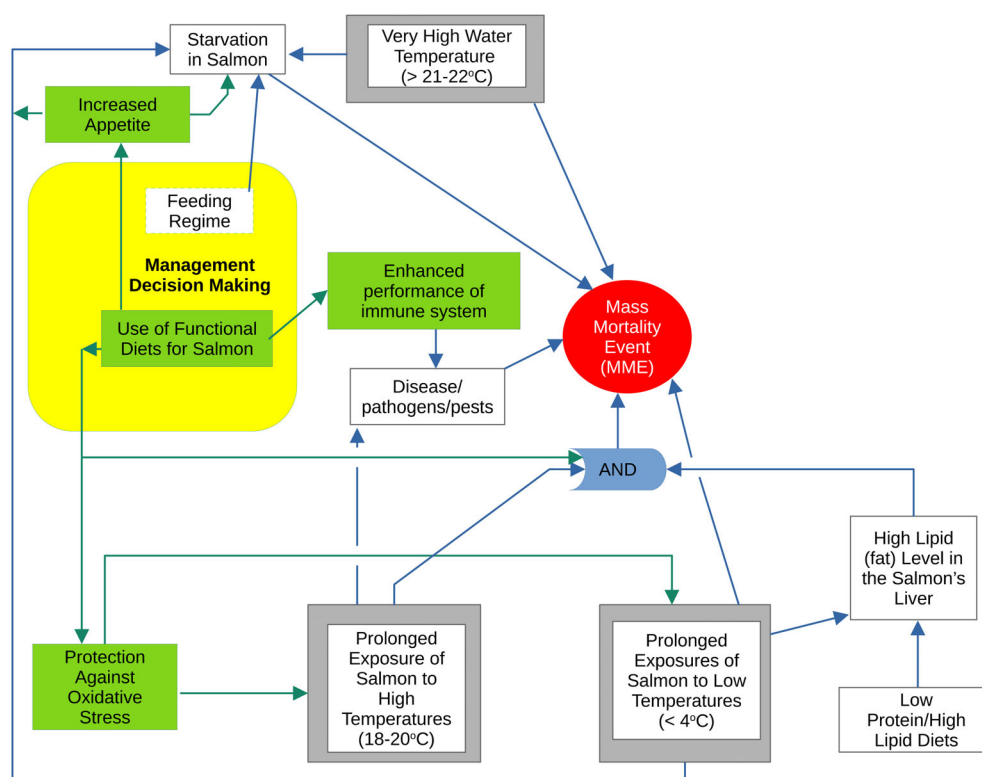


FIGURE 4 Salmon nutrition model. Green lines (with arrows) indicate risk mitigation effects and blue lines indicate the connections between risk factors. The legend for Figure 2 also applies to this figure.

changes in features of the transcriptome related to inflammation, and the antiviral and antibacterial immune responses of Atlantic salmon.¹²⁶⁻¹²⁸ Some of these effects could be leveraged by tailoring novel feeds to prevent and mitigate diseases in aquaculture. Microbial cell components (e.g., cytosine-phosphate-guanine oligodeoxynucleotide motifs, peptidoglycans) have also been shown to exert interesting immunostimulatory effects on Atlantic salmon as feed additives.^{129,130} Sustainably formulated health-promoting feeds are key components of integrated disease management strategies in aquaculture and help to reduce the use of chemotherapeutants and antibiotics. As such, they could become a powerful tool to reduce the risk of MMEs.

3.4 | Aquaculture OHS model

Figure 5 shows that marine Atlantic salmon aquaculture is associated with potential exposure to diverse physical, chemical, biological, ergonomic, and psychosocial hazards aside from safety risks.^{26,27,131-134} It is also associated with an elevated risk of injury, illness, and death relative to other industrial sectors, based on national averages in countries where these comparisons are available (see reference 135). Large

MMEs are likely to contribute to even higher risk levels due to the nature and pressures associated with dead fish removal operations. Findings from an expert risk assessment synthesis of key existing sources on MMEs and OHS across five candidate countries indicate that MMEs fit a definition of 'significant accidents'.¹³⁶ That is, MMEs require rapid mobilization of workers, vessels and other supports. To varying degrees, they can also require staff working under pressure to investigate the extent and cause of the die-off and to remove, transport, and dispose of dead fish. MMEs are also often associated with regulatory and organizational pressures to change farm design, emergency planning, and other practices to reduce future MME risks that may have implications for OHS.

The MME and OHS risk analysis in Figure 5 highlights key hazards and potential pathways between MME-prevention planning, monitoring and response, and OHS risks. MMEs will affect work on vessels (including while transporting workers, feed, equipment, supplies, and dead and live fish). MME response also often encompasses underwater work around, under, and inside net pens, including gathering dead fish in various stages of decay and net cleaning and repair. MMEs can affect the types and levels of exposure to documented hazards, especially regarding diving, working on cages and around cages, seagoing workboats and wharves, and the onshore rendering of dead fish.

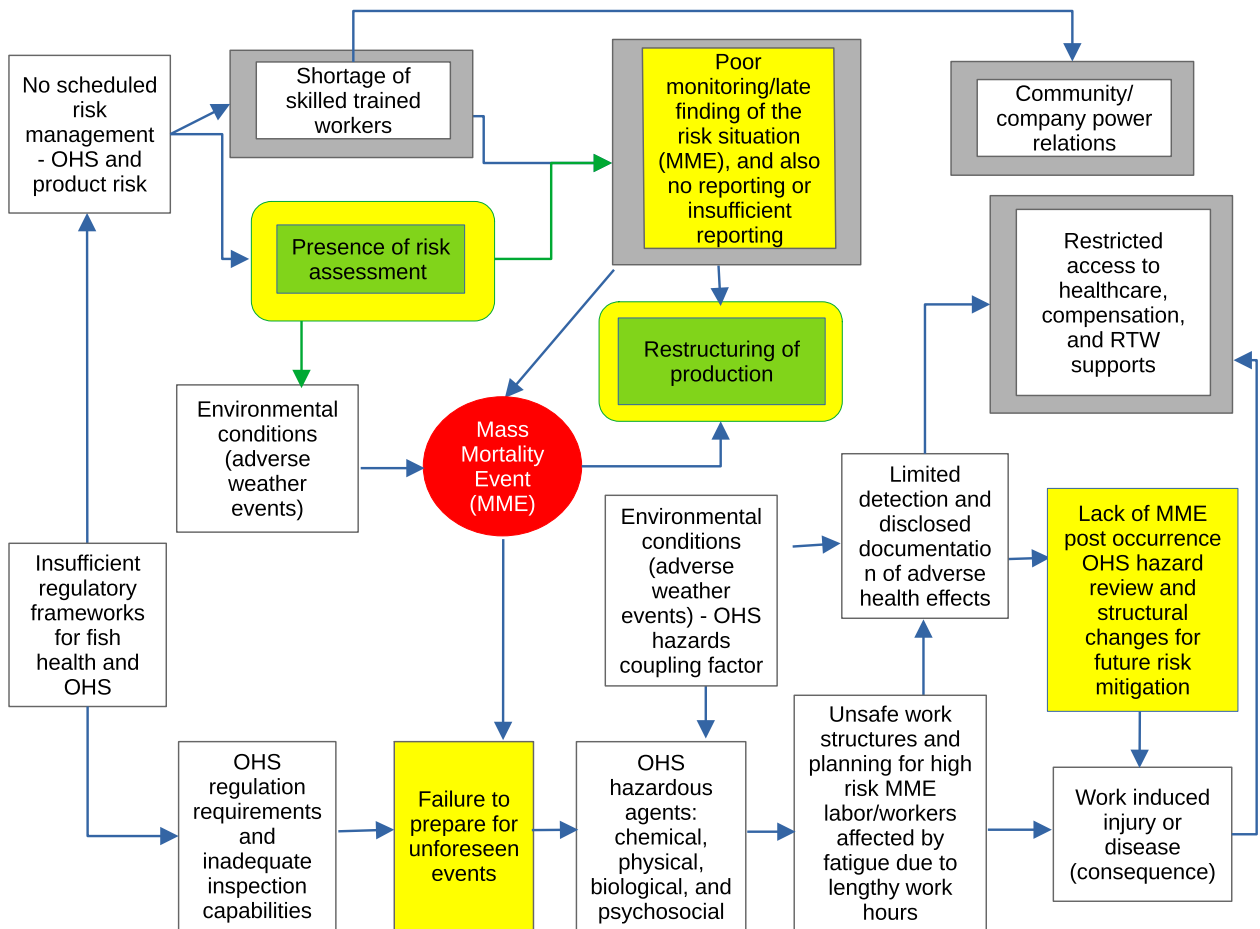


FIGURE 5 Aquaculture occupational health and safety (OHS) model. The legend for Figure 2 also applies to this figure. RTW stands for Return To Work.

Much of this work happens outdoors and is subject to weather-related hazards.

The relationship between MME and OHS risk depends on the cause, scale, duration, timing, and location of the MME, including its relation to adverse weather events. For example, larger MMEs and more extensive and prolonged mortality removal in exposed locations and seasons associated with bad weather are likely associated with higher risk. This means there are links between personnel training and skill levels, monitoring, contingency planning, emergency preparedness, and OHS at the company level.^{137–139} The presence and strength of health and safety regulations and inspection systems (including requirements to quickly notify government and health and safety departments at the onset of MMEs; company risk assessments, emergency preparedness, and contingency planning; labour force training and skill levels; and technology and work task design related to key tasks such as mort removal and transport) are all pre-event factors that will indirectly influence the relationship between MMEs and aquaculture OHS risks. Once MMEs begin to unfold, the relationship between these and injury, illness and fatality risk would also be determined by the cause and timing of the event with HABs (causal agent) and MMEs associated with periods of chemotherapeutic/antibiotic treatment, which are potentially associated with enhanced chemical and biological health risks to workers. Where divers primarily remove dead fish, MMEs can increase the already significant diving-related hazards associated with marine net pen aquaculture, including the risk of net entanglement, decompression sickness, and other adverse health events. The removal and transportation of large volumes of dead and decomposing fish may enhance the risk of chemical exposure and related illness among transport workers, including exposure to hydrogen sulfide (H₂S) and water transport-related incidents such as capsizing, slips, and falls. Risks to divers and transport workers are likely greater if MME remediation work requires recruiting inexperienced workers, contracting equipment not designed for aquaculture operations, and where such work takes place in the context of time and other pressures for rapid removal. These situations can increase the risk associated with inexperience and inadequate training, resulting in risk-taking and fatigue-related injuries. Potential longer-term post-event impacts on health and socio-economic implications for injured workers would be mediated by the adequacy of access to appropriate medical care and workers' compensation benefits for injured workers, access to return to work options and programming, as well as any potential OHS impacts of production reorganization triggered by the MME, such as changes in work design and farm locations.

Key intervention entry points for management to act upon and mitigate OHS risks associated with MMEs include: (1) taking OHS risk into account when doing broader risk assessments and contingency planning for MMEs; (2) including OHS agencies and OHS-risk-related details (such as staffing and work task changes associated with mort removal) in requirements for early reporting of emerging MMEs on the part of companies; (3) including OHS-related risks and incidents in MME investigation guidelines and reports to allow for improved surveillance, the mitigation of hazards and comparisons of risk across

different events and regional and national contexts; and, (4) implementing a post-MME OHS hazard review.

3.5 | Workers' livelihood model

Based on the workers' livelihood analysis shown in Figure 6, MMEs will have multiple impacts on workers and the communities in which they live. Both immediate short-term and potentially long-term effects will be associated with these events. In the short-term, there will likely be a loss of employment opportunities for workers involved in direct production and fish processing due to the loss of fish that would have been processed, but also potential long-term loss of employment if the MME results in the company losing their licence, as happened in the Newfoundland and Labrador (Canada) case.⁴³ Employment loss will significantly affect household income, which may not be covered through social assistance and other employment support mechanisms. Over the longer term, an MME may result in people seeking employment opportunities in other sectors of the economy that are considered more secure and not subject to disruptions of this kind. It may also lead to people seeking employment outside of the communities that are adjacent to aquaculture projects, which would, in turn, exacerbate the trend of outmigration with potentially serious impacts on community sustainability. Migrant workers may fill this gap, such as through temporary migrant worker programs in Canada, with short-term employment opportunities.¹⁴⁰ As identified in the aquaculture OHS section, these jobs range from collecting and disposing of dead fish to repairing and cleaning nets. However, the migrant workforce may face different impacts due to gender, race, citizenship status and age.¹⁴¹ Our model identifies critical intervention points for local governments and management, which can help to reduce the effects of an MME on the livelihood of workers. For example, a weak social security system (such as inadequate employment insurance) can contribute to the loss of local employment and income of the people associated with aquaculture. Such economic hardship may lead employees to lose their health benefits and health facilities for their immediate family members. Therefore, the national, federal, and provincial regulatory systems can play a vital role in minimizing the impact of MMEs on people's livelihoods. Figure 6 suggests that if the government can provide alternate employment and economic safeguards to aquaculture workers and their families, the social implications of MMEs can be minimized.

Additional longer-term impacts relate to an industry's commitment to a production region and an industry's social licence to operate (SLO).¹⁴² MMEs, especially when they happen more frequently, may result in a company deciding to either limit its exposure to a specific production site by reducing investments or, more dramatically, by withdrawing from the site/region altogether. MMEs, again, when they happen on a regular basis, may raise questions about whether the site or region is suitable for intensive, industrial forms of aquaculture production.¹⁴³ Sites affected by regular mass die-offs due to environmental, disease, and operational reasons may be considered too risky as production sites. In a changing ocean environment and with parasites

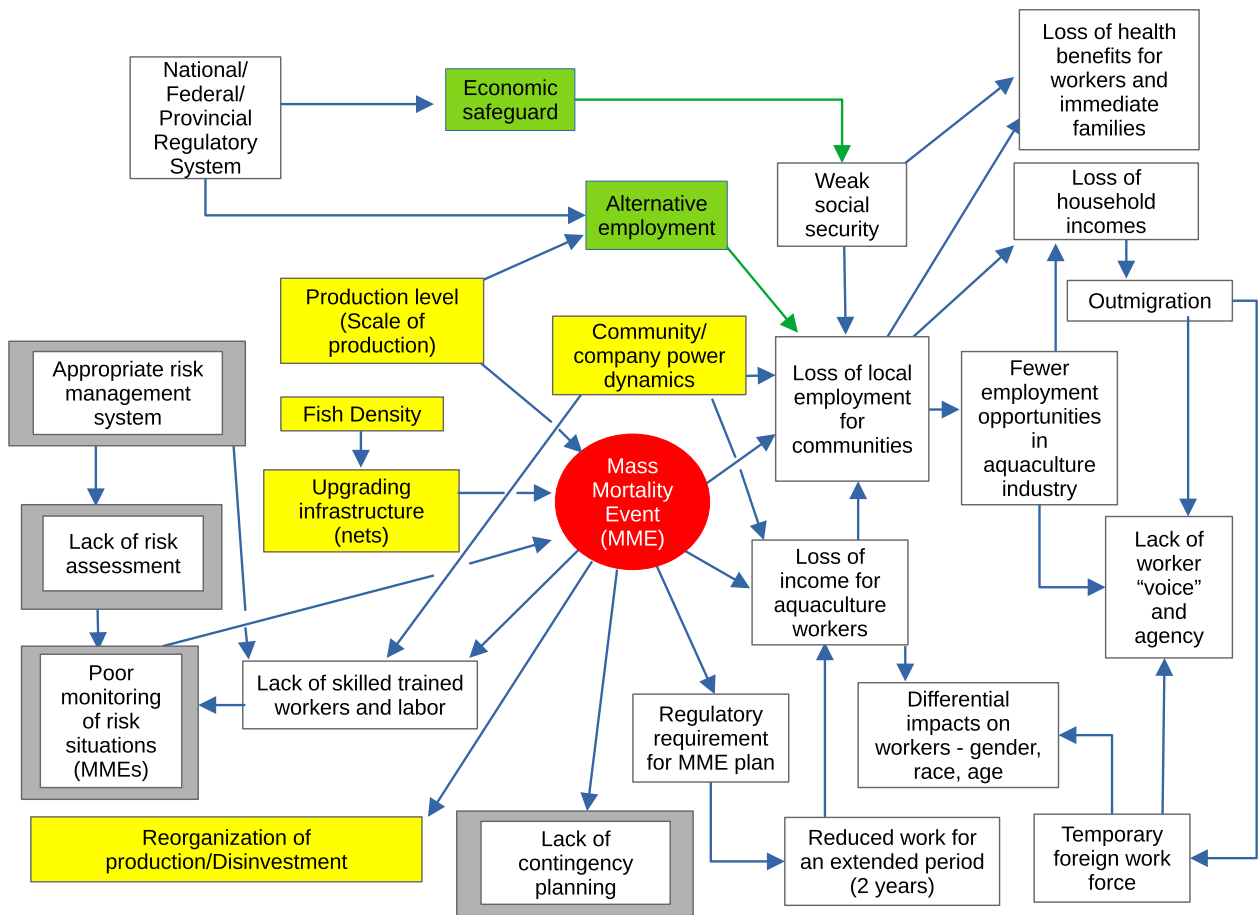


FIGURE 6 Workers' livelihood model for aquaculture. The legend for Figure 2 also applies to this figure.

increasingly resistant to standard treatments, we can expect that some previously productive sites may no longer be suitable for intensive aquaculture production, with potentially serious implications for communities that rely on this industry.¹⁴⁴

Regarding crucial intervention points for management, Figure 6 shows pre-event and post-event intervening points. Pre-event intervening points for leadership are critical to reducing the occurrence of MMEs. These actions include upgrading infrastructure, production levels, health monitoring and treatment protocols, actively participating in research, and a robust and appropriate risk management system. As discussed in the aquaculture OHS section, a lack of risk assessment and poor monitoring can lead to more and larger MMEs. Community and company dynamics are categorized as pre-event and post-event. The community and company dynamics also play a crucial role in causing MMEs and can help minimize the economic impacts of MMEs on aquaculture workers and the local community. Our findings reveal that MMEs can force production to be reorganized and lead to the development of regulatory requirements to better deal with post-event situations.

3.6 | Implications of this study and future work

This study provides interactive models that help to understand the causes and effects of MMEs in Atlantic salmon sea-cage aquaculture.

The networks developed in this study are called qualitative Bayesian networks (BNs), which help to systematically map our current understanding of the structural dependencies among aquaculture risk factors without specifying numerical values. These qualitative BN models aid in visualizing causal reasoning by indicating which risk factors are directly influencing others¹⁴⁵ towards causing MMEs, as well as the direction of their influence. The directional links in each network provide insights into the model's sensitivity to risk factor relationships and dynamics between them.¹⁴⁶

This work finds significant value in science policy related to aquaculture research. In mapping the causal systems that contribute to MMEs, as well as their impacts, this work identifies critical mechanistic pathways and interactions that should be prioritized in further research. In particular, it can help develop new hypotheses for research into interventions to forestall and mitigate MMEs. Broadly, by mapping the current understanding of the causes and effects of MMEs, this work also provides a baseline understanding that can be updated as new research is done and our understanding of aquaculture risk improves. For example, a next step of this study could be to transform the qualitative BN models presented into quantitative BN models. Given observed evidence, the quantitative BN model will allow probabilistic inference, enabling the calculation of probabilities (likelihood) for MMEs' occurrences. Such an approach could facilitate decision-making under uncertainty by providing a framework¹⁴⁷ to compute the optimal values of each parameter for the aquaculture

industry. Quantitative BNs can also help in predictive modelling and forecasting by estimating the probabilities or chances of future MME occurrences, and hence can help the industry to take proactive actions to avoid MMEs or reduce losses due to MMEs.

The model developed in this study can also aid in developing contingency planning to mitigate MMEs. Industry stakeholders can benefit significantly from this research as they seek to implement effective risk management strategies within their aquaculture operations. By utilizing the qualitative BN models of this study, aquaculture companies can consider the system of variables that affect the most influential factors driving salmon mortality, especially interactions that enhance or mitigate these risk factors, and enable them to tailor risk mitigation measures to address specific stressors or vulnerabilities. This targeted approach empowers industry players to make informed decisions regarding site selection, stocking densities, feeding regimes and environmental monitoring protocols, ultimately minimizing the likelihood of MMEs and enhancing the overall resilience of their operations.

In parallel, government policymakers have a crucial role to play in leveraging the insights provided by our research to establish robust regulatory frameworks and guidelines for the aquaculture industry. Equipped with an understanding of the interplay between different risk factors, policymakers can develop regulations that promote sustainable and responsible aquaculture practices while safeguarding environmental integrity, public health and worker safety. Furthermore, the findings from this study can inform the design of monitoring and compliance programs, enabling regulators to prioritize inspections and enforcement actions based on the key risk factors identified in the study. This proactive approach ensures that industry practices align with established standards and guidelines, fostering a culture of accountability and continuous improvement within the aquaculture sector.

It is essential to emphasize the importance of stakeholder collaboration and ongoing monitoring and evaluation in mitigating the risks associated with salmon MMEs. By fostering partnerships amongst aquaculture companies, research institutions, government agencies and non-governmental organizations, stakeholders can collectively develop and implement innovative solutions to address the identified risk factors. Additionally, a commitment to continuous monitoring and evaluation allows industry stakeholders and policymakers to assess the effectiveness of risk mitigation measures and adapt management practices in response to changing environmental conditions and emerging threats. Through these collaborative efforts and dedication to evidence-based decision-making, stakeholders can work together to enhance the resilience and sustainability of the aquaculture sector, ultimately reducing the incidence of salmon MMEs and safeguarding the long-term viability of this vital industry.

4 | CONCLUSION

The demand for Atlantic salmon products has grown enormously in recent years due to their high market value. Atlantic salmon

aquaculture has emerged as a promising way to meet such demand and provide additional high-quality protein to the increasing human population. However, MMEs are an important risk to the sustainability of the aquaculture of this species when fish are grown in open net pens/at cage sites. Several environmental, nutritional and disease/pathogen challenges can affect the health and welfare of salmon in complex and non-linear ways, given the difficulty in mitigating these challenges and because intense farming can lead to stressful conditions that exacerbate these factors. This study also identifies and analyses risk factors causing MMEs and post-MME impacts on aquaculture workers and communities. This study has proposed a robust and sustainable Atlantic salmon aquaculture system where MMEs are minimized, and risks to aquaculture production systems are predictable.

The study identifies that, when required, various fish health management strategies such as rigorous vaccination programs, responsible antibiotic and other therapeutic treatments, and integrated pest management strategies, can help prevent MMEs. However, warm and cold temperatures at/or beyond the salmon's tolerances, decreased water or systemic (internal) oxygen levels, increased HABs, sea lice infestations, and jellyfish blooms leave fish more susceptible to physiological stress and secondary (opportunistic) infections.²¹ Further, many of these challenges are being exacerbated by climate change.²³ This study identifies that the cumulative effect of all these risks results in significant production losses. However, being a qualitative BN study, the loss's magnitude is impossible to report. For such activity, a quantitative BN model is recommended. Crucially, the complexity of causes leading to MMEs, coupled with the increasing uncertainty and variability from climate change, mean that some interventions intending to reduce mortality may exacerbate MME risk, and such risk is unlikely to be eliminated entirely.

In conclusion, this research underscores the importance of understanding and addressing the complex interplay of risk factors contributing to MMEs in Atlantic salmon aquaculture. Using qualitative BN models, we have elucidated vital risk categories and their relationships, providing valuable insights for industry stakeholders and government policymakers. Moving forward, we must translate these findings into actionable strategies and policies aimed at mitigating risks, promoting sustainability, and safeguarding the health and welfare of salmon populations. Through collaborative efforts and ongoing monitoring and evaluation, we can work towards a future where aquaculture operations thrive in harmony with the environment, ensuring the continued viability and sustainability of the aquaculture industry for generations to come.

AUTHOR CONTRIBUTIONS

Zaman Sajid: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; data curation; project administration. **A. Kurt Gamperl:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing. **Christopher C. Parrish:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization;

writing – review and editing. **Stefanie M. Colombo:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing. **Javier Santander:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing. **Charles Mather:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing. **Barbara Neis:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing. **Ingunn Marie Holmen:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Ramón Filgueira:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Cynthia H. McKenzie:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Lissandra Souto Cavalli:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Mohamed Jeebhay:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Wenzhao Gao:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **María Andréa López Gómez:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Cory Ochs:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Sarah Lehnert:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Cyr Couturier:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Christine Knott:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **João F. Romero:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Albert Caballero-Solares:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Allan Cembella:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Harry M. Murray:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Ian A. Fleming:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Joel Finnis:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Mark D. Fast:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Mark Wells:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing. **Gerald G. Singh:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; project administration; supervision; resources.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the financial support from the Government of Newfoundland and Labrador's Department of Industry, Energy and Technology, Canada (grant number 20210487) and the Ocean Frontier Institute, Memorial University of Newfoundland,

Canada through an award from the Canada First Research Excellence Fund. GGS acknowledges support from the Nippon Foundation Ocean Nexus Center at EarthLab, University of Washington. The authors also thank Texas A&M University for covering Open Access (OA) charges for this paper. Thanks to Nikhilesh Paliath and Jadyn Godfrey for their help with data management. Special thanks to Beverley Brown for proofreading this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no data sets were generated or analysed during the current study.

ORCID

Zaman Sajid  <https://orcid.org/0000-0003-4318-4690>

Stefanie M. Colombo  <https://orcid.org/0000-0003-1828-7145>

Ramón Filgueira  <https://orcid.org/0000-0002-3332-8649>

Lissandra Souto Cavalli  <https://orcid.org/0000-0001-8531-7362>

María Andréa López Gómez  <https://orcid.org/0000-0002-1198-4530>

João F. Romero  <https://orcid.org/0000-0001-5869-7769>

Albert Caballero-Solares  <https://orcid.org/0000-0001-7693-0739>

Ian A. Fleming  <https://orcid.org/0000-0002-5541-824X>

Gerald G. Singh  <https://orcid.org/0000-0003-4333-1988>

REFERENCES

1. FAO. The State of World Fisheries and Aquaculture. Towards Blue Transformation. FAO; 2022. <https://doi.org/10.4060/cc0461en>
2. Cotello C, Cao L, Gelcich S, et al. The future of food from the sea. *Nature*. 2020;588(7836):95-100.
3. Campbell LM, Fairbanks L, Murray G, Stoll JS, D'Anna L, Bingham J. From Blue Economy to Blue Communities: reorienting aquaculture expansion for community wellbeing. *Mar Policy*. 2021;124:104361. doi:10.1016/j.marpol.2020.104361
4. Kayansamruaj P, Areechon N, Unajak S. Development of fish vaccine in Southeast Asia: a challenge for the sustainability of SE Asia aquaculture. *Fish Shellfish Immunol*. 2020;103:73-87. doi:10.1016/j.fsi.2020.04.031
5. Askew K. Troubled Waters: How High Fish Mortality and Poor Animal Welfare Threaten the Profitability of Aquaculture. Published 2021. Accessed October 19, 2022. <https://www.foodnavigator.com/Article/2021/08/05/Troubled-waters-How-high-fish-mortality-and-poor-animal-welfare-threaten-the-profitability-of-aquaculture>
6. Singh GG, Sajid Z, Mather C. Quantitative analysis of mass mortality events in salmon aquaculture shows increasing scale of fish loss events around the world. *Sci Rep*. 2024;14:3763. doi:10.1038/s41598-024-54033-9
7. Dyreveralliansen. Staggering Mortality Rates Reveal Significant Health and Welfare Challenges in Norwegian Fish Farming. Eurogroup for Animals. Published 2022. Accessed October 19, 2022. <https://www.eurogroupforanimals.org/news/staggering-mortality-rates-reveal-significant-health-and-welfare-challenges-norwegian-fish#:~:text=In%202020%2C%2052.1%20million%20farmed,mortality%20rate%20of%2014.8%20percent>
8. Kibria G. Global Fish Kills: Causes and Consequences. Tech Report. 2014.

9. Fey SB, Siepielski AM, Nusslé S, et al. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proc Natl Acad Sci U S A*. 2015;112(4):1083-1088. doi:10.1073/pnas.1414894112
10. Lande R. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am Nat*. 1993; 142(6):911-927.
11. Reed DH, O'Grady JJ, Ballou JD, Frankham R. The frequency and severity of catastrophic die-offs in vertebrates. *Animal Conservation Forum*. Vol 6. Cambridge University Press; 2003:109-114.
12. Edwards R. Farmed Salmon Deaths from Disease Reach Record High. *The Ferret*. Published July 13, 2020. Accessed March 8, 2022. <https://thoferret.scot/farmed-salmon-deaths-disease-reach-record-high/>
13. Oliveira VHS, Dean KR, Qviller L, Kirkeby C, Bang JB. Factors associated with baseline mortality in Norwegian Atlantic salmon farming. *Sci Rep*. 2021;11(1):14702. doi:10.1038/s41598-021-93874-6
14. Sommerset I, Walde CS, Bang Jensen B, Bornø G, Haukaas A, Brun E. *The Health Situation in Norwegian Aquaculture 2019*. Norwegian Veterinary Institute. 2020. https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=&ved=2ahUKEwin-aKnnNnzAhVsUd8KHZPnDq8QFnoECAKQAQ&url=https%3A%2F%2Fwww.vetinst.no%2Frapporter-og-publikasjoner%2Frapporter%2F2020%2Ffish-health-report-2019%2F_%2Fattachment%2Fdownload%2F7507c5b.
15. León-Muñoz J, Urbina MA, Garreaud R, Iriarte JL. Hydroclimatic conditions trigger record harmful algal bloom in western Patagonia (summer 2016). *Sci Rep*. 2018;8(1):1330. doi:10.1038/s41598-018-19461-4
16. SEPA. Scotland's Aquaculture Fish Farms Monthly Biomass & Treatment. Scottish Environment Protection Agency (SEPA) via "Scotland's Aquaculture." Published April 12, 2020. Accessed October 20, 2022. http://aquaculture.scotland.gov.uk/data/fish_farms_monthly_biomass_and_treatment_reports.aspx
17. Salmon Scotland. Mortality Rates in Scottish Salmon Farming. Salmon Scotland. Published 2022. Accessed October 21, 2022. <https://www.salmonscotland.co.uk/facts/fish-welfare#:~:text=Over%20the%20course%20of%20a,loss%20of%201.3%25%20each%20month>
18. Burt K, Hamoutene D, Perez-Casanova J, Kurt Gamperl A, Volkoff H. The effect of intermittent hypoxia on growth, appetite and some aspects of the immune response of Atlantic salmon (*Salmo salar*). *Aquacult Res*. 2013;45(1):124-137.
19. Gairn L. Harmful Algal Bloom in Chile Triggers Mass Salmon Mortality Event. We are Aquaculture. Published 2024. Accessed March 4, 2024. <https://weareaquaculture.com/news/aquaculture/harmful-algal-bloom-in-chile-triggers-mass-salmon-mortality-event>
20. Johnston J. Chile Loses Thousands of Salmon and Trout to Algal Blooms. *Fish Farmer Magazine*. Published 2023. Accessed March 4, 2024. <https://www.fishfarmermagazine.com/2023/11/20/chile-loses-thousands-of-salmon-and-trout-to-algal-blooms/#:~:text=According%20to%20the%20figures%20Sernapesca,has%20now%20reached%201%2C100%20tons>
21. Gamperl AK, Ajiboye OO, Zanuzzo FS, Sandrelli RM, Ellen de Fátima CP, Beemelmanns A. The impacts of increasing temperature and moderate hypoxia on the production characteristics, cardiac morphology and haematology of Atlantic Salmon (*Salmo salar*). *Aquaculture*. 2020;519:734874.
22. Persson D, Nødtvedt A, Aunsmo A, Stormoen M. Analysing mortality patterns in salmon farming using daily cage registrations. *J Fish Dis*. 2022;45(2):335-347.
23. Falconer L, Telfer TC, Garrett A, et al. Insight into real-world complexities is required to enable effective response from the aquaculture sector to climate change. *PLoS Clim*. 2022;1(3):e0000017.
24. CBC. Company Accepts Suspension of Licences After 2.6 million Dead Salmon, Insists Gerry Byrne. Canadian Broadcasting Corporation. Published November 21, 2019. Accessed October 28, 2022. <https://www.cbc.ca/news/canada/newfoundland-labrador/gerry-byrne-licences-back-northern-harvest-salmon-1.5368299>
25. CDC. Center for Maritime Safety and Health Studies: Aquaculture, The National Institute for Occupational Safety and Health (NIOSH). Centers for Disease Control and Prevention. Published January 9, 2020. Accessed October 28, 2022. <https://www.cdc.gov/niosh/programs/cms/shs/aquaculture.html>
26. Ngajilo D, Jeebhay MF. Occupational injuries and diseases in aquaculture—a review of literature. *Aquaculture*. 2019;507:40-55. doi:10.1016/j.aquaculture.2019.03.053
27. Watterson A, Jeebhay MF, Neis B, Mitchell R, Cavalli L. The neglected millions: the global state of aquaculture workers' occupational safety, health and well-being. *Occup Environ Med*. 2020;77(1): 15-18.
28. CBC News(b). Harbour Breton Fish Plant Workers Concerned for the Future After Northern Harvest Fish Die-Off. Canadian Broadcasting Corporation. Published September 26, 2019. Accessed October 28, 2022. <https://www.cbc.ca/news/canada/newfoundland-labrador/plant-workers-without-work-harbour-breton-1.5297255>
29. Ban SS, Pressey RL, Graham NAJ. Assessing interactions of multiple stressors when data are limited: a Bayesian belief network applied to coral reefs. *Glob Environ Chang*. 2014;27:64-72. doi:10.1016/j.gloenvcha.2014.04.018
30. Sajid Z, Khan F, Zhang Y. Integration of interpretive structural modelling with Bayesian network for biodiesel performance analysis. *Renew Energy*. 2017;107:194-203. doi:10.1016/j.renene.2017.01.058
31. Sajid Z, Khan F, Zhang Y. A novel process economics risk model applied to biodiesel production system. *Renew Energy*. 2018;118: 615-626. doi:10.1016/j.renene.2017.11.022
32. Dao U, Sajid Z, Khan F, Zhang Y, Tran T. Modeling and analysis of internal corrosion induced failure of oil and gas pipelines. *Reliab Eng Syst Saf*. 2023;234:109170.
33. Dao U, Sajid Z, Khan F, Zhang Y. Safety analysis of blended hydrogen pipelines using dynamic object-oriented bayesian network. *Int J Hydrogen Energy*. 2024;52:841-856.
34. Singh GG, Sinner J, Ellis J, et al. Group elicitation yield more consistent, yet more uncertain experts in understanding risks to ecosystem services in New Zealand bays. *PLoS One*. 2017;12(8):e0182233.
35. Rensel JE, Whyte JNC. Finfish mariculture and harmful algal blooms. *Manual on Harmful Marine Microalgae*. Monographs on Oceanographic Methodology. Vol 11. Intergovernmental Oceanographic Commission; 2003:693-722.
36. Matsuyama Y, Oda T. Toxic effects of harmful algal blooms on finfish and shellfish. *Handbook of Algal Science, Technology and Medicine*. Elsevier; 2020:543-560.
37. McKenzie CH, Bates SS, Martin JL, et al. Three decades of Canadian marine harmful algal events: phytoplankton and phycotoxins of concern to human and ecosystem health. *Harmful Algae*. 2021;102: 101852.
38. Holbrook NJ, Scannell HA, Sen Gupta A, et al. A global assessment of marine heatwaves and their drivers. *Nat Commun*. 2019;10(1): 2624.
39. Oliver ECJ, Donat MG, Burrows MT, et al. Longer and more frequent marine heatwaves over the past century. *Nat Commun*. 2018;9(1): 1-12.
40. Viglione G. Fevers are plaguing the oceans—and climate change is making them worse. *Nature*. 2021;593(7857):26-28.
41. Intergovernmental Panel on Climate Change. In: Pörtner HO, Roberts DC, Tignor M, et al., eds. *Impacts, adaptation, and vulnerability. Contribution of working group II to the sixth assessment report of*

- the intergovernmental panel on climate change. Cambridge University Press; 2022:3056.
42. Wade NM, Clark TD, Maynard BT, et al. Effects of an unprecedented summer heatwave on the growth performance, flesh colour and plasma biochemistry of marine cage-farmed Atlantic salmon (*Salmo salar*). *J Therm Biol*. 2019;80:64-74.
 43. Burke H, Gardner I, Farrell AP. A Review of the 2019 Newfoundland and Labrador South Coast Cultured Atlantic Salmon Mortality Event. Department of Fisheries and Aquaculture, Government of Newfoundland and Labrador, Spec Stud Reports. 2020.
 44. Ignatz EH, Sandrelli RM, Vadboncoeur É, et al. The Atlantic salmon's (*Salmo salar*) incremental thermal maximum is a more relevant and sensitive indicator of family-based differences in upper temperature tolerance than its critical thermal maximum. *Aquaculture*. 2023;574:739628.
 45. Benfey TJ, Gonen S, Bartlett CB, Garber AF. High heritability for thermal tolerance in Atlantic salmon, *Salmo salar*. *Res Sq*. 2022; 1:1-27.
 46. Godwin SC, Fast MD, Kuparinen A, Medcalf KE, Hutchings JA. Increasing temperatures accentuate negative fitness consequences of a marine parasite. *Sci Rep*. 2020;10(1):18467.
 47. Sae-Lim P, Kause A, Mulder HA, Olesen I. Breeding and genetics symposium: climate change and selective breeding in aquaculture. *J Anim Sci*. 2017;95(4):1801-1812.
 48. Zanuzzo FS, Ellen de Fátima CP, Sandrelli RM, St-Hilaire S, O'Brien N, Gamperl AK. Temperature has considerable effects on plasma and muscle antibiotic concentrations in Atlantic salmon (*Salmo salar*). *Aquaculture*. 2022;546:737372.
 49. Gamperl AK, Zrini ZA, Sandrelli RM. Atlantic salmon (*Salmo salar*) cage-site distribution, behavior, and physiology during a Newfoundland heat wave. *Front Physiol*. 2021;12:719594.
 50. Overton K, Dempster T, Oppedal F, Kristiansen TS, Gismervik K, Stien LH. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. *Rev Aquac*. 2019;11(4):1398-1417.
 51. Sviland Walde C, Bang Jensen B, Pettersen JM, Stormoen M. Estimating cage-level mortality distributions following different delousing treatments of Atlantic salmon (*Salmo salar*) in Norway. *J Fish Dis*. 2021;44(7):899-912.
 52. Østevik L, Stormoen M, Evensen Ø, et al. Effects of thermal and mechanical delousing on gill health of farmed Atlantic salmon (*Salmo salar* L.). *Aquaculture*. 2022;552:738019.
 53. Catto JL, Ackerley D, Booth JF, et al. The future of midlatitude cyclones. *Curr Clim Change Rep*. 2019;5:407-420.
 54. Gubbins M, Bricknell I, Service M. Impacts of climate change on aquaculture. *MCCIP Sci Rev*. 2013;318-327.
 55. Maulu S, Hasimuna OJ, Haambiya LH, et al. Climate change effects on aquaculture production: sustainability implications, mitigation, and adaptations. *Front Sustain Food Syst*. 2021;5:609097.
 56. Huang J, Hitchcock P, Maycock AC, McKenna CM, Tian W. Northern hemisphere cold air outbreaks are more likely to be severe during weak polar vortex conditions. *Commun Earth Environ*. 2021;2(1):147.
 57. Smith ET, Sheridan SC. Where do cold air outbreaks occur, and how have they changed over time? *Geophys Res Lett*. 2020;47(13):e2020GL086983.
 58. Szekeres P, Eliason EJ, Lapointe D, Donaldson MR, Brownscombe JW, Cooke SJ. On the neglected cold side of climate change and what it means to fish. *Climate Res*. 2016;69(3):239-245.
 59. Canadian Broadcasting Corporation. Harsh Weather Linked to Die-Off at Newfoundland Salmon Farm. 2020. Accessed July 4, 2023 <https://www.cbc.ca/news/canada/newfoundland-labrador/another-salmon-die-off-1.5483364>
 60. Fletcher GL, Kao MH, Dempson JB. Lethal freezing temperatures of Arctic char and other salmonids in the presence of ice. *Aquaculture*. 1988;71(4):369-378.
 61. Čirić J. 500 Tonnes of Salmon Die in Arnarlax Fish Farms. Iceland Review. Published 2020. Accessed July 4, 2023. <https://www.icelandreview.com/economy/500-tonnes-of-salmon-die-in-arnarlax-fish-farms/#:~:text=Kjartan%20C3%93lafsson%2C%20the%20chairman%20of,lead%20to%20the%20fish%27s%20death>
 62. Vadboncoeur É, Nelson C, Hall JR, et al. Lowering temperature to 1°C results in physiological changes, stress and mortality in cultured Atlantic Salmon (*Salmo salar*). *Aquaculture*. 2023;568:739313.
 63. Vadboncoeur É, Nelson C, Ignatz EH, et al. Increased liver size and dysfunction, ionoregulatory disturbance and opportunistic infections in cultured post-smolt Atlantic salmon (*Salmo salar*) at low temperatures. *J Fish Dis*. 2022.
 64. Ibarz A, Padrós F, Gallardo MÁ, Fernández-Borràs J, Blasco J, Tort L. Low-temperature challenges to gilthead sea bream culture: review of cold-induced alterations and 'winter syndrome'. *Rev Fish Biol Fish*. 2010;20:539-556.
 65. Bakun A, Black BA, Bograd SJ, et al. Anticipated effects of climate change on coastal upwelling ecosystems. *Curr Clim Change Rep*. 2015;1:85-93.
 66. Karlson B, Andersen P, Arneborg L, et al. Harmful algal blooms and their effects in coastal seas of northern Europe. *Harmful Algae*. 2021;102:101989.
 67. Stehfest KM, Carter CG, McAllister JD, Ross JD, Semmens JM. Response of Atlantic salmon *Salmo salar* to temperature and dissolved oxygen extremes established using animal-borne environmental sensors. *Sci Rep*. 2017;7(1):4545.
 68. Baxter EJ, Rodger HD, McAllen R, Doyle TK. Gill disorders in marine-farmed salmon: investigating the role of hydrozoan jellyfish. *Aquac Environ Interact*. 2011;1(3):245-257.
 69. Baxter EJ, Sturt MM, Ruane NM, et al. Gill damage to Atlantic salmon (*Salmo salar*) caused by the common jellyfish (*Aurelia aurita*) under experimental challenge. *PLoS One*. 2011;6(4):e18529.
 70. Powell MD, Harris JO, Carson J, Hill JV. Effects of gill abrasion and experimental infection with *Tenacibaculum maritimum* on the respiratory physiology of Atlantic salmon *Salmo salar* affected by amoebic gill disease. *Dis Aquat Organ*. 2005;63(2-3):169-174.
 71. Småge SB, Brevik ØJ, Frisch K, Watanabe K, Duesund H, Nylund A. Concurrent jellyfish blooms and tenacibaculosis outbreaks in Northern Norwegian Atlantic salmon (*Salmo salar*) farms. *PLoS One*. 2017;12(11):e0187476.
 72. Bertness MD, Bruno JF, Silliman BR, Stachowicz JJ. Marine Community Ecology and Conservation. Sinauer. 2014. <https://books.google.com/books?id=LndEnwEACAAJ>
 73. Hajek AE, Shapiro-Ilan DI. *Ecology of Invertebrate Diseases*. Wiley; 2018. <https://books.google.com/books?id=Klw6DwAAQBAJ>.
 74. Tully O. Predicting infestation parameters and impacts of caligid copepods in wild and cultured fish populations. *Invertebr Reprod Dev*. 1992;22(1-3):91-102.
 75. Brooks KM. The effects of water temperature, salinity, and currents on the survival and distribution of the infective copepodid stage of sea lice (*Lepeophtheirus salmonis*) originating on Atlantic salmon farms in the Broughton Archipelago of British Columbia, Canada. *Rev Fish Sci*. 2005;13(3):177-204.
 76. Groner ML, Gettinby G, Stormoen M, Revie CW, Cox R. Modelling the impact of temperature-induced life history plasticity and mate limitation on the epidemic potential of a marine ectoparasite. *PLoS One*. 2014;9(2):e88465.
 77. Groner ML, Rogers LA, Bateman AW, et al. Lessons from sea louse and salmon epidemiology. *Philos Trans R Soc Lond B Biol Sci*. 2016;371(1689):20150203.
 78. Vezzulli L, Colwell RR, Pruzzo C. Ocean warming and spread of pathogenic vibrios in the aquatic environment. *Microb Ecol*. 2013;65:817-825.

79. Stene A, Bang Jensen B, Knutsen Ø, Olsen A, Viljugrein H. Seasonal increase in sea temperature triggers pancreas disease outbreaks in Norwegian salmon farms. *J Fish Dis.* 2014;37(8):739-751.
80. Zanuzzo FS, Beemelmanns A, Hall JR, Rise ML, Gamperl AK. The innate immune response of Atlantic salmon (*Salmo salar*) is not negatively affected by high temperature and moderate hypoxia. *Front Immunol.* 2020;11:1009.
81. Groves L, Whyte SK, Purcell SL, et al. Temperature impacts Atlantic salmon's (*Salmo salar*) immunological response to infectious salmon anemia virus (ISAV). *Fish Shellfish Immunol Rep.* 2023;4:100099.
82. Purcell MK, McKibben CL, Pearman-Gillman S, Elliott DG, Winton JR. Effects of temperature on *Renibacterium salmoninarum* infection and transmission potential in Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *J Fish Dis.* 2016;39(7):787-798.
83. Holt RA, Amandi A, Rohovec JS, Fryer JL. Relation of water temperature to bacterial cold-water disease in coho salmon, chinook salmon, and rainbow trout. *J Aquat Anim Health.* 1989;1(2):94-101.
84. Tunsjø HS, Paulsen SM, Mikkelsen H, L'Abée-Lund TM, Skjerve E, Sørum H. Adaptive response to environmental changes in the fish pathogen *Moritella viscosa*. *Res Microbiol.* 2007;158(3):244-250.
85. Ugelvik MS, Mæhle S, Dalvin S. Temperature affects settlement success of ectoparasitic salmon lice (*Lepeophtheirus salmonis*) and impacts the immune and stress response of Atlantic salmon (*Salmo salar*). *J Fish Dis.* 2022;45(7):975-990.
86. Abram QH, Dixon B, Katzenback BA. Impacts of low temperature on the teleost immune system. *Biology.* 2017;6(4):39.
87. Virtanen MI, Brinckmann MF, Patel DM, Iversen MH. Chronic stress negatively impacts wound healing, welfare, and stress regulation in internally tagged Atlantic salmon (*Salmo salar*). *Front Physiol.* 2023;14:1147235.
88. Costello MJ. Ecology of sea lice parasitic on farmed and wild fish. *Trends Parasitol.* 2006;22(10):475-483.
89. Lepe-López M, Escobar-Dodero J, Rubio D, Alvarez J, Zimin-Veselkoff N, Mardones FO. Epidemiological factors associated with *Caligus rogercresseyi* infection, abundance, and spatial distribution in southern Chile. *Front Vet Sci.* 2021;8:595024.
90. Costello M. The global economic cost of sea lice to the salmonid farming industry. *J Fish Dis.* 2009;32(1):115-118.
91. Barrett LT, Oppedal F, Robinson N, Dempster T. Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. *Rev Aquac.* 2020;12(4):2527-2543.
92. Aaen SM, Helgesen KO, Bakke MJ, Kaur K, Horsberg TE. Drug resistance in sea lice: a threat to salmonid aquaculture. *Trends Parasitol.* 2015;31(2):72-81.
93. Brooks KM. Considerations in developing an integrated pest management programme for control of sea lice on farmed salmon in Pacific Canada. *J Fish Dis.* 2009;32(1):59-73.
94. Treasurer JW. A review of potential pathogens of sea lice and the application of cleaner fish in biological control. *Pest Manag Sci Former Pestic Sci.* 2002;58(6):546-558.
95. Erkinharju T, Dalmo RA, Hansen M, Seternes T. Cleaner fish in aquaculture: review on diseases and vaccination. *Rev Aquac.* 2021;13(1):189-237.
96. Skiftesvik AB, Blom G, Agnalt A-L, et al. Wrasse (Labridae) as cleaner fish in salmonid aquaculture—the Hardangerfjord as a case study. *Mar Biol Res.* 2014;10(3):289-300.
97. Powell A, Treasurer JW, Pooley CL, et al. Use of lumpfish for sea-lice control in salmon farming: challenges and opportunities. *Rev Aquac.* 2018;10(3):683-702.
98. Sayer MDJ, Reader JP. Exposure of goldsinny, rock cook and corkwing wrasse to low temperature and low salinity: survival, blood physiology and seasonal variation. *J Fish Biol.* 1996;49(1):41-63.
99. Imsland AK, Reynolds P, Eliassen G, et al. Investigation of behavioural interactions between lumpfish (*Cyclopterus lumpus*) and goldsinny wrasse (*Ctenolabrus rupestris*) under controlled conditions. *Aquac Int.* 2016;24:1509-1521.
100. Charmley KJ. Habitat selection by two species of cleaner fishes that may be beneficial in removing sea lice from cultured salmon. *Surg J.* 2019;11.
101. Marcos-López M, Donald K, Stagg H, McCarthy U. Clinical *Vibrio anguillarum* infection in lumpfish *Cyclopterus lumpus* in Scotland. *Vet Rec.* 2013;173(319):10-1136.
102. Imsland AK, Reynolds P, Eliassen G, et al. The use of lumpfish (*Cyclopterus lumpus* L.) to control sea lice (*Lepeophtheirus salmonis* Krøyer) infestations in intensively farmed Atlantic salmon (*Salmo salar* L.). *Aquaculture.* 2014;424:18-23.
103. Whittaker BA, Consuegra S, de Leaniz CG. Genetic and phenotypic differentiation of lumpfish (*Cyclopterus lumpus*) across the North Atlantic: implications for conservation and aquaculture. *PeerJ.* 2018;6:e5974.
104. Figueroa C, Bustos P, Torrealba D, et al. Coinfection takes its toll: sea lice override the protective effects of vaccination against a bacterial pathogen in Atlantic salmon. *Sci Rep.* 2017;7(1):17817.
105. Kotob MH, Menanteau-Ledouble S, Kumar G, Abdelzaher M, El-Matbouli M. The impact of co-infections on fish: a review. *Vet Res.* 2017;47(1):1-12.
106. Kibenge FSB. Emerging viruses in aquaculture. *Curr Opin Virol.* 2019;34:97-103.
107. Yáñez JM, Houston RD, Newman S. Genetics and genomics of disease resistance in salmonid species. *Front Genet.* 2014;5:415.
108. Mustafa A, MacKinnon BM. Genetic variation in susceptibility of Atlantic salmon to the sea louse *Caligus elongatus* Nordmann, 1832. *Can J Zool.* 1999;77(8):1332-1335.
109. Glover KA, Solberg MF, McGinnity P, et al. Half a century of genetic interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. *Fish Fish.* 2017;18(5):890-927.
110. Guy DR, Bishop SC, Brotherstone S, et al. Analysis of the incidence of infectious pancreatic necrosis mortality in pedigreed Atlantic salmon, *Salmo salar* L., populations. *J Fish Dis.* 2006;29(11):637-647.
111. Blix TB, Dalmo RA, Wargelius A, Myhr AI. Genome editing on finfish: current status and implications for sustainability. *Rev Aquac.* 2021;13(4):2344-2363.
112. Schar D, Klein EY, Laxminarayan R, Gilbert M, Van Boeckel TP. Global trends in antimicrobial use in aquaculture. *Sci Rep.* 2020;10(1):21878.
113. Henriksen PJG, Rico A, Troell M, et al. Unpacking factors influencing antimicrobial use in global aquaculture and their implication for management: a review from a systems perspective. *Sustain Sci.* 2018;13:1105-1120.
114. Watts JEM, Schreier HJ, Lanska L, Hale MS. The rising tide of antimicrobial resistance in aquaculture: sources, sinks and solutions. *Mar Drugs.* 2017;15(6):158.
115. Dessen J-E, Østbye TK, Ruyter B, Bou M, Thomassen MS, Rørvik K-A. Sudden increased mortality in large seemingly healthy farmed Atlantic salmon (*Salmo salar* L.) was associated with environmental and dietary changes. *J Appl Aquac.* 2021;33(2):165-182. doi:10.1080/10454438.2020.1726237
116. Grisdale-Helland B, Helland SJ. Replacement of protein by fat and carbohydrate in diets for Atlantic salmon (*Salmo salar*) at the end of the freshwater stage. *Aquaculture.* 1997;152(1-4):167-180.
117. Torstensen BE, Espe M, Stubhaug I, Lie Ø. Dietary plant proteins and vegetable oil blends increase adiposity and plasma lipids in Atlantic salmon (*Salmo salar* L.). *Br J Nutr.* 2011;106(5):633-647.
118. Poppe TT, Johansen R, Gunnes G, Tørud B. Heart morphology in wild and farmed Atlantic salmon *Salmo salar* and rainbow trout *Oncorhynchus mykiss*. *Dis Aquat Organ.* 2003;57(1-2):103-108.
119. Hixson SM, Parrish CC, Anderson DM. Full substitution of fish oil with camelina (*Camelina sativa*) oil, with partial substitution of fish

- meal with camelina meal, in diets for farmed Atlantic salmon (*Salmo salar*) and its effect on tissue lipids and sensory quality. *Food Chem.* 2014;157:51-61.
120. Hansen AKG, Kortner TM, Krasnov A, Björkhem I, Penn M, Krogdahl Å. Choline supplementation prevents diet induced gut mucosa lipid accumulation in post-smolt Atlantic salmon (*Salmo salar* L.). *BMC Vet Res.* 2020;16(1):1-15.
 121. Hansen AKG, Kortner TM, Denstadli V, et al. Dose-response relationship between dietary choline and lipid accumulation in pyloric enterocytes of Atlantic salmon (*Salmo salar* L.) in seawater. *Br J Nutr.* 2020;123(10):1081-1093.
 122. Adjoumani J-JY, Wang K, Zhou M, Liu W, Zhang D. Effect of dietary betaine on growth performance, antioxidant capacity and lipid metabolism in blunt snout bream fed a high-fat diet. *Fish Physiol Biochem.* 2017;43:1733-1745.
 123. Volkoff H, Rønnestad I. Effects of temperature on feeding and digestive processes in fish. *Temperature.* 2020;7(4):307-320.
 124. Dawood MAO, Koshio S, Esteban MÁ. Beneficial roles of feed additives as immunostimulants in aquaculture: a review. *Rev Aquac.* 2018;10(4):950-974.
 125. Dantagnan P, Gonzalez K, Hevia M, et al. Effect of the arachidonic acid/vitamin E interaction on the immune response of juvenile Atlantic salmon (*Salmo salar*) challenged against *Piscirickettsia salmonis*. *Aquacult Nutr.* 2017;23(4):710-720.
 126. Caballero-Solares A, Hall JR, Xue X, et al. The dietary replacement of marine ingredients by terrestrial animal and plant alternatives modulates the antiviral immune response of Atlantic salmon (*Salmo salar*). *Fish Shellfish Immunol.* 2017;64:24-38.
 127. Emam M, Eslamloo K, Caballero-Solares A, et al. Nutritional immunomodulation of Atlantic salmon response to *Renibacterium salmoninarum* bacterin. *Front Mol Biosci.* 2022;9:931548.
 128. Eslamloo K, Xue X, Hall JR, et al. Transcriptome profiling of antiviral immune and dietary fatty acid dependent responses of Atlantic salmon macrophage-like cells. *BMC Genomics.* 2017;18(1):1-28.
 129. Xue X, Woldemariam NT, Caballero-Solares A, et al. Dietary immunostimulant CpG modulates microRNA biomarkers associated with immune responses in Atlantic salmon (*Salmo salar*). *Cells.* 2019;8(12):1592.
 130. Sutherland BJB, Covello JM, Friend SE, et al. Host-parasite transcriptomics during immunostimulant-enhanced rejection of salmon lice (*Lepeophtheirus salmonis*) by Atlantic salmon (*Salmo salar*). *Facets.* 2017;2(1):477-495.
 131. Thorvaldsen T, Kongsvik T, Holmen IM, et al. Occupational health, safety and work environments in Norwegian fish farming-employee perspective. *Aquaculture.* 2020;524:735238.
 132. Cole DW, Cole R, Gaydos SJ, et al. Aquaculture: environmental, toxicological, and health issues. *Int J Hyg Environ Health.* 2009;212(4):369-377.
 133. Moreau DTR, Neis B. Occupational health and safety hazards in Atlantic Canadian aquaculture: laying the groundwork for prevention. *Mar Policy.* 2009;33(2):401-411.
 134. Cavalli L, Jeebhay MF, Marques F, et al. Scoping global aquaculture occupational safety and health. *J Agromedicine.* 2019;24(4):391-404.
 135. McGuinness E, Aasjord HL, Utne IB, Holmen IM. Fatalities in the Norwegian fishing fleet 1990-2011. *Saf Sci.* 2013;57:335-351.
 136. Neis B, Gao W, Cavalli L, et al. Mass mortality events in marine salmon aquaculture and their influence on occupational health and safety hazards and risk of injury. *Aquaculture.* 2023;566:739225. doi:10.1016/j.aquaculture.2022.739225
 137. Thorvaldsen T, Holmen IM, Moe HK. The escape of fish from Norwegian fish farms: causes, risks and the influence of organisational aspects. *Mar Policy.* 2015;55:33-38.
 138. Føre HM, Thorvaldsen T. Causal analysis of escape of Atlantic salmon and rainbow trout from Norwegian fish farms during 2010-2018. *Aquaculture.* 2021;532:736002.
 139. Holmen IM, Utne IB, Haugen S. Identification of safety indicators in aquaculture operations based on fish escape report data. *Aquaculture.* 2021;544:737143.
 140. Knott C, Marschke M. Flagpoling: inter-provincial mobility of international migrants within Canada's temporary foreign worker program. *Int Migr.* 2021;59(2):25-40.
 141. Knott C. Contentious mobilities and cheap (er) labour: temporary foreign workers in a New Brunswick seafood processing community. *Can J Sociol.* 2016;41(3):375-398.
 142. Knott C, Mather C. Ocean frontier assemblages: critical insights from Canada's industrial salmon sector. *J Agrar Change.* 2021;21(4):796-814.
 143. Mather C, Fanning L. Social licence and aquaculture: towards a research agenda. *Mar Policy.* 2019;99:275-282.
 144. Martin SJ, Mather C, Knott C, Bavington D. Landing'salmon aquaculture: ecologies, infrastructures and the promise of sustainability. *Geoforum.* 2021;123:47-55.
 145. Dao U, Sajid Z, Khan F, Zhang Y. Dynamic Bayesian network model to study under-deposit corrosion. *Reliab Eng Syst Saf.* 2023;237:109370.
 146. Sajid Z. A dynamic risk assessment model to assess the impact of the coronavirus (COVID-19) on the sustainability of the biomass supply chain: a case study of a US biofuel industry. *Renew Sustain Energy Rev.* 2021;151:111574.
 147. Sajid Z, Khan F, Veitch B. Dynamic ecological risk modelling of hydrocarbon release scenarios in Arctic waters. *Mar Pollut Bull.* 2020;153:111001. doi:10.1016/j.marpolbul.2020.111001

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sajid Z, Gamperl AK, Parrish CC, et al. An aquaculture risk model to understand the causes and consequences of Atlantic Salmon mass mortality events: A review. *Rev Aquac.* 2024;16(4):1674-1695. doi:10.1111/raq.12917

APPENDIX A

Risk category	Risk factor
Environmental stressors (abiotic and biotic) model	<p>Amoebic gill disease</p> <p>Bacterial pathogens (bacteria, viruses, sea lice, amoebic gill disease)</p> <p>Cage damage/collapse</p> <p>Climate change</p> <p>Cold temperature</p> <p>Extreme weather events</p> <p>Gill damage</p> <p>High water temperature (18 – 20°C)</p> <p><i>In vivo</i> systemic hypoxia</p> <p>Increased runoff and nutrients</p> <p>Jellyfish</p> <p>Low ocean salinity (< 20 PSU)</p> <p>Low water oxygen level (< 70% air saturation)</p> <p>Net fouling</p> <p>Ocean acidification</p> <p>Reduced antibiotic levels/effectiveness</p> <p>Reduced cage water flow</p> <p>Skin damage</p> <p>Storms (wind/waves)</p> <p>'Super Chill' (< -0.5°C) 'Winter Syndrome' (< 4°C)?</p> <p>Very high water temperature (> 21 – 22°C)</p> <p>Viral pathogens (incl. ISA)</p>
Infectious diseases and pathogens model	<p>Bacterial diseases (pathogens)</p> <p>Fish immune suppression</p> <p>Harmful algal blooms (HABs)</p> <p>High fish densities</p> <p>High ocean salinity (> 20 PSU)</p> <p>High ocean temperature (> 18° C)</p> <p>Low ocean temperature (< 4°C)</p> <p>Low oxygen level in water (hypoxia)</p> <p>Sea lice</p> <p>Viral diseases</p>
Salmon nutrition model	<p>Diseases/pathogens/pests</p> <p>Feeding regime</p> <p>High lipid (fat) level in the salmon's liver</p> <p>Low protein/high lipid diets</p> <p>Starvation in salmon</p>
Aquaculture occupational health and safety (OHS) model	<p>Community/company power relations</p> <p>Environmental conditions (adverse weather events)</p> <p>Environmental conditions (adverse weather events) - OHS hazards coupling factor</p> <p>Failure to prepare for unforeseen events</p> <p>Insufficient regulatory frameworks for fish health and OHS</p> <p>Limited detection and disclosed documentation of adverse health effects</p> <p>No scheduled risk management - OHS and product risk</p>

(Continues)

Risk category	Risk factor
	<p>OHS hazardous agents: chemical, physical, biological, and psychosocial</p> <p>OHS regulation requirements and inadequate inspection capabilities</p> <p>Poor monitoring/late finding of the risk situation (MME), and also no reporting or insufficient reporting</p> <p>Restricted access to healthcare, compensation, and RTW supports</p> <p>Unsafe work structures and planning for high - risk MME labor/workers affected by fatigue due to lengthy work hours</p> <p>Work - induced injury or disease (consequence)</p>
Workers' livelihood model	<p>Appropriate risk management system</p> <p>Differential impacts on workers - gender, race, age</p> <p>Fewer employment opportunities in aquaculture industry</p> <p>Lack of contingency planning</p> <p>Lack of risk assessment</p> <p>Lack of skilled trained workers and labor</p> <p>Lack of worker "voice" and agency</p> <p>Loss of health benefits for workers and immediate families</p> <p>Loss of household incomes</p> <p>Loss of income for aquaculture workers</p> <p>Loss of local employment for communities</p> <p>national/federal/provincial regulatory system</p> <p>outmigration</p> <p>Poor monitoring of risk situations (MMEs)</p> <p>Reduced work for an extended period (2 years)</p> <p>Regulatory requirement for MME plan</p> <p>Shortage of skilled trained workers</p> <p>Temporary foreign workforce</p> <p>Weak social security</p>
Risk factors shared between two or more risk categories	<p>Appropriate risk management system</p> <p>Bacterial pathogens</p> <p>Cold temperatures (< 4°C)/low ocean temperature (< 4°C)</p> <p>Community/company power relations</p> <p>Extreme weather events</p> <p>Fish immune suppression</p> <p>Harmful algal blooms (HABs)</p> <p>High water/ocean temperature (18 - 20°C)</p> <p>Lack of contingency planning</p> <p>Lack of risk assessment</p> <p>Low water oxygen level (hypoxia; < 70%)</p> <p>Poor monitoring of risk situations</p> <p>Poor monitoring/late finding of the risk situation (MME), and also no reporting or insufficient reporting</p> <p>Presence of sea lice</p> <p>Prolonged exposure of salmon to high temperatures (18 - 20°C)</p> <p>Prolonged exposure of salmon to low temperatures (< 4°C)</p> <p>Restricted access to according health care, compensation, and RTW supports</p> <p>Shortage of skilled trained workers</p> <p>Very high water temperatures (> 21 - 22°C)</p> <p>Viral pathogens (incl. ISA)</p>

Risk category	Risk factor
Management decision - making and mitigating risk factors	Alternative employment Antibiotics Cage siting/construction/depth Cleaner fish Community/company power dynamics Community/company power relations Diets Economic safeguard Enhanced performance of immune system Feeding regime/nutrition (High) fish densities Increased appetite Lack of MME post - occurrence OHS hazard review and structural changes for future risk mitigation Mort collection Net cleaning Oxygenation/aeration Poor monitoring/late finding of the risk situation (MME), and also no reporting or insufficient reporting Presence of risk assessment Production level (scale of production) Protection against oxidative stress Reorganization of production/disinvestment Restructuring of production Sea lice treatment (incl. cleaner fish) Selective breeding Stocking densities Stocking density Upgrading infrastructure (nets) Use of functional diets for salmon Vaccination