



REVIEW

Offshore aquaculture of finfish: Big expectations at sea

Bernat Morro¹  | Keith Davidson² | Thomas P. Adams² | Lynne Falconer¹  |
 Max Holloway² | Andrew Dale² | Dmitry Aleynik²  | Philipp R. Thies³ |
 Faryal Khalid³ | Jon Hardwick³ | Helen Smith³ | Philip A. Gillibrand⁴ |
 Sonia Rey-Planellas¹ 

¹Institute of Aquaculture, Faculty of Natural Sciences, University of Stirling, Stirling, UK

²Scottish Association for Marine Science (SAMS), Scottish Marine Institute, Oban, UK

³Renewable Energy Group, College of Engineering, Mathematics, and Physical Sciences, University of Exeter, Penryn, UK

⁴Mowi Scotland Ltd, Fort William, UK

Correspondence

Sonia Rey-Planellas, Institute of Aquaculture, Faculty of Natural Sciences, University of Stirling, Stirling, UK.
 Email: sonia.reyplanellas@stir.ac.uk

Funding information

Biotechnology and Biological Sciences Research Council, Grant/Award Number: BB/S004246/1; Natural Environment Research Council, Grant/Award Number: NE/R00675X/1

Abstract

Offshore aquaculture has gained momentum in recent years, and the production of an increasing number of marine fish species is being relocated offshore. Initially, predictions of the advantages that offshore aquaculture would present over nearshore farming were made without enough science-based evidence. Now, with more scientific knowledge, this review revisits past predictions and expectations of offshore aquaculture. We analysed and explained the oceanographic features that define offshore and nearshore sites. Using Atlantic salmon (*Salmo salar*) as a case study, we focussed on sea lice, amoebic gill disease, and the risk of harmful algal blooms, as well as the direct effects of the oceanography on the health and physiology of fish. The operational and licencing challenges and advantages of offshore aquaculture are also considered. The lack of space in increasingly saturated sheltered areas will push new farms out to offshore locations and, if appropriate steps are followed, offshore aquaculture can be successful. Firstly, the physical capabilities of the farmed fish species and infrastructure must be fully understood. Secondly, the oceanography of potential sites must be carefully studied to confirm that they are compatible with the species-specific capabilities. And, thirdly, an economic plan considering the operational costs and licencing limitations of the site must be developed. This review will serve as a guide and a compilation of information for researchers and stakeholders.

KEYWORDS

amoebic gill disease, Atlantic salmon, harmful algal blooms, oceanography, policy, sea lice

1 | INTRODUCTION

Over half of global human fish consumption today (52% in 2018), a number equivalent to 82 million tonnes and valued at £190 billion (241.3 billion US\$), depends on aquaculture production systems. Demand for fish is growing, with average annual increases of 3.1%

between 1961 and 2017 (almost twice that of annual world population growth at 1.6%). This places annual consumption at 20.5 kg per capita and has turned aquaculture into the fastest-growing animal protein food-production sector.¹ In the next decade, fish aquaculture is expected to keep growing steadily, with an estimated 14.5% increase in production by 2030, by which time it is

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Reviews in Aquaculture* published by John Wiley & Sons Australia, Ltd.

predicted that 62% of all seafood consumed will be farm raised.^{1,2} Whilst aquaculture production is projected to continue growing on all continents, Asia is expected to account for the biggest growth (at 19.2%), with Europe and North America among the lowest (6.6% and 6.8%, respectively). Aquaculture in places like Northern Europe, North America, and Chile, unable to compete in volume, will continue to focus on 'premium' products like Atlantic salmon (*Salmo salar*).

The marine fish aquaculture industry in its current form, and especially Atlantic salmon aquaculture, is based primarily on sea cage production within sheltered, fjordic sea lochs with restricted water exchange. Countries such as Scotland, Chile and Norway, have a geography that benefits from an abundance of these fjordic enclosures, but they are less common in other countries. In recent years, countries including Scotland, Ireland, Norway, Spain, Italy, USA and Australia have invested in moving cages to locations further from the coast,³⁻⁵ known as offshore aquaculture. Initially, 'offshore' mainly referred to activities located in open waters kilometres from the coast, the so called open-ocean aquaculture. More recently, the term 'offshore aquaculture' has been used in other contexts. For example, Lester et al.⁶ defined it as farming beyond the nearshore and inshore coastal zone, where waters are typically deeper than 20 m. However, no consensus has yet been achieved between different disciplines.⁴ Likewise, different interpretations of the term 'offshore' are used for aquaculture governance purposes. Regional and national regulations do not use a common definition and often the term is not even covered in the regulations.⁷ The lack of an agreed definition of 'offshore aquaculture' has been complicated further by the emergence of other terms that mean roughly the same. The term 'moving offshore' is sometimes used to describe the transition of aquaculture from sheltered to more exposed areas, which emphasises the idea that aquaculture is moving towards the open-ocean (i.e. areas beyond the continental shelf) but not quite reaching it. 'Exposed aquaculture' (as opposed to 'sheltered aquaculture') is also used in a very similar context.

For the purpose of this review, 'offshore aquaculture' will refer to farming in generally remote locations that are exposed (have little shelter) and display high energy currents and waves comparable to those of the open-ocean but are located relatively close to the coast. Due to the high energy, these farms require specialised equipment and practices (e.g. longer and stronger moorings).⁸ Therefore, this review focuses on coastal offshore aquaculture and not on open-ocean aquaculture but in many aspects it will also be relevant for the latter. Differences between 'nearshore', 'offshore' and 'open-water' farms will be pointed out when relevant.

Restricted water exchange can result in a reduction in cage space: temperature and dissolved oxygen gradients effectively limit the space that fish utilise within a cage, increasing fish density and health risks.⁹ Health risks and mass mortalities resulting from harmful algal blooms (HABs) (e.g. Atlantic salmon mortalities in the Los Lagos, the Aysén and the Magallanes regions in Chile in 2018¹⁰) can be particularly acute in restricted water exchange environments, as they can promote conditions for their proliferation.^{11,12}

Other potential benefits of offshore aquaculture relate to the control of fish parasites. The proliferation of parasites is one of the most serious threats to the aquaculture industry.^{13,14} Sea cages with high fish densities offer an ideal habitat for parasites to thrive and reproduce. Amoebic gill disease (AGD), caused by the amphizoid protozoan amoeba *Neoparamoeba perurans*, and sea lice (mainly *Lepeophtheirus salmonis* and *Caligus elongates* in Northern Europe) infestations occur rapidly, cannot be predicted reliably, and cannot be completely palliated with current anti-parasite treatments.^{15,16} The infection of fish by both parasites results in weakening of the immune system, poor welfare and can lead to death. Parasite control is made harder when several farms occupy the same region, such as the same fjordic enclosure, particularly if farms from different companies fail to coordinate their anti-parasite treatments.^{17,18} There is a clear potential to reduce parasite pressure by placing cages far from existing cages in more open and dispersive environments.

The current lack of development of offshore aquaculture is attributable to many factors. Moving further offshore incurs extra transport costs, leading to higher operation and servicing costs, which in turn need to be compensated by performance benefits of the cultured species in the offshore location. There is uncertainty in criteria choice for site selection, how to use technology that has been designed for nearshore farms in offshore farms, and which environmental conditions can each species of fish cope with. Nonetheless, research in these topics is very active.¹⁹⁻²¹ Other issues relate to onsite operations that need to be carried out regularly and which may not be possible offshore due to bad weather and adverse conditions.²² These issues create uncertainty, and investment in offshore farms is, therefore, still low. To overcome this, the industry needs to understand the tolerance of each target species to the relevant environmental factors (e.g. current speed and temperature) and select sites accordingly. Further issues are related to licencing,^{23,24} including concerns regarding socio-economic impacts, impact on marine wildlife, visual impact and competition for space.

Open-ocean aquaculture has been carried out for decades in countries like Hawaii and Australia, to produce species like cobia (*Rachycentron canadum*).²⁵ For other species such as Atlantic salmon, the concept of offshore aquaculture has gained momentum in recent years, with expected benefits lacking detailed science-based evidence.^{21,26} However, recent research provides a base upon which this can now be revisited. The objective of this document is, therefore, to review new evidence relating to offshore aquaculture, focussing on European Atlantic salmon production as a case study. The following expectations will be evaluated:

- Dispersive environments and greater separation between farms will reduce the pressure of sea lice via reducing retention and exchange of lice between sites.²⁶
- Offshore environments will be more dispersive of wastes and chemical treatments,²⁷ leading to increased dilution and reduced negative impact. This would improve the production environment and lower the cost of environmental monitoring, and it may result in higher carrying capacities, justifying larger farms.²⁸

- Offshore environments will be less likely to be impacted by HABs, since these proliferate more easily in the 'incubator' of a restricted exchange sea loch.²⁹
- Salmon health and welfare are likely to be impacted by more exposed environments and unpredictable events (i.e. storms, thermal gradients, fluctuations in temperature, feeding restriction during storms).³⁰ For example, gill health will likely be affected positively by offshore environments due to increased oxygen and water exchange but negatively by higher salinity.¹⁶

The following sections provide a state-of-the-art review of knowledge to assess the above claims. Knowledge gaps, where further research is needed, are also identified.

2 | OCEANOGRAPHY OF OFFSHORE SITES

2.1 | Differing physical environments

The lack of a consistent definition of the term 'offshore' in an aquaculture context was highlighted above. The picture with respect to physical characteristics is not straightforward, and it is important to recognise that exposed environments are not always more energetic than more sheltered and constrained coastal sites. Tidal flows, in particular, are greatest where they are most constricted. In the complex and often fjordic environments that typically host marine aquaculture, there exists a continuum of oceanographic conditions, varying according to the relative importance of different influences and processes (e.g. in Scotland³¹ or Norway³²). For example, the fjordic coastline of western Scotland includes: (i) constrained sea lochs (fjords), frequently heavily stratified, dominated by freshwater dynamics and restricted exchange through narrows and across sills^{33,34}; (ii) tidally well-mixed regions characterised by unstratified, highly energetic and stirred flows^{35,36}; and (iii) open shelf regions less constrained than those above and characterised by seasonal development and breakdown of stratification (e.g. Gillibrand et al.³⁷). The last two environments could be classified as offshore depending on the chosen metric. Many farm sites are likely to experience transitional or mixed physical conditions in that they can experience a variety of dynamics, the dominance of which varies in response to meteorological, spring-neap and seasonal forcing.

2.2 | Physical conditions sought by offshore expansion

The hypothesised physical benefits of moving aquaculture to offshore locations include more space to expand farm operations and more dispersive environments. With strategic planning, these conditions can be found at close proximity to coastlines, reducing operational costs.

Dispersion (whether of treatment chemicals, wastes or sea lice and HABs) is complex and hence difficult to evaluate. It results from dynamic stretching, shearing and stirring by currents both vertically and horizontally.³⁸ If waste material is released from a farm site, its initial dilution depends on the volume of the water that receives it. This is effectively increased by rapid flow past the site and by vertical mixing (if the farm is in a surface mixed layer, the material will rapidly mix throughout this layer). In strongly stratified systems, initial dispersion of material may be vertically restricted and may even occur as a sub-surface layer.³⁹ Whether initial dilution is greater in more open/offshore sites depend on the nature of the sites concerned. Whilst reduced freshwater influence or increased stirring by wind and waves means less stratification and potentially greater vertical dilution, typical current speeds may be weaker and hinder dilution.

In unconstrained environments, horizontal dispersion becomes more effective with increased timespan and scale because, as the material being dispersed increases in extent, larger eddies and motions contribute to this process.⁴⁰ It is here that the greatest dispersive benefits of more open, offshore sites are expected. In constrained coastal environments, scales of motion are capped by the proximity of boundaries, so whilst initial dispersion may be rapid, the increase with scale is less than would be expected without constraints. An extreme example of this would be in an enclosed inlet or fjord where mixing can fill the water body and subsequent dilution results only from the limited exchanges with adjoining water bodies.

2.3 | Role of physical modelling

Relatively simple physical models have often been used in aquaculture, for instance dispersion models based on mixing into a receiving volume of water,⁴¹ or box models that represent the external exchanges of an enclosed body of water.^{42,43} Simple models have benefits from a regulatory perspective in that they can be applied consistently in a relatively prescriptive manner.^{44,45} Hydrodynamic models, in contrast, provide a fuller description of the host environment by simulating three-dimensional flow processes. As such, they provide an important tool for identifying and evaluating potential sites for offshore aquaculture. Model-based knowledge of the environmental conditions over a large area facilitates intelligent, targeted site selection. Simulated local dynamics, such as tides, wind-driven flows, freshwater layers and local mixing processes, should be used in conjunction with in-situ observational data to validate the simulation quality and ensure that a model adequately captures the site conditions. Models can also then inform regional studies of interaction or connectivity between farms, for instance in the dispersal of sea lice and other pathogens that can infect finfish.⁴⁶ Oceanographic and hydrodynamic modelling applications for the simulation of coastal and open waters are now well developed. A range of tools is available to predict spatial and temporal variability in currents, temperature and salinity (notably, the Finite-Volume Coastal Ocean Model FVCOM,^{47,48} WeStCOMS-FVCOM⁴⁹ and FVCOM-SWAN wave-current model⁵⁰), and to generate long term 'climatological'

scenarios.⁵¹ These models enable determination of areas with suitable conditions, the risk of exceeding operational thresholds, and prediction of future scenarios.

The multi-scale requirements of aquaculture modelling are most cleanly handled by unstructured grid models, where the environment is represented on a variable-resolution mesh, which allows enhanced resolution in areas of constrained or complex environmental factors or close to a site of interest. Fine-scale local modelling can then be seamlessly coupled to regional dynamics. Such models have been developed for a number of key aquaculture regions: all over the North Atlantic,⁵² Norway,^{53,54} Canada,⁵⁵ Scotland,⁴⁹ also in Chile⁵⁶ and Tasmania.⁵⁷ It is important to recognise the shortcomings of hydrodynamic models, however. Especially challenging environments are those where there is dependence of larger scale flows on small-scale processes that are parametrised rather than explicitly represented. Fjordic environments where aquaculture proliferates are just such environments in view of the key role of mixing and freshwater dynamics in governing their behaviour. Modelling the physical complexity of the coastal environment, where most aquaculture farms are currently located, therefore, requires frequent enhancements in horizontal and vertical resolution to improve the accuracy in predicting the spread of sea lice, diseases, wastes and the environmental footprint of a farm. Operational coastal ocean physical models now resolve the coastal environment at sub-kilometre scales. For example, the Norwegian Met Office recently upgraded their forecasting Regional Ocean Modelling System (ROMS) model, NorKyst, from a resolution of 2.4 km to 800 m,³² and the Scottish Association for Marine Science (SAMS) West Scotland Coastal Ocean Modelling System (WeStCOMS2; <https://www.sams.ac.uk/facilities/thredds/>)⁴⁹ has been enhanced with horizontal resolutions locally as low as ~100 m.

Recent adaptations to fine-scale hydrodynamic modelling have enabled investigation of interactions between human-made static structures and the ocean, such as drag forces, alterations to local flow regimes,^{58,59} and physical stresses that may lead to structural failure.²¹ Adaptation of fine-scale models to study how sea pens interact with high energy waves and currents has been carried out in a small number of cases, based upon idealised flows.^{60,61} Understanding these interactions in realistic flows is essential to select the most appropriate location for any offshore structures and farms.⁶² Models resolving aquaculture sites at very high resolution (~<30 m) also demonstrate that cage effects should be considered in aquaculture environmental interactions as they directly impact dispersal simulations and the concentrations of effluents in both the near and far field.⁶³ Indeed, sub-metre scale non-hydrostatic simulations of aquaculture cages suggest that the impact of increased drag acts to increase the local deposition footprint, both increasing maxima and volume average concentrations.⁶⁴ This impact is dependent on local oceanography and will likely vary between inshore and offshore environments. For example, the extension of wake downstream of a cage depends directly on current intensity, with larger extensions associated with higher current velocities.⁶⁰ Field data have shown that current patterns, oxygen levels, fish behaviour and

vertical exchange, relevant to predict fall rates of faecal and feed material and a cage's material footprint, are strongly influenced by the strength of stratification.⁶⁵ Therefore, it is important that modelling tools used to assess the suitability of potential offshore aquaculture sites can adequately resolve pycnocline dynamics, which are likely to be seasonal and weaker than the more traditional freshwater influenced fjordic and nearshore environments.

Modelling is also important for assessing environmental interactions and connectivity between farm developments. In particular, tracing the dispersal of waste materials, water-borne parasites, pathogens and HABs, both to and from sites of interest. Models can be used to predict the level of risk that may affect a new or existing aquaculture development, informing planning decisions and allowing for effective husbandry and prophylactic measures. In the case of parasites and pathogens, for management and control purposes it is important to understand the level of population 'connectivity' between networks of sites^{18,66} and the likely spatial extent of larval spread. Larval behaviour adds additional complexity, as larvae cannot be depicted simply as passively dispersing particles within a reliable management tool.⁶⁷⁻⁶⁹ For waste materials, the location and intensity of the seabed footprint has direct implications for benthic fauna,^{28,70,71} in addition to oxygen availability in the overlying water. Benthic impacts are subject to direct regulation in many salmon producing areas.^{10,44,45,72} For HABs, understanding the biology of the different harmful species and genera, as well as the oceanographic features of the area near the site of interest, is of crucial importance for effective monitoring and prediction.⁷³ Approaches used to model impacts in coastal waters appear to be broadly applicable in more exposed locations.

3 | IMPACTS OF OFFSHORE AQUACULTURE ON FISH HEALTH AND WELFARE

Offshore conditions will affect farmed fish both directly and indirectly. Strong currents and relatively frequent storms can change the behaviour of the fish and may result in health and welfare benefits or detriments. Other factors such as sea lice and AGD prevalence are indirect consequences of the location.

3.1 | Direct effects of offshore locations on farmed fish health and welfare

3.1.1 | Overview

Whilst wild Atlantic salmon are resilient animals capable of survival in extreme conditions,⁷⁴ captivity in cages limit their ability to avoid exposure to unfavourable conditions. Research can give insights into how Atlantic salmon can cope and adapt to the high energy currents, strong waves, stratified waters, etc. characteristic of an offshore farm. Unpredictable events, like food deprivation due to bad

weather, preventing fish farmers from carrying out their husbandry duties in offshore sites, would also have a negative impact on farmed fish.

The offshore environment is harsher and weaker animals will likely die more easily. Hence, when comparing the welfare of animals in offshore and nearshore farms, fish in offshore farms may present better operational welfare indicator (OWI) scores than fish in nearshore farms. However, such observations may be biased by fish with deformities, cataracts, injuries, etc. being more likely to die in offshore, thus often being counted as mortalities and not as low OWI scores.

3.1.2 | Currents

Atlantic salmon are fast, long-distance swimmers with high aerobic capacities that can achieve extremely long migrations,^{75,76} and therefore, can maintain high physical performance over long periods. However, during these migrations they have the option to pace themselves and to choose when and where they travel, taking advantage of currents that aid in their movement and choosing the depth that opposes less resistance to their advance.^{75,77} In captivity, these choices are very limited, and fish must swim at speeds dictated by the farm environment. Depending on the fish species and the current speeds, this forced swimming for long periods at a high speed can become a legitimate welfare concern.^{30,78} Resultant high energy expenditure can also lead to a decrease in production, as part of the energy that could be directed to fish growth is diverted to exercise.⁷⁹ Contrary to this, moderate water velocity (0.36–0.63 body lengths per second, BL per s) has been shown to be beneficial for growth, increasing growth rate for Atlantic salmon of 894 ± 4.6 g during their entire on-growing stage,⁸⁰ likely involving an increase in feed intake and energy conversion efficiency.⁸¹ In recirculation aquaculture systems (RAS) this optimal water velocity for growth has been suggested to be 1 BL per s.⁸² Higher current speeds up to 2.5 BL per s increase growth, muscle fibre size, insulin-like growth factor 1 expression and several metabolic pathways, but at the expense of fish welfare, which suffered from a higher incidence of inflammation and skin and pelvic lesions.⁸²

Given the environmental conditions of offshore locations, it is likely that the maximum current speed and duration may exceed the physical capabilities of Atlantic salmon in some locations, leading to detrimental effects on physiological function and welfare.⁸³ However, as observed in sea cages, fish circle around the cages in low currents but when these exceed around 45 cm/s, they all swim into the current.^{84,85} Low frequency and duration exposure to this high-speed current may improve fish welfare, allowing them to behave as they would during their foraging migrations. Benefits of aerobic swimming for fish and applications under farming conditions have been covered recently in the review of McKenzie et al.⁸⁶

Experiments using a swim tunnel determined that Atlantic salmon post-smolts of around 43 cm (850 g) were capable of a critical

swimming speed (Ucrit) of 97.2 cm/s on average when tested individually (not as a group).⁷⁶ Fish were then tested for endurance (i.e. sustained swimming capacity) for 4 h and only a fraction of the fish (1/12) could sustain this speed for the whole duration. Conversely, all fish coped with a speed of 78 cm/s for the full four hours. Also tested individually in a similar setup, Atlantic salmon post-smolts of around 29.2 cm (300 g) achieved a Ucrit of 65.5 cm/s.⁸³ Then, when tested in a bigger swimming tunnel as groups of fish of around 19.6 cm (80 g, groups of 28 fish), 29.0 cm (289 g, groups of 16 to 17) or 51.9 cm (1750 g, groups of 3 to 4), they achieved average Ucrits of 80.6, 90.9 and 99.5 cm/s, respectively. This showed a significant increase in performance when swimming as a group (shown by the 289–300 g groups) due to a reduction in the overall effect of drag. Big post-smolts of around 63.5 cm (3.4 kg) could withstand even higher currents speeds but would become fatigued above 125 cm/s.⁸⁵ Importantly, smolts are generally transferred to seawater at a weight of around 300g, a size, which should not be exposed to maximum currents over 80.6 cm/s. Their sustained swimming capacity is likely to be around 80% of that value,^{76,83,87} suggesting that prolonged exposure to current speeds higher than around 64.48 cm/s should be avoided, although this remains to be tested. Alternatively, current speed reducing technology such as skirts or double nets could be deployed.⁸⁸

The period of adaptation to seawater after smoltification is a particularly critical time for salmonids, partly because the rate of gas exchange may be compromised when osmoregulation is prioritised, limiting the respiratory function of the gills and the physical capacity of the fish to cope with intense exercise.^{75,89} This further suggests that to avoid mortalities at deployment, smolts might need to be transferred to offshore cages at a bigger size or to be first transferred to seawater in low energy sites. The deployment size at which they can be transferred to an offshore cage will depend on the oceanographic conditions, which will require study on a farm-to-farm basis.

Another consideration regarding current velocities is the swimming ability of other species in polyculture with Atlantic salmon. These are mainly the cleaner fish lumpfish and ballan wrasse. Lumpfish, are not the most adept of swimmers, having difficulty swimming against currents of more than 1.3 to 1.7 BL/s (approximately 24.7 to 32.3 cm/s in 300 g lumpfish)⁹⁰ and this can have negative consequences for their welfare.⁹¹ When attached to an (ideal) surface using their sucker, they can resist currents of between 70 and 110 cm/s, with bigger fish resisting less, but can only remain attached for around 1 to 8 min, and do not consciously resort to attaching to surfaces when they feel unable to swim against the current. Similar results were reported for ballan wrasse, that demonstrated swimming speeds of up to 27.3 cm/s, and a very strong reliance on warm temperatures that are unlikely to be found where Atlantic salmon are produced.⁹² With temperatures below 25°C, ballan wrasse were sluggish and reluctant to swim for prolonged periods of time. Therefore, lumpfish and ballan wrasse are less suited to be used in offshore farms.^{78,92} Hence, many offshore farms will not be able to benefit from the use of

cleaner fish. However, some offshore sites in Faroe Islands do deploy lumpfish in salmon sea cages with good survival rates by offering sheltered areas that protect them during storms and high waves and currents.⁹³

When studying the potential locations for an offshore farm, and when monitoring an existing one, not only the average current speeds are of interest.⁷⁸ The maximum magnitude, as well as the duration and frequency of the currents are largely what determines the suitability of a farm for a species of fish at a specific size.

3.1.3 | Waves

The existing site classification for aquaculture⁹⁴ was devised for nearshore farms where sites with significant wave height of greater than 3 m, associated peak period above 5.3 s or mid-current speed greater than 1.5 m/s are classified as extreme exposure sites. It is expected that for most offshore sites, one or all of these conditions will apply during normal operation and during storm conditions, waves in offshore locations can exceed several metres. Numerical modelling and physical testing can address the need for further research to understand the influence of these dynamic conditions on the structural components of the farm as well as fish behaviour.

Offshore fish farmers have noted that waves can submerge feed barges (floating structures the size of small apartments with living commodities). In such circumstances, fish farmers must leave the farms for safety. These large waves may cause salmon to collide with each other and the cage netting, which has the potential of causing injuries, stress and discomfort.⁹⁵ However, provided that they have sufficient depth range in a cage, Atlantic salmon can move to deeper waters during a storm, as the power of waves decreases in the water column. Contrary to this, an acoustic telemetry study on fish movement inside an Atlantic salmon sea cage detected no changes in behaviour (distance from the centre of the cage [m], depth [m], velocity [m/s], and turning angle [°]) during a storm event.⁹⁶ Fish behaviour during a storm is complex and depends on the power and frequency of the waves, as well as the current speed and time of day. The objective of this behaviour is to minimise collision risk.⁹⁷ However, due to cage deformations and the unpredictability of these movements, fish may still be at risk.⁹⁸

Atlantic salmon are physostomes; they need to surface to fill their swimming bladders with air to maintain buoyancy. Whilst they have been shown to cope for 17 days without access to air, their buoyancy decreased and their swimming speed increased, and they schooled more tightly.⁹⁹ With waves, currents and a deforming cage, and fish that struggle to maintain buoyancy, swim faster and aggregate tightly, the risk of collision during a long storm could increase. Not surprisingly, reports of significant fish mortalities and escapes are common after a storm, often as a result of cage damage (e.g. Cooke's farm in Newfoundland¹⁰⁰ and Bakkafröst's in the Faroe Islands in March 2020,¹⁰¹ and Mowi's Argyll fish farm in August 2020¹⁰²).

3.1.4 | Oxygen

Sufficient oxygen is an important factor for the survival of cultured fish, which relies on water currents to flush old water that carry waste and is partly depleted of oxygen. Oxygen can be a constraint in shallow waters, estuarine and sea loch areas with poor water renewal and few currents. In general, stronger currents provide better oxygenation inside cages.⁹⁵ Algal blooms can also restrict oxygen availability.¹⁰³

In case of hypoxia (45–55% dissolved oxygen), Atlantic salmon lower their swimming speed, with pronounced effects on the swimming capacity of small (around 26 cm in length, decreasing Ucrit from 91 ± 0.7 to 70 ± 0.7 cm/s) medium-sized (around 46 cm, Ucrit from 98 ± 3.4 to 89 ± 4.9 cm/s) and large fish (around 64 cm, Ucrit from ≥ 124 to 101 cm/s), being these differences significant at all three sizes.¹⁰⁴ Atlantic salmon can avoid hypoxic water layers when more oxygenated layers exist. Fish distribution in the vertical column was shown to be determined first by salinity, second by temperature and third by dissolved oxygen.¹⁰⁵ Intermittent hypoxia has also been shown to reduce Atlantic salmon appetite and growth, and compromise their innate immune system,¹⁰⁶ which is consistent with an accelerated the progression of AGD.¹⁰⁷

The size of the fish cage is also relevant. Oldham et al.¹⁰⁸ showed that oxygen becomes lower with increasing cage sizes (168 m vs. 240 m). Burke et al.¹⁰⁹ showed dissolved oxygen levels of 8.24 ± 0.29 mg/L going into 32 m in diameter cages stocked at 16.4 kg/m³ with Atlantic salmon. At the other end of the cage dissolved oxygen levels of 5.38 ± 0.34 mg/L were measured. Furthermore, the oxygen concentration inside a cage could be decreased by the deployment of lice shielding skirts, due to the reduction in current speeds.⁸⁸

Future studies will need to address how the water flow changes through biomasses of 1000–10,000 tonnes of fish in a cage and the consequences on oxygenation. Hypoxic deep-water upwellings and oxygen minimum zones could also be a problem that needs to be studied in order to predict, locate and avoid them.^{110,111}

3.1.5 | Stratification

Due to complex oceanography in some offshore areas, the water column can show (permanent/seasonal) stratification in temperature, salinity, dissolved oxygen, and current velocity.^{33,34} When this happens, it allows more choice for fish in offshore cages than they would have nearshore (moreover, offshore cages tend to be much deeper; 40–50 m, as opposed to 20–25 in nearshore farms). Temperature (and temperature choice) can be a crucial determinant of fish survival upon pathogen infection or under stress.^{112,113} Fish with the potential to move to different water temperatures can modulate their immune system depending on their physiological status, effectively having the ability to express behavioural fever on themselves and maximise their survival in response to an infection. It is possible that Atlantic salmon fight pathogenic infections by seeking higher temperatures, but it has not been investigated in response

to bacterial infections, AGD or sea lice. If this was the case, their survival from infection could be higher in offshore locations. Fish can also choose different temperatures to cope with stressors or disease.^{112,113} Daily thermal cycles related to diurnal rhythms are also common in fish. Offshore conditions might, therefore, offer them more opportunities to better express this natural behaviour than in less stratified systems in shallower coastal areas.

3.2 | Direct effects of offshore locations on farmed fish health

3.2.1 | Sea lice risk. Will offshore environments reduce sea lice pressure?

Sea lice are parasitic copepods (crustaceans) that infect a wide diversity of hosts by feeding on their flesh or secretions.¹¹⁴ The most relevant to the aquaculture industry are the sea lice that specialise in feeding on mucus and skin of finfish. In Northern Europe, these are mainly *Lepeophtheirus salmonis* and *Caligus elongatus*, and other species of the same genera. If left uncontrolled, infestations by this type of sea lice reach great numbers in marine fish cages, leading to skin lesions, stress and weight loss, opening gateways for secondary infections and, ultimately, high disease and mortality.^{115,116}

Anti-parasite chemotherapeutant treatments can decrease sea lice infestations but can have a detrimental impact on the environment.^{15,117,118} Their use can lead to treatment resistant parasites, a phenomenon, which has been reported for all chemical treatments currently in use.¹¹⁹ Initially, the industry met this resistance with increased dosages,¹¹⁹⁻¹²¹ potentially damaging not only the environment but also the fish, as they do not develop resistance at the same pace as the parasites.¹²² In fact, the cost of sea lice control in the United Kingdom was highest across the salmon industry when last compared in 2009, £0.17 (0.31 US\$) per kg versus £0.13 (0.24 US\$) per kg in Norway in 2006.¹⁵ Other control measures, including mechanical and biological approaches, have become common. Whilst the efficacy of mechanical and thermal anti-parasite treatments like Hydrolicer and Thermolicer is generally high, the abrasiveness of the procedure raises concerns about fish welfare and health, leading to scale loss, gill bleeding, wounds, pain and death.¹²³⁻¹²⁵ Sviland Walde et al.¹²⁶ determined that mortality after mechanical and thermal treatment was several times higher (median delta mortality 6.3 and 5.4 times higher, respectively) than after chemical treatments. Further, the immunodepression caused by such treatments risk making the fish more vulnerable to re-infection.¹²⁴ Cleaner fish have been confirmed to feed on sea lice and, though they offer a greener option to the other treatments, their beneficial effects remain largely unproven. Farms that use lumpfish (*Cyclopterus lumpus*), ballan wrasse (*Labrus bergylta*) or other cleaner fish species still rely heavily on chemical and mechanical anti-parasite treatments and continue to report high sea lice prevalence.¹²⁷ Furthermore, both lumpfish^{128,129} and ballan wrasse^{130,131} have been identified as vectors for several Atlantic salmon pathogens and their translocation

and use in aquaculture carry a genetic risk (i.e. interbreeding and hybridisation) to wild cleaner fish populations in the event of escapes.¹³²⁻¹³⁴ Overall, when accounting for the total cost of sea lice control treatments, decreased fish growth, administering more feed, and sea lice related mortality, it is expected that up to 10% of the industry's revenue is lost.^{14,15,135} Since it is the costliest issue to the industry, thousands of studies have been published on the topic in the last decade. Nonetheless, in-situ studies of sea lice prevalence with offshore farms remain anecdotal in the literature.

Biology and life cycle of sea lice

Focussing on *Lepeophtheirus salmonis* and *Caligus elongatus*, both species go through non-infective planktonic nauplius I and II stages, before becoming infective in their planktonic copepodid stages, when they actively seek to infect a host.^{136,137} After attaching to this host, they develop into chalimus, followed by their adult stage. Egged females are known as gravids.

During their nauplius and copepodid stages, sea lice are carried away from their point of origin, which is likely to be a salmonid farm.^{138,139} By 2017, farmed salmonids accounted for 99.6% of available hosts, and produced 99.1% of adult female salmon lice and 97.6% of mated (ovigerous) adult female salmon lice in Norwegian coastal waters.¹³⁴ The duration of the nauplius stages is dependent on temperature. Tully¹⁴⁰ estimated them to last for 223.3 h at 5°C, 87.4 h at 10°C, and 50.0 h at 15°C in the case of *L. salmonis*. For *Caligus* spp. they last 60–70 h at 10°C.¹⁴¹ Development into copepodids is similarly affected by temperature. Temperatures of 3°C or lower completely inhibit this development in *L. salmonis* as 100% of nauplii died in the process.¹⁴² *C. elongatus*, survival from hatching to the copepodid decreased from 90% at 15°C to 60% at 5°C.¹⁴⁰ On development into copepodids, lice are still nonfeeding but become positively phototactic, which increases the chances of finding a host during a crossover in the vertical water column, as salmonids display the opposite behaviour, migrating downwards at daybreak, as shown for *L. salmonis*.¹⁴³ Copepodids of *L. salmonis* are most abundant in the top four metres of the water column,¹³⁹ and therefore, infest salmon residing close to the surface at much higher rates than fish forced to swim deeper down or protected by the surface water.¹⁴⁴ The process of seeking a host is energetically demanding and, therefore, after moulting from nauplius into copepodid, lice can only survive as free swimmers for a few (temperature dependent) days.¹⁴⁵ Copepodids of *L. salmonis* can last 2 up to 8 days at 15°C as free swimmers¹⁴⁶ and Hamre et al.¹⁴⁷ showed that development of copepodids into adults is severely compromised at 3 and 24°C, whilst it proceeds normally at temperatures between 6 and 21°C. For *Caligus* spp., copepodid survival can reach 50 h at 13°C.¹⁴¹

As a result of the prolonged nauplius stage, it has often been assumed that sea lice are unlikely to infect fish from their farm of origin.^{146,148} Recent work has shown that vertical movements could, however, allow lice to remain close to their natal farm.¹⁴⁹ Given the right temperature and water current conditions, sea lice will typically travel 10–50 km during their free-swimming stages (nauplius and copepodid),¹³⁹ which is more than enough to reach other farms

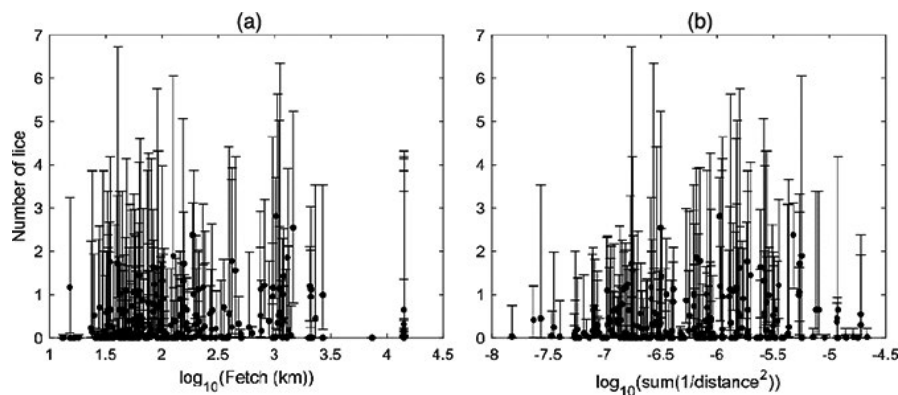


FIGURE 1 Relationship of observed site sea lice count per fish to (a) exposure (higher fetch = more exposure) and (b) isolation (higher absolute value of sum of inverse-squared distances = more isolation)

and wild salmonid populations. Even offshore farms can receive sea lice from nearshore farms,⁶⁷ and vice-versa. In fact, a recent study showed that sea lice spreading could occur over much larger distances than previously thought, with specific strains of resistant sea lice found in Iceland, where chemical treatments are forbidden.⁵² A major difference between *L. salmonis* and *Caligus* spp. is that, whilst *L. salmonis* mainly infects salmonids, *Caligus* spp. are less host specific.^{150,151} This means that *Caligus* species are able to find a host more easily, being able to form reservoirs using both migrating and non-migrating fish species, and, therefore, their spread is not constrained by seasonal fluctuations of salmonids, although temperature fluctuations remain important.

Sea lice proliferation is strongly modulated by environmental conditions.¹⁵² Temperature, besides being a major controller of the duration of their different life stages, also directly affects their infectivity and survival. With *L. salmonis*, a higher number of copepodids fail to successfully attach to a host at lower temperatures.^{142,153} Atlantic salmon presented 0.62 ± 0.12 lice-fish⁻¹ at 5°C (2.1% \pm 0.4% infestation success), 16.0 ± 0.6 lice-fish⁻¹ at 10°C (53.2% \pm 2.3% infestation success) and 13.3 ± 0.6 lice-fish⁻¹ at 20°C (41.6% \pm 2.0% infestation success),¹⁴² agreeing with an increase in the copepodid's capacity to infect at between 5 and 15°C reported by Skern-Mauritzen et al.¹⁵⁴ and an optimal of 10°C.¹⁵⁵ Hatching is also severely affected by temperature. As shown by Samsing et al.,¹⁴² 100% of *L. salmonis* eggs hatched at 20 and 15°C, 87% at 10°C, 90% at 7°C, 85% at 5°C, and 28% at 3°C. Importantly, time to hatching increased at lower temperatures (20.8 ± 1.5 days at 3°C compared to 1.8 ± 0.1 days at 20°C). Furthermore, the number of eggs per gravid was significantly lower at the lowest (3°C) and highest tested temperatures (20°C) than at 5, 7, 10 or 15°C. Salinity also has a strong effect, with low salinities (<12‰) preventing survival of adults and salinities below <30‰ partly preventing development of nauplii into the copepodid stage.¹⁵⁰ Bricknell et al.¹⁵⁶ reported that salinities lower than 29‰ severely reduce survival of free-swimming stages (50% survival after 24 h at 29‰, 11 h at 26‰, 8 h at 23‰, 6 h at 19‰, 4 h at 16‰ and >1 h at 12, 9 and 5‰). When given a choice, most copepodids sit in salinities of 34‰¹⁴³ and actively avoid salinities below 27‰.¹⁵⁶ The potential of sea lice to increase their tolerance to freshwater

was reviewed by Groner et al.¹⁵⁷, who concluded that this question cannot be elucidated with the current knowledge.

Sea lice and offshore farms

Ten years since its publication, Kirchoff et al.²⁶ remains the only study to report the impact of sea lice on farmed fish in contrasting inshore and offshore environments. It was carried out in Australia and it used wild Southern bluefin tuna (*Thunnus maccoyii*) that had been caught and grown in sea cages. These tuna were reared in either a 'nearshore' (16 nautical miles from the coast) or an 'offshore' (25 nautical miles from the coast) farm site and their health and performance compared. Besides reporting an overall better growth and health in the offshore site, the study concluded that sea lice prevalence (*Cardicola forsteri* and *Caligus* spp.) was significantly lower offshore. The study reported no *Cardicola forsteri* and a 5% prevalence of *Caligus* spp. offshore, compared to a prevalence of 85% for *Cardicola forsteri* and 55% for *Caligus* spp. nearshore at 6 weeks after transfer. Despite reporting very promising results for the future of offshore farming, the study only considered one nearshore and one offshore farm, sampled at three different timepoints with an *n* of either 10 or 20. More such studies are needed to compare the effects of rearing in nearshore and offshore farms, as results, which likely will vary strongly depending on the farmed species. Interestingly, sea lice infestation in the first Atlantic salmon farm, Ocean Farm 1, appeared after only six weeks of its first fish stocking, despite being located 3 miles off Norway's coast.¹⁵⁸

In Scotland, monthly site lice abundances,¹⁵⁹ and site location data¹⁶⁰ are published online. A proxy for site exposure was obtained in the form of a wave fetch index, measured in km to nearest coastline, summed over 16 fixed directions.¹⁶¹ Site isolation was calculated as the sum of inverse-squared distances to all other sites using MATLAB. Figure 1 shows a scatterplot of median lice abundances against site fetch and isolation, with error bars indicating 10th and 90th percentiles, over 24 months (2018 and 2019) of data. Due to the nature of the data, relevant variables like intensity of anti-parasite treatment or fish size could not be incorporated into the analysis. The results suggest that the most exposed (and more physically isolated) sites have the lowest median number of lice per fish,

suggesting that moving cages further offshore decreases sea lice infestation risk. Interestingly, it is sites with intermediate exposure, which tend to have the highest lice abundances. However, some very exposed and isolated sites can still receive high numbers of sea lice, suggesting that the dynamics of sea lice movement cannot be explained by only these two variables and a more detailed study of the oceanography of each site is required.

The oceanographic complexity of offshore environments, which may present marked layers of water at different current speeds, temperature, oxygen content, and salinity¹⁶²⁻¹⁶⁴ will affect the biology of sea lice, determining their vertical distribution, infectivity, survival, reproduction, and spread. Generally, offshore environments present higher surface salinity, although subject to strong seasonal variation, than their nearshore counterparts.^{10,44,45,72} As a result of the more dispersive environments, the probability of sea lice infecting fish from their farm of origin is very low in offshore farm sites.¹⁶⁵ And since the distance between offshore farms will be generally greater than between nearshore farms, sea lice 'connectivity' among farms will be reduced but it will not be null unless they are very distant (>50 km).¹³⁹ If currents are strong, this may prevent and even negate sea lice attachment.^{166,167} In terms of salinity, nearshore farms that are close to river openings could benefit from the deleterious effects of low salinity to sea lice, provided that they reach concentrations under 30%.¹⁵⁰

3.2.2 | Will offshore environments reduce AGD incidence?

Worldwide, AGD is caused by the protozoan amoeba species *Neoparamoeba perurans*. Economic losses due to AGD-related farmed fish mortality were estimated at £50 million (80 million US\$) in 2011 for Scotland alone,¹³ with reported farm mortalities of up to 70% due to the disease. The parasite infects gills of fish and causes a proliferative response within the gill epithelium. In healthy gills this epithelium layer is thin, allowing efficient exchange of gases, acids, ammonia, ions and water. However, in the case of AGD-infected gills this layer is thickened with inflamed gill tissue and excess production of mucous, causing respiratory problems, thus increasing the diffusion distance in the water-blood barrier¹⁶⁸ (see Figure 2).

The biology, life cycle and natural distribution and reservoirs outside of fish farms of *N. perurans* remain largely unknown.¹⁶⁹ They are free-living, facultative ectoparasites able to quickly replicate asexually. They can be found in four stages depending on the environment or when exposed to chemicals: pseudocyst, trophozoite, cyst and attached to the gill using pseudopods.^{170,171} *N. perurans* host endosymbionts of the flagellate protist family Kinetoplastea. One of these, *Perkinsella* sp., has been shown to be an obligate symbiont of *N. perurans* that lost its flagellum and feeds on the hosts cytoplasm whilst sharing the function of its organelles and the products of crucial kinetoplastid-specific metabolic pathways with the amoeba.¹⁷²

Fish suffering from AGD have shown clinical signs of inanition, respiratory distress and lethargy.¹⁶⁹ In severe and chronic cases, the

hypoxic conditions caused by suffocation have deleterious effects on the liver and heart.^{173,174} Affected Atlantic salmon also showed elevated concentrations of cortisol and lower haematocrit, suggesting stress and a susceptibility to incur further diseases.¹⁷⁵ Proliferative gill disease (PGD) is closely linked to AGD and often the two are not routinely distinguished. In this case, *N. perurans* infestation can be just one component. PGD is a multifactorial disease, resulting from a combination of different bacteria, viruses and parasites that cause proliferative gill inflammation and can affect other organs. Fish suffering from PGD also show respiratory problems and many other health problems.¹⁷⁶

AGD and offshore farms

To date, no comprehensive evaluation of the incidence of AGD in offshore locations has been published. However, Figure 2 confirms the presence of all stages of infection in Atlantic salmon gill samples collected from an offshore farm. Since offshore conditions require fish to exercise more vigorously than in nearshore locations, and AGD may limit aerobic capacity, the effects of AGD could be more severe in offshore farms.

Several apparently contradictory studies on the effects of AGD on gas transfer in gills and metabolic rate of Atlantic salmon have been published.¹⁷⁷⁻¹⁸⁰ These results likely reflect differences in the stage of the disease, with more severe cases resulting in reduced gas transfer, which can be especially harmful in poorly oxygenated water.¹⁶ As a result of this reduction in maximum oxygen uptake due to AGD, the aerobic scope of Atlantic salmon is severely affected (from 406 mg O₂ per kg per h in healthy fish to 203 mg O₂ per kg per h).¹⁷⁵ In turn, high-intensity swimming performance in strong currents is negatively affected (from 3 body lengths per s in healthy fish to 2.5 body lengths per s) and cortisol levels increase during exercise.¹⁷⁵ As a result, AGD-related mortalities due to suffocation in offshore situations where high swimming performance is needed are expected to be more frequent and happen at an earlier disease stage.

A decrease in the number of chloride cells in AGD lesions suggests that the osmoregulatory capacity of affected fish may be compromised,^{168,181,182} reducing their tolerance of high salinities. This could indicate that offshore locations are even more unforgiving for affected fish.

There is still discussion community about the environmental risk factors that promote AGD, but it is generally accepted that high temperature and salinity promote and speed up its development. For example, outbreaks may be more likely to occur after abnormally high temperatures in a region.¹⁶⁹ However, as outbreaks have also been reported at relatively low temperatures of 7°C,^{174,176} it is clear that temperature is not the sole controlling factor.

3.2.3 | Are offshore environments less likely to be impacted by HABs?

Blooms of phytoplankton are primarily natural events¹⁸³ and an important part of the annual cycle of phytoplankton growth, but some

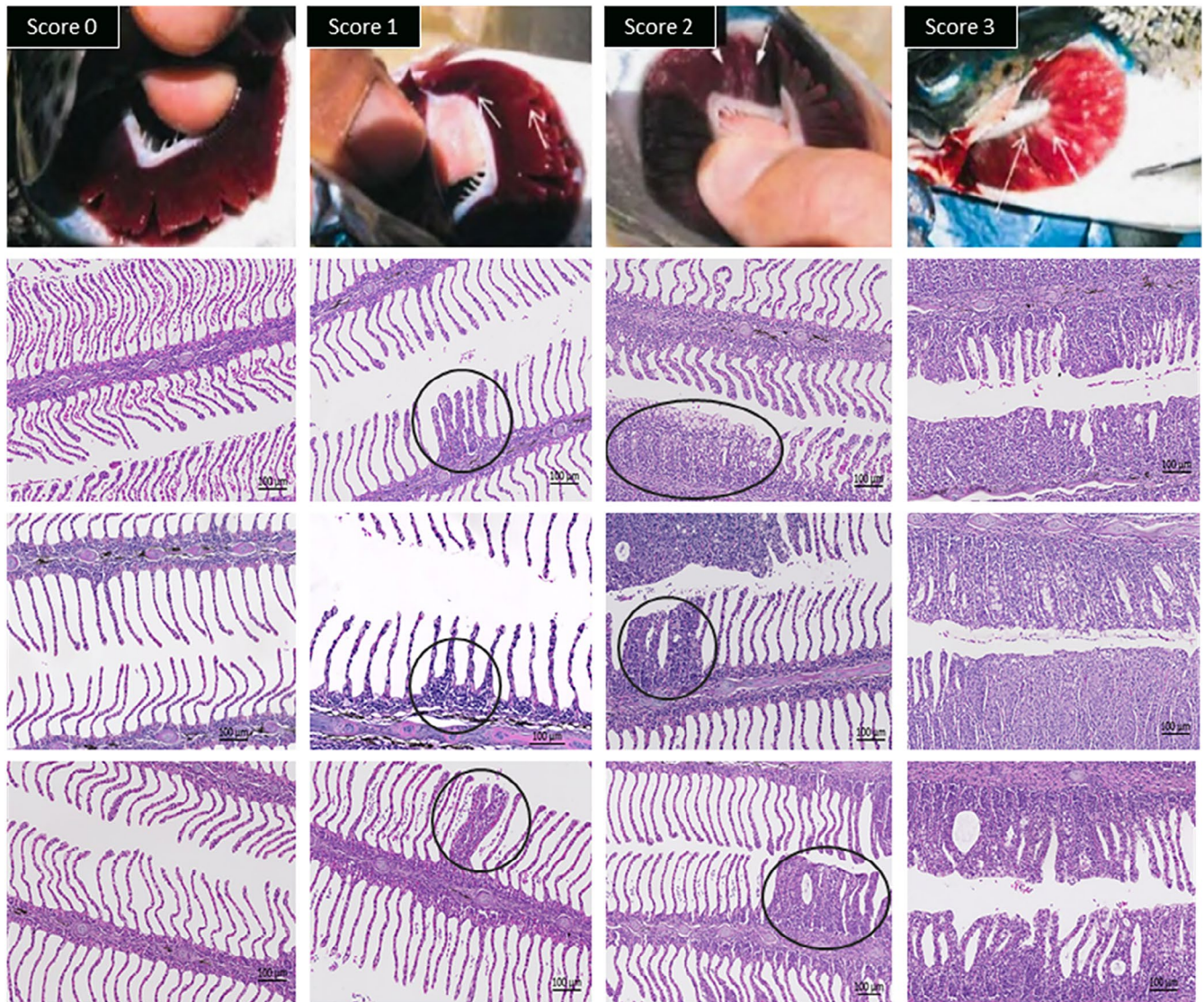


FIGURE 2 Macroscopic (top row) and histological pictures (other rows) of healthy (Score 0; first column) and different stages of progression of amoebic gill disease (AGD) infection (Scores 1–3; second to fourth columns) in gills of Atlantic salmon raised in an offshore farm. White arrows show areas where the AGD infection is more obvious. For histological pictures, gills (second left gill arch) were fixed in 10% formalin, embedded in paraffin wax and, after 2 h in rapid decalcification, 5 μ m sections were stained with routine haematoxylin and eosin. Black circles indicate areas where the AGD infection is more obvious. This figure was adapted from Wilford³⁰⁰

blooms are associated with 'harmful events', ranging from ecosystem disturbance to serious threats to human health.¹⁸⁴ These harmful blooms impact on the human use of ecosystem services such as fish farming.¹⁸⁵

Mortalities of fish associated with harmful algal blooms (HABs)

On a global scale, HABs have had a major economic impact on fish farming¹⁸⁶ and their occurrence has posed a significant impediment to the development of fish farming in some coastal regions.¹⁸⁵ For example, blooms of *Chatonella antiqua* have regularly resulted in large scale mortalities of farmed fish in the Seto inland Sea of Japan,^{183,187} a bloom of the genus *Pseudochatonella* in Chile in 2016 resulted in mass farmed fish mortalities with an estimated value of £593 million

(806.5 million US\$)¹⁸⁸ and a 2019 bloom of *Chrysochromulina lead-beateri* in Norway killed 8 million salmon, total tonnage 14,000, with a direct value of over 850 million NOK.¹⁸⁵

Fish killing HABs can be divided into three lifeform categories, diatoms, dinoflagellates and microflagellates.¹⁸⁹ The siliceous cell walls and spines of some diatoms can harm and kill fish.¹⁹⁰ Dinoflagellate generated biotoxins can also impair the health and cause mortality of fish.¹⁹¹ Microflagellates, are a taxonomically diverse group of small ($\sim 20 \mu$ m) organisms, with various members of the group having been found responsible for fish mortality.¹⁸⁹ If any phytoplankton species reaches sufficiently high density, deoxygenation during bloom senescence can also result in fish kills.¹⁰³

The potential for harm to fish from diatoms is primarily physical in nature. Diatoms typically cause gill-based histological damage in fish and hence species with setae (such as the genus *Chaetoceros*) are most likely to result in mortality.¹⁹² However, mortalities of Atlantic Salmon mediated by other diatom species (without setae) have also been reported, most likely due to gill lesions caused by algal cells.¹⁹³

In Scottish waters, separate fish health incidents related to diatom blooms occurred on the west coast (Loch Torridon) and in the Shetland Islands in June and July 1988¹⁹⁴ when mortalities of farmed fish coincided with the presence of the chain forming diatom *Chaetoceros* spp. The silicoflagellate *Dictyocha speculum* was also present in Shetland.¹⁹⁴ Treasurer et al.¹⁹⁵ reported the occurrence of a mixed bloom of *Chaetoceros wighamii* and an unidentified flagellate during the Loch Torridon incident. Subsequent reported mortalities of farmed fish associated with diatom blooms are rare. However, as diatoms are not routinely monitored by HAB regulatory programmes that focus on shellfish biotoxin producing organisms,^{196,197} and aquaculture companies often consider mortality events commercially confidential, it is likely that many fish health HAB events are not recorded in the scientific literature.

The production of known biotoxins by diatoms is restricted to the genus *Pseudo-nitzschia*.¹⁹⁸⁻²⁰⁰ The causative toxin domoic acid (DA) is primarily a human health problem since its accumulation in molluscan shellfish can cause amnesic shellfish poisoning (ASP). Whilst some studies have indicated a behavioural effect of *Pseudo-nitzschia* produced DA on fish populations,²⁰¹ subsequent work²⁰² by the same authors indicates that this was due to the extremely high concentrations used in laboratory studies and that at ecologically relevant DA concentrations, fish are not behaviourally effected by DA (even though they may contain high concentrations of the toxin that are vectored to seabirds and marine mammals²⁰³). We are unaware of any published reports of fish kills related to blooms of *Pseudo-nitzschia* in northern European waters, but verbal information from fish farmers indicates these events occur. In addition to mortality, diatom blooms may result in sub-lethal impacts. Sub-lethal effects associated with diatom blooms include loss of appetite, lethargy and respiratory distress.¹⁹⁵

The main threat posed to fish from blooms of dinoflagellates is through the production of toxins, and there are well documented examples of farmed and wild fish mortalities from different regions of the world.^{204,205} The dinoflagellate genus *Karenia* contains several species that have been linked fish mortality²⁰⁶ with *Karenia mikimotoi* being of particular importance for the salmon farming regions of Northern Europe.²⁰⁷ *K. mikimotoi* blooms have occurred in Scottish waters in multiple years with a particularly extensive blooms in 2006 extending over most of the country.²⁰⁸ Most recently, a significant *K. mikimotoi* bloom occurred in the Firth of Clyde in 2016.²⁰⁹ This resulted in hypoxic conditions and mass mortalities of marine organisms, but as the areas has a low density of fish farming the impact on aquaculture was low.

Blooms of microflagellates have resulted in extensive fish kills worldwide,²¹⁰ with a recent bloom of the raphidophyte *Heterosigma akishiwo* killing 200,000 salmon in British Columbia in 2018.²¹¹

These organisms have caused a surprisingly small impact on Scottish aquaculture, with the most prominent incidents related to an unidentified flagellate (designated as Flagellate X) that bloomed in Loch Striven and Loch Fyne between 1972 and 1982 and was implicated in three major kills of farmed salmon.²¹²⁻²¹⁵

HABs in offshore locations

The major salmon farming countries: Norway, Chile, Scotland, Canada make use of their fjordic coastline to provide partially sheltered locations for salmon aquaculture. Such restricted exchange environments can in some circumstances promote the environmental conditions needed for HAB events. These blooms can on occasions be related to a supply of anthropogenic nutrients. For example, Gowen et al.¹⁸³ demonstrated the relationship between nitrogen load and red tide frequency in the Seto Inland Sea in Japan, but such anthropogenic nutrient loading conditions are unusual in, typically remote, salmon farming regions. However, whilst a lack of monitoring data prevents full confirmation, Anderson et al.¹⁸⁸ discussed the possibility that both natural and anthropogenic nutrient sources may have exacerbated the massive fish killing harmful bloom in Reloncavi Sound Chile in 2016.

A majority of reported HAB associated fish kills in seawater were located in areas close to the shore, especially when in partially sheltered locations. Whilst this is not surprising, since most aquaculture and monitoring effort occurs in coastal regions, these areas are more likely to exhibit low energy currents and perhaps eutrophic conditions that favour dinoflagellate blooms.²⁹ Greater turbulence also favours the growth of the non-motile diatoms that can be particularly problematic for fish farming.

Open-ocean locations are often where HAB events originate either at offshore cyst beds²¹⁶ or at frontal regions.²¹⁷ These blooms can then be transported advectively.^{49,218} Should they reach coastal waters, physical concentrating mechanism can increase cell density to harmful levels.²¹⁹ Whilst one might, therefore, expect offshore locations to be less impacted by HABs as the physical transport of a HAB might make it a transitory event in an offshore location, the relative lack of monitoring in these locations means that the extent of offshore HABs is poorly quantified, and satellite-based studies have demonstrated offshore HAB events can be geographically extensive.²²⁰ Moreover, local hydrodynamics can sometimes protect fisheries located in coastal waters from HABs. For example, Paterson et al.²²¹ demonstrated a temperature front acting as a barrier at the mouth of Loch Fyne in southwest Scotland, protecting it from the ingress of harmful cells.

Worryingly, HABs risk is expected to increase as a result of climate change,²²²⁻²²⁴ but the specific location and timing of such blooms remains uncertain. Planning where to place farms will need to take into close consideration the physical oceanography of a region, especially the role of seasonal mixing and stratification, the formation of frontal regions and the influence of upwelling areas, as well as the biology of the local phytoplanktonic species. Additionally, jellyfish blooms are also an issue that can cause mass mortalities in fish farms. The damage they inflict is particularly pronounced in the gills of the fish. This topic

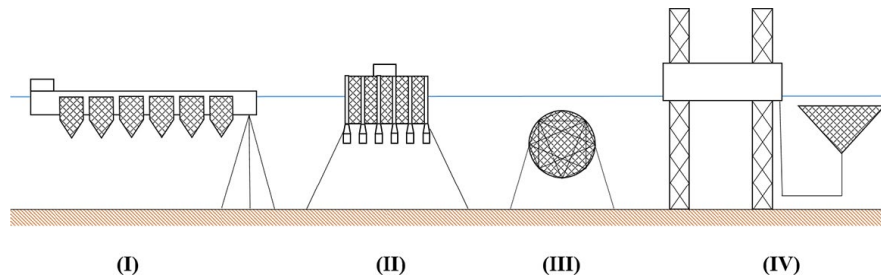


FIGURE 3 Classification of the offshore fish farm units: (I) Ship-shaped - Havfarm²³⁵ (II) Column-stabilised - OceanFarm 1 (Jin, 2021) (III) Circular, submerged - Aquapod²³⁷ and (IV) Self-elevating - Roxel.²³⁸ Categories based on DNV-GL.²³³ Blue line represents sea surface, orange lines represent sea bottom, square pattern represents netting and thin straight lines represent moorings

has been reviewed by Callaway et al.²²⁵ and recently by Clinton et al.²²⁶ In offshore waters, jellyfish may be less abundant due to the distance to the hard substrate where polyps live, despite the large range of dispersion of some species (10s to 1000s of km).²²⁷ However, offshore structures can serve as propagators of jellyfish²²⁸ and offshore farms are affected by jellyfish blooms.²²⁹

4 | OPERATIONAL CONSIDERATIONS

4.1 | Overview

Environmental capacity limitations and social and environmental issues make the space for new nearshore farms less and less available.²⁴ However, the aquaculture of Atlantic salmon in offshore locations faces more challenges to operations, staff, animal health, structures and equipment due to the harsh environmental conditions and the remoteness of offshore locations. These results in extra costs that need to be matched by benefits in production. These challenges demand innovation in both technology and strategies to adapt current practices to farming in offshore locations.²¹ In an effort to minimise these challenges, offshore Atlantic salmon farms so far have mostly been located within partly sheltered coastal sites, rather than fully open areas.

4.2 | Structural integrity and reliability

The structural integrity of an offshore fish farm can be compromised in a variety of ways. As reported in various media sources, this included storm damage,²³⁰ design life exceedance²³¹ and human error.²³² The consequence of such failures may involve fish escape, structural damage, complete loss of a farm and even loss of personnel. Active measures must thus be taken to mitigate the risk of failure.

From a structural point of view, the expansion of fish farming into more dynamic offshore conditions is a combination of two developed industries: offshore technology, and aquaculture. The structural integrity of a fish farm depends on site-specific environmental conditions and structural design. Since offshore fish farming

involves the adaptation of existing concepts to new loading conditions or adopting innovative designs, there is little relevant service history to develop robust guidance and standards. Therefore, existing guidance²³³ relies heavily on other industries.

A fish farm system is generally composed of numerous key components, including fish cages, feed barge, feeding tubes, a mooring system, and auxiliary instruments to support and monitor performance. It is important to characterise the individual and combined dynamic response of these components in operational and extreme conditions to ensure structural integrity of the system and develop an effective maintenance regime. This need can be addressed through numerical modelling or physical testing at test facilities or in the field.

Conventional fish cages are designed as semi-submersible systems with a net cage and floating collar for buoyancy in sheltered environments.²³⁴ As the industry expands further offshore, innovative concepts like the vessel-like Havfarm,²³² submarine-like closed-containment system Preline,²³⁵ closed deep-water Aquapods,²³⁶ repurposed oil rijgs²³⁷ and submerged cage by Atlantis²³⁸ have been developed. For deployment at sites with rough surface conditions, it is argued^{239,240} that submerged fish cages such as those by Atlantis Subsea Farming AS²⁴¹ offer reduced wave loads on the structure. Figure 3 shows the classification of some of these novel concepts based on existing guidance by DNV-GL²³³ and Table 1 provides further details regarding the state-of-art and development status and potential.

Numerical modelling has been used to predict the dynamic response of the various components in a fish farm and their mutual interaction.²⁴² Structural response modelling of conventional farms was first performed by Tsukrov et al.²³⁹ using the finite element method to establish a baseline system design for a demonstration site. The publication identified the problem of accurately modelling the net cage that has been the focus of further research. Computational fluid dynamics analysis of a fish farm is challenging since the number of twines for the nets is typically in the order of tens of millions. Other modelling methods often applied to calculate the hydrodynamic response of cage structures and flexible nets include the screen model²⁴³ and Morison element model.²⁴⁴ Whilst the Morison model determines drag coefficients based on the Reynolds number and twine diameter, the screen model

TABLE 1 Classification of offshore fish farm units and installations with relevant examples, applicability to exposed conditions, development stage and expected development limitations

Type	Design Class of Unit or Installation	Example	Development stage	Applicability to Exposed conditions	Salient features	Limitations and future work
I	Vessel-like	Havfarm	Operational	5	Largest semi-submersible structure ever built. Weathering allows minimal environmental footprint. Dynamic positioning system reduces structural loads.	Designed for maximum significant wave height of ten metres. After the test phase, the unit is expected to be autonomously operated.
II	Column-stabilised	Ocean Farm 1	Operational - 2nd production cycle	4	First deep-sea aquaculture project in 2017. Semi-submersible system with revolving self-cleaning technology to reduce biofouling on the structure.	Expected deployment depth up to 300 m. Two failures experienced: damage to net and tilting of structure. Eight further lease sites granted.
		Smart Farm	Pilot project – Permit acquired	4	Twice the capacity of Ocean Farm 1. Designed to treat salmon against lice and disease in closed system.	Unforeseen environmental loads. Developing maintenance strategies.
		Shenlan 1	Operational	4	Fully submerged so reduced risk of wave loads and sea lice.	The size limits the harvest.
		Shenlan 2	Manufacturing	4	First harvest of warm water salmon aquaculture. Equivalent in size to Ocean Farm 1 to improve yield.	Larger footprint increases the risk of collision.
		Arctic Offshore Farm	Manufacturing	4	Fully submerged with air pocket. Designed to withstand waves of up to 13 metres.	Mooring system requirements must be accurately quantified.
III	Circular	Aquapod	Prototype tested	3	Fully submerged system. Tow testing of system with vessel performed.	Adaptable buoyancy mooring systems are under consideration. Full system deployment and dynamic interactions to be demonstrated.
IV	Self-elevating	Roxel Aqua AS	Concept stage	3	Repurposed unused jack-up rigs from the oil and gas exploration industry. Modular adaptation of existing rigs that can be converted back for oil and gas exploration.	Active control required to adjust the depth of conventional fish pens to avoid large waves.

calculates them depending on the ratio of the screen solidity, inflow angle and Reynolds number. For nets with low solidity ratio, the Morison model, screen model and experimental investigations show agreement for a larger range of current speeds. However, for higher solidity ratio, the results show variation for speeds larger than 0.5 m/s. In situations where the net is deformed due to high current speeds, the screen model is more accurate relative to the Morison model as the latter over predicts the drag forces for inflow angles larger than 45 degrees. Comparison of the screen and Morison cage model shows that both provide a suitable margin of confidence for the determination of the resulting mooring line tension.²⁴⁰

Commercial offshore technology software such as OrcaFlex²⁴⁵ uses the Morison equation to model the loading mechanisms on slender elements such as fish cage twines, mooring lines and feeding tubes. The model accounts for the normal relative velocity and acceleration between the structural components and fluid flow.

Offshore locations experience combined wave and current loading, where mooring line forces are strongly dependent on wave elevation²⁴⁰ and volume reduction in flexible net cages is driven by the viscous drag due to currents.²⁴⁶ For most wave frequencies, the cage motion is governed by the waves except at low wave frequency where current dominates motion and at high frequencies where the floating collar exhibits local deformations.²⁴⁰ It is, therefore, crucial to accurately predict the incident wave conditions and to model the resultant hydrodynamic loads.

Causes of offshore fish farm structural failure include metocean loads (i.e. combined wind, wave, climate, etc.), biofouling, erosion and corrosion. In addition to damage by extreme events, the accumulation of stresses over the design lifetime of the system (envisaged at 25 years) may lead to fatigue damage based on the prevalent wave and current conditions.²¹

Based on existing experience²⁴⁷ and modelling,²³⁴ feeding tubes are reliability critical structures that are essential for sustained farm operation. This is because they are partly submerged and oscillations in the tube may subject them to snap loads. Brusset²³⁴ analysed the dynamic response of the feeding tube for wave conditions with 1 and 50 year return periods. The feeding tube tension and bending moment are seen to increase significantly under extreme conditions. The maximum tension increases from 16 to 87 kN and the tube oscillates between tension and compression loading that is likely to cause damage due to snap loads, which can increase fatigue damage and ultimately leads to the rupture of the tube.

The shorter lifetime of feeding tubes, estimated at 5 years²⁴¹ relative to the fish cages is expected to further decrease at more exposed offshore locations.²⁴⁸ The maintenance and repair effort required to address damaged feeding tubes can lead to a significant additional farm operational costs, thereby reducing profitability. Existing research demonstrates that the large bending moment at the connection points of the feeding tube (i.e. at the fish cage and the feed barge) can be reduced significantly by introducing bend stiffeners.²⁴⁸

A robust mooring system provides station-keeping for the fish farm; as the farms move further offshore, longer mooring lines will be required in deeper waters and optimal configurations may vary.⁸ The prevalent environmental conditions and site water depth will be the primary drivers for mooring system design decisions.²⁴⁹ Environmental load monitoring during field testing is important to validate the numerical and experimental test results. Existing projects have recognised this need, for example, Atlantis Subsea Farming AS has deployed load shackles during the second round of trials at the demonstration site to better understand their structural loads.

Using environmental data from the North Sea, existing research demonstrates that mooring lines installed on conventional fish cages can exhibit a 45% and 100% increase in tension for operational and extreme conditions respectively.²³⁴ Therefore, the mooring systems must be designed to withstand these loads to avoid catastrophic system failure. A possible solution is to introduce non-linear mooring components in the system that provide the necessary compliance and stiffness based on the prevalent environmental conditions to reduce peak loads.^{250,251}

It is important to note that aquaculture systems come in several forms, with fundamental differences. The present review focuses on open aquaculture systems. Due to their self-contained nature, isolated from the environment, closed-containment and semi closed-containment systems have not been considered but were recently reviewed by Chu et al.²⁵²

Fish net cages affect the current flow within the cage and the wake for nearshore sites.²⁵³ This can have a significant effect on fish health as it directly impacts the dispersal potential. As the fouling on the net structure increases, the porosity of the cage is reduced resulting in reduced circulation inside the cages and the dispersal of effluent in the near wake. The effect of farm structure on flow speeds is useful to inform farm siting decisions in nearshore aquaculture zones using model-based systems to manage pathogen transport such as sea lice contamination.²⁵⁴ For offshore sites with more dynamic conditions, fine-scale models can be used to fully quantify this interaction of cage structures and the wave-current environment to understand the reduction in dispersal potential due to the flow-structure interaction.

4.3 | Operational and economic challenges

Offshore farms are expensive and potentially risky.²⁵⁵ The initial cost of the infrastructure is increased by the need for more resistant and expensive structures. These structures also have higher maintenance costs, since they wear down quickly due to the weather and require more frequent repair and maintenance.²⁴⁸ Offshore operations are also capital intensive. Remote locations require more self-sufficient infrastructures and makes transport to/from shore more time-consuming and expensive. Regular operations like size grading and redistribution of fish among cages to maintain acceptable stocking densities, routine monitoring of fish health, welfare and parasite prevalence, administration of anti-parasite treatments, net cleaning,

and structural maintenance are crucial to run a profitable and sustainable farm.²² However, bad weather may limit the ability of an operator to undertake these activities safely. This inability to look after the fish and structures has caused some offshore farms to be abandoned due to production losses.

As aquaculture moves further from the shore, sites may not be as easily accessible as those that are nearshore, particularly during bad weather and storms, so it may not be possible to observe the fish on site.²⁵⁶ Remote monitoring and Precision Fish Farming (PFF) can be used to control and automate important tasks from a land base.²⁵⁷ Acoustic technology and underwater cameras can be used to monitor feeding behaviour and ensure that feed is delivered at optimal times.^{258,259} Real-time sensors can also be used to monitor water quality and can provide alerts, *for example* if oxygen levels are too low and may affect fish health and welfare.¹⁰⁹ The cage infrastructure can even be monitored using sensors and models to provide advance warning of cage deformation.²⁶⁰ Though sensors are available, connectivity to the wider network and infrastructure, can be a challenge, particularly in more remote locations.²⁶¹ Cables would interfere with farm management practices and the physical distance mean they are impractical for offshore locations so wireless solutions are more appropriate.²⁵⁶ Weather can interfere with signals from sensors to the network, affecting overall reliability of the PFF system for monitoring and control of aquaculture.²⁶² Cost-efficient and reliable network solutions are required.²⁵⁶ Power supply is also an issue and there is a need for devices that have low-power consumption and can be deployed for long periods of time without the need for regular maintenance.^{256,262} PFF is still emerging within aquaculture and many of the challenges will be overcome with ongoing research, development and innovation.²⁶¹

4.4 | Feed withdrawal and production

Fish feed represents one of the greatest costs to fish farmers and its use has been carefully optimised to minimise losses.²⁶³ The feeding of fish can be difficult during storms. Should personnel have to evacuate the farm, fish can experience feed withdrawal for several days in a row. However, Atlantic salmon can cope with starvation for weeks at a time.²⁶⁴ However, data from a published study showed that after 1 to 4 weeks of feed withdrawal, the effects on fish welfare were negligible, despite a significant reduction in standard metabolic rate of the salmon to preserve energy and a reduction in growth rate. These food deprived fish maintained their full swimming capacity and their ability to respond and recover from acute stress.²⁶⁵ The effects of colder water and growth energy being diverted to exercise could result in decreased growth and production in offshore farms.²⁶⁶ Contrarily, these seemingly detrimental events have been shown to change the physiology of the animals, resulting in increased growth,^{80,82} or a subsequent compensatory growth that may even result in bigger fish at harvest.^{267,268} Regardless, this hypothesis remains to be tested in offshore-grown Atlantic salmon.

4.5 | Biofouling

Biofouling is the growth of organisms (i.e. microorganisms, plants, algae, or small animals) on submerged structures. It is an ongoing issue in aquaculture due to its negative impact on farming operations, farm component risk, as well as fish health and welfare.²⁶⁹ In the absence of intervention, the main issues include the occlusion of the pen net, increased disease risk, altered behaviour of cleaner fish, and its function as a reservoir for non-indigenous species (reviewed in Bloecher and Floerl²⁶⁹). Interventions to prevent and remove biofouling include mainly the use of biocidal coatings and the mechanical cleaning of the nets and structures, respectively. The associated costs of these procedures can be high.²⁶⁹

Biofouling in offshore locations can have even greater impacts on operations, since the drag they cause increases with current speed.²³⁴ However, these locations might benefit from reduced pressure from certain biofouling species. Strong currents above 1.03 m/s have the potential to reduce the need for intervention, preventing the settlement of the initial stages of some bivalves and other invertebrates.²⁷⁰⁻²⁷³ Nonetheless, bivalve settlement and growth can be abundant in offshore locations, particularly of mussels (*Mytilus* spp.), which can be partly attributed to a lack of some of their natural predators in floating structures.²⁷⁴ Another potential advantage comes from locating farms further from the coast, where short-dispersing coastal organisms cannot reach, as is the case of ascidians.²⁷⁵ The benefits of strong currents and the low connectivity with coastal organisms will need to be studied on a local basis, as the prevention of the settlement by some organisms may lead to reduced competition for more damaging biofouling species, depending on the communities that are present in the region.

4.6 | Dispersal of wastes

Waste dispersion depends on the physical characteristics of the environment, the feeding regime and/or chemotherapeutant use, properties of feed and/or chemotherapeutant, and the structure of the cage system. Offshore environments are generally more exposed than inshore or coastal locations and so waste may disperse further and dilute quicker than in more sheltered locations due to site hydrodynamic conditions. A comprehensive review by Holmer²⁸ highlighted environmental issues associated with offshore aquaculture and identified research needs that should be addressed. Although there has been an increase in the number of studies considering offshore aquaculture, many knowledge gaps remain.

Since Holmer,²⁸ one of the major advances has been the development and application of more sophisticated approaches to model particulate and soluble waste dispersion using hydrodynamic models.^{53,276,277} Such approaches are extremely important for more exposed and offshore locations as they can simulate the hydrographic conditions, transport, and deposition of wastes, and can support assessment of environmental impacts. A key advantage is the ability to model far-field dispersal of wastes and studies have shown

that wastes can be dispersed several km from farms.^{53,276,277} Even in offshore sites, patterns of waste dispersion will be highly variable between sites and will depend on the specific characteristics of a farm and location. These factors will also influence the effect that aquaculture waste has on the environment.

Holmer,²⁸ stated that benthic impacts can be expected in offshore locations, even if they are in deeper water and more exposed locations. Increased current speeds may increase dispersion, but large particles are often still deposited near the cages. Thus, there is a need to consider the effect of waste deposition. The benthic environment and communities at offshore sites may be different to those in coastal or inshore locations; for example deep and/or dispersive locations may have hard substrates,²⁷⁸ and consequently waste loading may have different impacts. Most studies on the effects of salmon waste have focussed on infauna, but epibenthic communities are more common in hard substrate sites.²⁷⁹ At a dispersive location in Norway, Woodcock et al.⁷¹ showed uptake of salmon waste by epibenthic invertebrates 1 km from a site. Many of the environmental monitoring approaches that have been established for salmon farming are based on soft sediments and are not appropriate for other substrate types.^{278,280} In areas where grab sampling is difficult, or not possible, then other monitoring techniques include the use of video monitoring^{281,282} and surveying bacterial communities.²⁸³ Potentially, environmental DNA (eDNA) could also be used to detect the presence of these communities.²⁸⁴ Regulators will need to define the monitoring approaches that are most relevant and should be used for offshore aquaculture in their jurisdiction.²⁸⁵

Holmer²⁸ also highlights the need to understand the conditions within the water column, and potential effect of developing an offshore farm. Water quality sampling and monitoring can be difficult, especially in more exposed locations.²⁸⁶ At highly dispersive sites, soluble wastes will be diluted quicker than they would be in more sheltered, less dispersive sites, which is an advantage of offshore production. However, as with other aspects, there will be variability between sites and the production technology, farm management methods and environmental conditions will all influence the release of wastes and their effects on the environment.

5 | REGULATORY ISSUES

One of the bottlenecks to offshore aquaculture at present is the lack of governance and regulatory systems for development.⁷ Political will, proactive policies, and appropriate regulatory mechanisms are all required to support development of offshore aquaculture.²⁸⁷ In most countries there is no specific licencing or regulation system in place to cover 'offshore' aquaculture.⁷ This may be due to confusion over what 'offshore' actually refers to amongst different stakeholders and use of alternative terminology.²⁸⁵ As aquaculture moves offshore, the biophysical and environmental characteristics of new production areas could be different to those where farms are already established and existing regulations may not be appropriate.²⁸⁵

In addition to the environmental characteristics of the area, the technology of offshore farms will also need to be considered in the licencing process. At present, most salmon farms are circular cages, and whilst these may be suitable for some coastal offshore sites, they are unlikely to be suitable for open-ocean conditions that have higher waves and so there is a need for cage systems that are designed for that particular type of environment. For new and emerging technology, such as those highlighted in Table 1, installation of the farm may also have adverse impacts on the environment. The potential impact of construction, ongoing operation and decommission, would be considered within an Environmental Impact Assessment (EIA), but lack of knowledge on such impacts may be a limitation for development of some offshore aquaculture systems if regulators do not have sufficient information to make decisions on licencing applications. For some structures, it may be possible to transfer knowledge and approaches used for the offshore energy sectors.

Licensing applications for coastal fish farms are often rejected due to concerns over visual impacts,²³ but a move further from the coast, away from sensitive seascapes and landscapes may remove this issue, although this will still depend on the physical characteristics of the coastline and location of the site. Visual impact will also depend on the size and scale of the offshore aquaculture operation as a large rig system may still have a visual impact that is considered unacceptable, but a submerged cage system may not. Visual impact assessments and visualisations using computer software can be used as part of the planning process to identify areas with minimal impact and used for engagement with local communities as part of public consultations.^{23,288} Social acceptability of aquaculture is an important issue and there are differences in perception that affect how aquaculture is developed at local and national scales.²⁸⁹ Issues around social licence to operate may be different for offshore and inshore locations, but this will also vary depending on other socio-economic factors and the communities involved.

One of the advantages of moving offshore is less competition for space as there are fewer activities than in the more crowded coastal and inshore locations. Although in some offshore waters, for example the German section of the North Sea, there are still many different user groups and activities, including fishing, offshore energy, undersea cables, military and protected areas so there is high competition for space.²⁹⁰ The types of activities and user groups may be different from those encountered in more coastal and inshore environments.

In addition to human activities, potential interactions with wild fish stocks and the wider ecosystem must also be considered and some of the key issues that would also be considered as part of the planning process such as sea lice and effects of wastes have been discussed earlier in this review. For salmon aquaculture, a key concern is escapes.²⁹¹ As offshore locations are in more exposed locations, then there is a higher risk of escape events due to rough weather conditions; therefore, the technology used to contain the fish must be suitable for such environments. Aquaculture sites can also act as aggregation devices for fish, birds and marine mammals.²⁹² The effect of offshore aquaculture on wild populations

would be considered in the planning process and may require the use of ecosystem modelling to assess the potential effect of establishing a farm site. Species distribution modelling can also be used to help identify potential habitat range of wild organisms. Migratory routes should also be considered, as attraction to aquaculture sites can lead to changes in migration patterns.²⁹² For some species, this information may already be available and there may be regulatory or policy mechanisms in place to protect them. Offshore locations may include formal protected areas such as Marine Protected Areas (MPAs), where development may be restricted or subject to more conditions than in other locations to protect sensitive species, habitats, and features. Marine spatial plans that outline the natural resources, wild populations and human activities of coastal and offshore locations would be useful. Such assessments could also be used to identify potential zones for aquaculture where development should be prioritised due to favourable conditions for production and minimal effects on other activities.²⁹³

Many studies on offshore aquaculture promote the concept of co-location, particularly with offshore wind farms.^{290,294} Co-location is seen as a way of maximising economic output of an area, sharing some resources and optimising use of space by having multiple activities on the same platform or within close proximity. However, multi-functional use of a site will also create new biological, legal, technical and operational challenges.²⁹⁵ The different activities will have different priorities that may not be compatible with each other. Most attention has focussed on shellfish and seaweeds,²⁹⁶⁻²⁹⁸ though some studies have also considered finfish.²⁹⁴ Christie et al.²⁹⁵ noted that there are few examples, where wind farms and aquaculture have actually been co-located, and suggested this is due to the lack of licencing and regulatory framework to establish such systems, but also that commercial viability for each component still needs to be proven. Most studies have been conceptual or theoretical, with some small-scale pilot studies taking place. Though co-location may offer advantages for marine spatial planning and space allocation, for aquaculture, health and welfare of the animals is top priority and selection of sites, whether individual or co-located, must not compromise aquaculture operations. Consequently, further work is required to determine whether or not commercial-scale fish production at offshore wind farms would be feasible, or even desirable, for both fish and energy producers given the added challenges.

6 | CONCLUSIONS AND FUTURE DIRECTION

Clearly, not all offshore locations are suitable for fish farming development, yet the number of locations that will be deemed appropriate after studying their oceanography will likely be high offering considerable potential for development of the industry. However, offshore farming faces limitations.²⁹⁹ Those who choose to start a farm in an offshore location will face important operational limitations and increased operational costs. In turn, they might benefit from some production advantages. Regardless, if not out of choice, many new

farms will have to be located in such environments due to the lack of available locations in sheltered areas. If the site selection is done properly, based on a clear understanding that the oceanography of the potential sites is suitable for the target farmed species, economic losses related to fish health and to damage to the structures will be minimised. This location must also be viable operationally (e.g. transport costs) and in terms of permits and licencing.

It is important to note that the definition of 'offshore aquaculture' can vary drastically between countries. Hence, as identified in this review, it is hard to harmonise numerous poorly defined concepts and terms (for example, 'moving offshore' or 'exposed'). Some readers will not agree with our approach, and this serves to confirm the need for a common set of terms and definitions obtained through consensus between stakeholders.

Salmon behaviour is governed by its environment and fish vertical distribution in the cages will be different in exposed and sheltered areas. Health and welfare will be also directly affected (both positively and negatively) by the harsher offshore conditions; mainly enhanced currents and waves and will need to be closely monitored. To avoid mass mortalities, smaller fish might have to be deployed in nearshore farms to then be transferred to offshore sites when bigger. Offshore aquaculture will benefit from careful monitoring and new technologies, as implemented by Precision Fish Farming.²⁵⁷

Whilst sea lice free Atlantic salmon farms can exist in nearshore waters (e.g. the Scottish Orkney Islands, SRP, pers obs), dispersive environments and the greater distance to the coast will in general reduce the pressure of sea lice via reducing retention and exchange of lice between sites. However, sea lice still reach these offshore sites and can still cause important infestations. The propagation of sea lice follows complex pathways that are not fully understood. Offshore fish farmers may be unable to carry out monitoring procedures routinely if there is extended bad weather, potentially reducing the operator's ability to control lice. A study comparing sea lice counts in farms situated in a range of oceanographic conditions is needed to understand how these conditions affect the prevalence of the parasite, and the ability to undertake anti sea lice treatments.

This dispersive environment in offshore locations is also likely to disperse farm wastes and chemical treatments away from farms. Intuitively there may be an expectation that increased dispersion is a benefit to benthic communities, and this will be the case in some locations, but, the impact of these wastes on wild fauna and flora will depend on the species that form these communities in offshore environments and site-specific characteristics. The ecological consequences of waste deposition will need to be considered, along with the oceanography of the site, before choosing a location for a new farm.

Dispersal will also affect HABs and jellyfish, which have mostly been reported in partly sheltered locations where restricted exchange may promote blooms. However, many of these organisms are known to develop and bloom offshore and move adjectively. A combination of satellite and in-situ monitoring combined with mathematical modelling will be required to provide early warning of

these events, with bioremediation procedures being adapted from nearshore protocols to minimise harm. In terms of AGD, its propagation mechanisms are mostly unknown, so it is hard to predict the potential of infection at offshore farms. However, whilst increased oxygen and water exchange offshore might lessen this problem, the swimming capacity and aerobic scope of afflicted fish is severely reduced. This may lead to AGD-related mortalities in offshore farms due to suffocation when high swimming performance is needed (i.e. in strong currents). A study comparing AGD prevalence in offshore and nearshore farms and accounting for the number of anti AGD treatments carried out and for AGD-related mortalities is needed to test these hypotheses.

Finally, most operational costs will increase, including the initial investment and all costs related to transport. The constant strain on the structures will require more expensive and specialised materials and they will need to be replaced more often than in nearshore farms. The overall usable life of the whole farm will, therefore, likely be reduced. Due to all this, there will be a requirement to spend more time and resources on in-depth studies of the oceanography, suitability to the target fish species, and operational and licencing costs and challenges for offshore compared with nearshore sites.

ACKNOWLEDGEMENTS

We would like to thank Dr Grigorios Moschonas for reading the manuscript and providing thoughtful comments. The work was primarily funded by the UK BBSRC/NERC funded project Off-Aqua (Evaluating the Environmental Conditions Required for the Development of Offshore Aquaculture) – BB/S004246/1. KD and DA were also funded by the NERC project CAMPUS (NE/R00675X/1).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Scottish Salmon Producers' Organisation at www.scottishsalmon.co.uk.

ORCID

Bernat Morro  <https://orcid.org/0000-0002-6799-3882>

Lynne Falconer  <https://orcid.org/0000-0002-1899-1290>

Dmitry Aleynik  <https://orcid.org/0000-0002-2066-1960>

Sonia Rey-Planellas  <https://orcid.org/0000-0002-3406-3291>

REFERENCES

1. FAO. *The State of World Fisheries and Aquaculture 2020. Sustainability in Action*. FAO; 2020.
2. World Bank. *Fish to 2030: Prospects for Fisheries and Aquaculture*. Italy: FAO. 2013.
3. Di Trapani AM, Sgroi F, Testa R, Tudisca S. Economic comparison between offshore and inshore aquaculture production systems of European sea bass in Italy. *Aquaculture*. 2014;434:334-339.
4. Froehlich HE, Smith A, Gentry RR, Halpern BS. Offshore aquaculture: I know it when I see it. *Front Mar Sci*. 2017;4:154.
5. Dale T, Cusack C, Ruiz M. Aquaculture site selection Report. 2017:39. AtlantOS Deliverable D82. http://oceanrep.geomar.de/39456/1/D.8.2_AtlantOS.pdf
6. Lester SE, Gentry RR, Kappel CV, White C, Gaines SD. Opinion: Offshore aquaculture in the United States: Untapped potential in need of smart policy. *Proc Natl Acad Sci USA*. 2018;115(28):7162-7165. <https://doi.org/10.1073/pnas.1808737115>
7. Davies IP, Carranza V, Froehlich HE, Gentry RR, Kareiva P, Halpern BS. Governance of marine aquaculture: Pitfalls, potential, and pathways forward. *Marine Policy*. 2019;104:29-36.
8. Li L, Jiang Z, Ong MC, Hu W. Design optimization of mooring system: an application to a vessel-shaped offshore fish farm. *Eng Struct*. 2019;197:109363.
9. 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):1-10.
10. Quinones RA, Fuentes M, Montes RM, Soto D, León-Muñoz J. Environmental issues in Chilean salmon farming: a review. *Rev Aquacult*. 2019;11(2):375-402.
11. Kim HG. Mitigation and controls of HABs. In: Turner, JT (Ed.), *Ecology of Harmful Algae*. USA: Springer. 2006;327-338.
12. Kudela RM, Berdalet E, Enevoldsen H, Pitcher G, Raine R, Urban E. GEOHAB: The Global Ecology and Oceanography of Harmful Algal Blooms program motivation, goals, and legacy. *Oceanography*. 2017;30(1):12-21.
13. Shinn AP, Pratoomyot J, Bron JE, et al. Economic costs of protozoan and metazoan parasites to global mariculture. *Parasitology*. 2015;142(1):196.
14. Abolofia J, Asche F, Wilen JE. The cost of lice: quantifying the impacts of parasitic sea lice on farmed salmon. *Mar Resour Econ*. 2017;32(3):329-349.
15. Costello M. The global economic cost of sea lice to the salmonid farming industry. *J Fish Dis*. 2009;32(1):115.
16. Marcos-López M, Rodger HD. Amoebic gill disease and host response in Atlantic salmon (*Salmo salar* L.): a review. *Parasite Immunol*. 2020;42(8):e12766.
17. Werkman M, Green DM, Murray AG, Turnbull JF. The effectiveness of fallowing strategies in disease control in salmon aquaculture assessed with an SIS model. *Prevent Vet Med*. 2011;98(1):64-73.
18. Samsing F, Johnsen I, Dempster T, Oppedal F, Tremli EA. Network analysis reveals strong seasonality in the dispersal of a marine parasite and identifies areas for coordinated management. *Landscape Ecol*. 2017;32(10):1953-1967.
19. Reijts TAM, Oorschot RWA, Poelman M, Kals J. *Aquacultuur op open zee*. TNO Bouw en Ondergrond No 2008-D-R1048/A. 2008.
20. Stelzenmüller V, Gimpel A, Gopnik M, Gee K. Aquaculture site-selection and marine spatial planning: the roles of GIS-based tools and models. In: Buck, BH & Langan, R (Eds.), *Aquaculture Perspective of Multi-Use Sites in the Open Ocean*. Springer; 2017:131-148.
21. El-Thalji I. Context analysis of offshore fish farming. *IOP Conf Series Mater Sci Eng*. 2019;700:012065.
22. Bjelland HV, Føre M, Lader P, et al. Exposed aquaculture in Norway. *IEEE*. 2015;1-10.
23. Falconer L, Hunter D-C, Telfer TC, Ross LG. Visual, seascape and landscape analysis to support coastal aquaculture site selection. *Land Use Policy*. 2013;34:1-10.
24. Galparsoro I, Murillas A, Pinarbasi K, et al. Global stakeholder vision for ecosystem-based marine aquaculture expansion from coastal to offshore areas. *Rev Aquacult*. 2020;12(4):2061-2079.
25. Benetti DD, O'Hanlon B, Rivera JA, Welch AW, Maxey C, Orhun MR. Growth rates of cobia (*Rachycentron canadum*) cultured in open ocean submerged cages in the Caribbean. *Aquaculture*. 2010;302(3-4):195-201.
26. Kirchhoff NT, Rough KM, Nowak BF. Moving cages further offshore: effects on southern bluefin tuna, *T. maccoyii*, parasites, health and performance. *PLoS One*. 2011;6(8):e23705.

27. Jansen HM, Van Den Burg S, Bolman B, et al. The feasibility of offshore aquaculture and its potential for multi-use in the North Sea. *Aquac Int*. 2016;24(3):735-756.
28. Holmer M. Environmental issues of fish farming in offshore waters: perspectives, concerns and research needs. *Aquacult Environ Interact*. 2010;1(1):57-70.
29. Smayda TJ, Reynolds CS. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *J Plankton Res*. 2001;23(5):447-461.
30. Hvas M, Folkedal O, Oppedal F. Fish welfare in offshore salmon aquaculture. *Rev Aquacult*. 2020;13(2):836-852.
31. Ellett DJ, Edwards A. Oceanography and inshore hydrography of the Inner Hebrides. *Proc R Soc Edinburgh B Biol Sci*. 1983;83:144-160.
32. Asplin L, Albretsen J, Johnsen IA, Sandvik AD. The hydrodynamic foundation for salmon lice dispersion modeling along the Norwegian coast. *Ocean Dyn*. 2020;70(8):1151-1167. <https://doi.org/10.1007/s10236-020-01378-0>
33. Thorpe SA, Hall AJ, Hunt S. Bouncing internal bores of Ardmucknish Bay, Scotland. *Nature*. 1983;306(5939):167-169.
34. Inall ME, Gillibrand PA. The physics of mid-latitude fjords: a review. *Geol Soc London, Special Publ*. 2010;344(1):17-33.
35. Jones KJ, Gowen RJ, Tett P. Water column structure and summer phytoplankton distribution in the Sound of Jura, Scotland. *J Exp Mar Biol Ecol*. 1984;78(3):269-289.
36. Easton MC, Woolf DK, Bowyer PA. The dynamics of an energetic tidal channel, the Pentland Firth, Scotland. *Continental Shelf Res*. 2012;48:50-60.
37. Gillibrand PA, Sammes PJ, Slesser G, Adams RD. Seasonal water column characteristics in the Little and North Minches and the Sea of the Hebrides. I. Physical and chemical parameters. *Fisheries Research Services Internal Report*. 2003;8:032003.
38. Zimmerman JTF. The tidal whirlpool: a review of horizontal dispersion by tidal and residual currents. *Neth J Sea Res*. 1986;20(2):133-154. [https://doi.org/10.1016/0077-7579\(86\)90037-2](https://doi.org/10.1016/0077-7579(86)90037-2)
39. Page FH, Losier R, Haigh S, et al. *Transport and Dispersal of Sea Lice Bath Therapeutants from Salmon Farm Net-Pens and Well-Boats Operated in Southwest New Brunswick: A Mid-Project Perspective and Perspective for Discussion*. Fisheries and Oceans Canada, Science. 2014.
40. Okubo A. Oceanic diffusion diagrams. *Deep Sea Res Oceanogr Abstracts*. 1971;18:789-802.
41. Gillibrand PA, Turrell WR. A management model to predict the dispersion of soluble pesticides from marine fish farms. *FRS ML Report*. 1999;2:99.
42. Gillibrand PA, Turrell WR. The use of simple models in the regulation of the impact of fish farms on water quality in Scottish sea lochs. *Aquaculture*. 1997;159(1-2):33-46.
43. Tett P, Portilla E, Gillibrand PA, Inall M. Carrying and assimilative capacities: the ACEXr-LESV model for sea-loch aquaculture. *Aquac Res*. 2011;42(s1):51-67. <https://doi.org/10.1111/j.1365-2109.2010.02729.x>
44. SEPA. *Aquaculture Modelling: Regulatory Modelling Guidance for The Aquaculture Sector*. Scottish Environmental Protection Agency. 2019.
45. SEPA. *Protection of the Marine Environment: Discharges from Marine Pen Fish Farms, a Strengthened Regulatory Framework*. Scottish Environmental Protection Agency (SEPA). 2019.
46. Aleynik D, Adams T & Davidson K, et al. Biophysical modelling of marine organisms: fundamentals and applications to management of coastal waters. In: Islam, MN & Jorgensen, SE (Eds.), *Environmental Management of Marine Ecosystems*. USA: CRC Press; 2018:65-98.
47. Chen C, Beardsley RC, Cowles G. Finite-volume coastal ocean. *Oceanography*. 2006;19(1):78.
48. Beardsley RC, Chen C, Xu Q. Coastal flooding in Scituate (MA): a FVCOM study of the 27 December 2010 nor'easter. *J Geophys Res Oceans*. 2013;118(11):6030-6045.
49. Aleynik D, Dale AC, Porter M, Davidson K. A high resolution hydrodynamic model system suitable for novel harmful algal bloom modelling in areas of complex coastline and topography. *Harmful Algae*. 2016;53:102-117.
50. Chen T, Zhang Q, Wu Y, Ji C, Yang J, Liu G. Development of a wave-current model through coupling of FVCOM and SWAN. *Ocean Eng*. 2018;164:443-454.
51. De Dominicis M, O'Hara Murray R, Wolf J, Gallego A. *Physical Variables from the Scottish Shelf Model 2038-2062 Future Climatology - 4 Monthly Averages on a Shelf Wide Regular Grid*. Scottish Government. 2019. <https://doi.org/10.7489/12039-1>
52. Fjørtoft HB, Nilssen F, Besnier F, et al. Losing the 'arms race': multi-resistant salmon lice are dispersed throughout the North Atlantic Ocean. *R Soc Open Sci*. 2021;8(5):210265.
53. Bannister RJ, Johnsen IA, Hansen PK, Kutti T, Asplin L. Near-and far-field dispersal modelling of organic waste from Atlantic salmon aquaculture in fjord systems. *ICES J Mar Sci*. 2016;73(9):2408-2419.
54. BarentsWatch. Norwegian fish health. www.barentswatch.no/en/fishhealth/
55. Ratsimandresy AW, Donnet S, Goulet P. Identification of geographic zones of influence associated with surface circulation for Aquaculture Bay Management Area application. *J Mar Syst*. 2020;204:103291.
56. Urbina MA. Temporal variation on environmental variables and pollution indicators in marine sediments under sea salmon farming cages in protected and exposed zones in the Chilean inland Southern Sea. *Sci Total Environ*. 2016;573:841-853.
57. Leith P, Ogier E, Haward M. Science and social license: defining environmental sustainability of Atlantic salmon aquaculture in south-eastern Tasmania, Australia. *Soc Epistemol*. 2014;28(3-4):277-296.
58. De Dominicis M, Murray ROH, Wolf J. Multi-scale ocean response to a large tidal stream turbine array. *Renewable Energy*. 2017;114:1160-1179.
59. Creech ACW, Borthwick AGL, Ingram D. Effects of support structures in an LES actuator line model of a tidal turbine with contra-rotating rotors. *Energies*. 2017;10(5):726.
60. Cornejo P, Sepúlveda HH, Gutiérrez MH, Olivares G. Numerical studies on the hydrodynamic effects of a salmon farm in an idealized environment. *Aquaculture*. 2014;430:195-206.
61. Bi C-W, Xu T-J. Numerical study on the flow field around a fish farm in tidal current. *Turk J Fish Aquat Sci*. 2018;18(5):705-716.
62. Faltinsen OM, Timokha AN. Analytically approximate natural sloshing modes and frequencies in two-dimensional tanks. *Eur J Mech B/Fluids*. 2014;47:176-187.
63. Broch OJ, Klebert P, Michelsen FA, Alver MO. Multiscale modelling of cage effects on the transport of effluents from open aquaculture systems. *PLoS One*. 2020;15(3):e0228502.
64. Rickard G. Three-dimensional hydrodynamic modelling of tidal flows interacting with aquaculture fish cages. *J Fluids Struct*. 2020;93:102871.
65. Johansson D, Juell J-E, Oppedal F, Stiansen J-E, Ruohonen K. The influence of the pycnocline and cage resistance on current flow, oxygen flux and swimming behaviour of Atlantic salmon (*Salmo salar* L.) in production cages. *Aquaculture*. 2007;265(1-4):271-287.
66. Adams TP, Aleynik D, Black KD. Temporal variability in sea lice population connectivity and implications for regional management protocols. *Aquacult Environ Interact*. 2016;8:585-596.
67. Gillibrand PA, Willis KJ. Dispersal of sea louse larvae from salmon farms: modelling the influence of environmental conditions and larval behaviour. *Aquat Biol*. 2007;1(1):63-75.

68. Salama NKG, Collins CM, Fraser JG, et al. Development and assessment of a biophysical dispersal model for sea lice. *J Fish Dis*. 2013;36(3):323-337.
69. Salama NKG, Dale AC, Ivanov VV, et al. Using biological-physical modelling for informing sea lice dispersal in Loch Linnhe, Scotland. *J Fish Dis*. 2018;41(6):901-919.
70. Pearson TH, Black KD. The environmental impacts of marine fish cage culture. In: Black, KD (Ed.), *Environmental Impacts of Aquaculture*. UK: Sheffield Academic Press; 2000;1-31.
71. Woodcock SH, Strohmeier T, Strand Ø, Olsen SA, Bannister RJ. Mobile epibenthic fauna consume organic waste from coastal finfish aquaculture. *Mar Environ Res*. 2018;137:16-23.
72. Cao L, Wang W, Yang Y, et al. Environmental impact of aquaculture and countermeasures to aquaculture pollution in China. *Environ Sci Pollut Res Int*. 2007;14(7):452-462.
73. Davidson K, Whyte C, Aleynik D, et al. HABreports: online early warning of harmful algal and biotoxin risk for the Scottish shellfish and finfish aquaculture industries. *Front Mar Sci*. 2021;8:350.
74. OECD. *Safety Assessment of Transgenic Organisms in the Environment, Volume 7*. France: OECD Publishing; 2017.
75. Hvas M, Nilsen TO, Oppedal F. Oxygen uptake and osmotic balance of Atlantic salmon in relation to exercise and salinity acclimation. *Front Mar Sci*. 2018;5:368.
76. Hvas M, Oppedal F. Sustained swimming capacity of Atlantic salmon. *Aquacult Environ Interact*. 2017;9:361-369.
77. Dadswell MJ, Spares AD, Reader JM, Stokesbury MJW. The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: The 'Merry-Go-Round' hypothesis. *J Fish Biol*. 2010;77(3):435-467.
78. Jónsdóttir KE, Hvas M, Alfredsen JA, et al. Fish welfare based classification method of ocean current speeds at aquaculture sites. *Aquacult Environ Interact*. 2019;11:249-261.
79. Solstorm F, Solstorm D, Oppedal F, Fernö A, Fraser TWK, Olsen R-E. Fast water currents reduce production performance of post-smolt Atlantic salmon *Salmo salar*. *Aquacult Environ Interact*. 2015;7(2):125-134.
80. Nilsen A, Hagen Ø, Johnsen CA, et al. The importance of exercise: Increased water velocity improves growth of Atlantic salmon in closed cages. *Aquaculture*. 2019;501:537-546.
81. Castro V, Grisdale-Helland B, Helland SJ, et al. Aerobic training stimulates growth and promotes disease resistance in Atlantic salmon (*Salmo salar*). *Comp Biochem Physiol A: Mol Integr Physiol*. 2011;160(2):278-290.
82. Timmerhaus G, Lazado CC, Cabillon NA, Reiten BKM, Johansen L-H. The optimum velocity for Atlantic salmon post-smolts in RAS is a compromise between muscle growth and fish welfare. *Aquaculture*. 2021;532:736076.
83. Remen M, Solstorm F, Bui S, et al. Critical swimming speed in groups of Atlantic salmon *Salmo salar*. *Aquacult Environ Interact*. 2016;8:659-664.
84. Johansson D, Laursen F, Fernö A, et al. The interaction between water currents and salmon swimming behaviour in sea cages. *PLoS One*. 2014;9(5):e97635.
85. Hvas M, Folkedal O, Solstorm D, et al. Assessing swimming capacity and schooling behaviour in farmed Atlantic salmon *Salmo salar* with experimental push-cages. *Aquaculture*. 2017;473:423-429.
86. McKenzie DJ, Palstra AP, Planas J, et al. Aerobic swimming in intensive finfish aquaculture: applications for production, mitigation and selection. *Rev Aquacult*. 2021;13(1):138-155.
87. Hvas M, Folkedal O, Oppedal F. What is the limit of sustained swimming in Atlantic salmon post smolts? *Aquacult Environ Interact*. 2021;13:189-198.
88. Jónsdóttir KE, Volent Z, Alfredsen JA. Current flow and dissolved oxygen in a full-scale stocked fish-cage with and without lice shielding skirts. *Appl Ocean Res*. 2021;108:102509.
89. Sardella BA, Brauner CJ. The osmo-respiratory compromise in fish: the effects of physiological state and the environment. In: Fernandes, MN, Rantin, FT, Glass, ML & Kapoor, BG (Eds.), *Fish Respiration and Environment*. USA: CRC Press; 2007;147-165.
90. Hvas M, Folkedal O, Imsland A, Oppedal F. Metabolic rates, swimming capabilities, thermal niche and stress response of the lumpfish, *Cyclopterus lumpus*. *Biol Open*. 2018;7(9):1-9.
91. Brooker AJ, Papadopoulou A, Gutierrez C, Rey S, Davie A, Migaud H. Sustainable production and use of cleaner fish for the biological control of sea lice: recent advances and current challenges. *Veterinary Record*. 2018;183(12):383.
92. Yuen JW, Dempster T, Oppedal F, Hvas M. Physiological performance of ballan wrasse (*Labrus bergylta*) at different temperatures and its implication for cleaner fish usage in salmon aquaculture. *Biol Control*. 2019;135:117-123.
93. Johannesen Á, Arge R, Eliassen K. Rearing, farm application, and behaviour of lumpfish (*Cyclopterus lumpus*) in the Faroes. In: Treasurer J, ed. *Cleaner Fish Biology and Aquaculture Applications*. 5m Publishing; 2018.
94. NAS. NS-9415 Marine fish farms—requirements for site survey, risk analyses, design, dimensioning, production, installation and operation. Vol. ICS 65.150;67.260. 2009.
95. Kapetsky JM, Aguilar-Manjarrez J, Jenness JA. *Global Assessment of Potential for Offshore Mariculture Development from a Spatial Perspective*, 181 pp. FAO Fisheries and Aquaculture Technical Paper. 2013;(549)
96. Stockwell CL, Filgueira R, Grant J. Determining the effects of environmental events on cultured Atlantic salmon behaviour using 3-dimensional acoustic telemetry. *Front Anim Sci*. 2021;2:26. <https://doi.org/10.3389/fanim.2021.701813>
97. Johannesen Á, Patursson Ø, Kristmundsson J, Dam SP, Klebert P. How caged salmon respond to waves depends on time of day and currents. *PeerJ*. 2020;8:e9313.
98. Klebert P, Patursson Ø, Endresen PC, Rundtop P, Birkevold J, Rasmussen HW. Three-dimensional deformation of a large circular flexible sea cage in high currents: field experiment and modeling. *Ocean Eng*. 2015;104:511-520.
99. Dempster T, Juell J-E, Fosseidengen JE, Fredheim A, Lader P. Behaviour and growth of Atlantic salmon (*Salmo salar* L.) subjected to short-term submergence in commercial scale sea-cages. *Aquaculture*. 2008;276(1-4):103-111.
100. Fish Farming Expert. Storms cause salmon deaths in Newfoundland. 2020. <https://www.fishfarmingexpert.com/article/storms-cause-high-mortality-at-newfoundland-fish-farm/>
101. Fish Farming Expert. 220,000 fish unaccounted for after Faroes storm deaths. 2020. <https://www.fishfarmingexpert.com/article/bakkafrost-fish-may-have-escaped-in-storm/>
102. Fish Farming Expert. Rope break blamed as Mowi puts Carradale farm escape total at 48,834. 2020. <https://www.fishfarmingexpert.com/article/rope-break-blamed-as-mowi-puts-carradale-farm-escape-total-at-48834/>
103. Matthews SG, Pitcher GC. Worst recorded marine mortality on the South African coast. In: Yasumoto, T, Oshima, Y & Fukuyo, Y (Eds.), *Harmful and Toxic Algal Blooms*. France: IOC-UNESCO; 1996;89-92.
104. Oldham T, Nowak B, Hvas M, Oppedal F. Metabolic and functional impacts of hypoxia vary with size in Atlantic salmon. *Comp Biochem Physiol A: Mol Integr Physiol*. 2019;231:30-38.
105. Oldham T, Dempster T, Fosse JO, Oppedal F. Oxygen gradients affect behaviour of caged Atlantic salmon *Salmo salar*. *Aquacult Environ Interact*. 2017;9:145-153.
106. 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*). *Aquac Res*. 2013;45(1):124-137.

107. Oldham T, Dempster T, Crosbie P, Adams M, Nowak B. Cyclic hypoxia exposure accelerates the progression of amoebic gill disease. *Pathogens*. 2020;9(8):597.
108. Oldham T, Oppedal F, Dempster T. Cage size affects dissolved oxygen distribution in salmon aquaculture. *Aquacult Environ Interact*. 2018;10:149-156.
109. Burke M, Grant J, Figueira R, Stone T. Oceanographic processes control dissolved oxygen variability at a commercial Atlantic salmon farm: application of a real-time sensor network. *Aquaculture*. 2021;533:736143.
110. Grantham BA, Chan F, Nielsen KJ, et al. Upwelling-driven near-shore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature*. 2004;429(6993):749-754.
111. Fuenzalida R, Schneider W, Garcés-Vargas J, Bravo L, Lange C. Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. *Deep Sea Res Part II*. 2009;56(16):992-1003.
112. Boltana S, Rey S, Roher N, et al. Behavioural fever is a synergic signal amplifying the innate immune response. *Proc R Soc B Biol Sci*. 2013;280(1766):20131381.
113. Rey S, Huntingford FA, Boltana S, Vargas R, Knowles TG, Mackenzie S. Fish can show emotional fever: stress-induced hyperthermia in zebrafish. *Proc R Soc B Biol Sci*. 2015;282(1819):20152266.
114. Nowak BF, Martin MB, Boltaña S. Parasitic crustaceans. *Fish Aquacult*. 2020;9:401.
115. Carvalho LA, Whyte SK, Braden LM, et al. Impact of co-infection with *Lepeophtheirus salmonis* and *Moritella viscosa* on inflammatory and immune responses of Atlantic salmon (*Salmo salar*). *J Fish Dis*. 2020;43(4):459-473.
116. Ugelvik MS, Skorping A, Moberg O, Mennerat A. Evolution of virulence under intensive farming: salmon lice increase skin lesions and reduce host growth in salmon farms. *J Evol Biol*. 2017;30(6):1136-1142.
117. Van Geest JL, Burrige LE, Kidd KA. Toxicity of two pyrethroid-based anti-sea lice pesticides, AlphaMax[®] and Excis[®], to a marine amphipod in aqueous and sediment exposures. *Aquaculture*. 2014;434:233-240.
118. Burrige LE, Lyons MC, Wong DKH, MacKeigan K, VanGeest JL. The acute lethality of three anti-sea lice formulations: AlphaMax[®], Salmosan[®], and Interox[®] Paramove[™] 50 to lobster and shrimp. *Aquaculture*. 2014;420:180-186.
119. 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.
120. Treasurer JW, Wadsworth S, Grant A. Resistance of sea lice, *Lepeophtheirus salmonis* (Krøyer), to hydrogen peroxide on farmed Atlantic salmon, *Salmo salar* L. *Aquac Res*. 2000;31(11):855-860. <https://doi.org/10.1046/j.1365-2109.2000.00517.x>
121. Barrett LT, Oppedal F, Robinson N, Dempster T. Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. *Rev Aquacult*. 2020;12(4):2527-2543.
122. Powell MD, Reynolds P, Kristensen T. Freshwater treatment of amoebic gill disease and sea-lice in seawater salmon production: Considerations of water chemistry and fish welfare in Norway. *Aquaculture*. 2015;448:18-28.
123. Gismervik K, Gåsnes S, Nielsen K, Mejdell C. *The Health Situation in Norwegian Aquaculture 2017. Fish Welfare*. Norwegian Veterinary Institute; 2018:18.
124. Overton K, Dempster T, Oppedal F, Kristiansen TS, Gismervik K, Stien LH. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. *Rev Aquacult*. 2019;11(4):1398-1417.
125. Nilsson J, Moltumyr L, Madaro A, et al. Sudden exposure to warm water causes instant behavioural responses indicative of nociception or pain in Atlantic salmon. *Veterinary and Animal Science*. 2019;8:100076.
126. 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.
127. Overton K, Barrett LT, Oppedal F, Kristiansen TS, Dempster T. Sea lice removal by cleaner fish in salmon aquaculture: a review of the evidence base. *Aquacult Environ Interact*. 2020;12:31-44.
128. Erkinharju T, Dalmo RA, Hansen M, Seternes T. Cleaner fish in aquaculture: review on diseases and vaccination. *Rev Aquacult*. 2021;13(1):189-237.
129. Haugland GT, Olsen A-B, Rønneseth A, Andersen L. Lumpfish (*Cyclopterus lumpus* L.) develop amoebic gill disease (AGD) after experimental challenge with *Paramoeba perurans* and can transfer amoebae to Atlantic salmon (*Salmo salar* L.). *Aquaculture*. 2017;478:48-55.
130. Karlsbakk E, Olsen AB, Einen A-CB, et al. Amoebic gill disease due to *Paramoeba perurans* in ballan wrasse (*Labrus bergylta*). *Aquaculture*. 2013;412:41-44.
131. Murray AG. A modelling framework for assessing the risk of emerging diseases associated with the use of cleaner fish to control parasitic sea lice on salmon farms. *Trans Emerg Dis*. 2016;63(2):e270-e277.
132. Blanco Gonzalez E, Espeland SH, Jentoft S, et al. Interbreeding between local and translocated populations of a cleaner fish in an experimental mesocosm predicts risk of disrupted local adaptation. *Ecol Evol*. 2019;9(11):6665-6677.
133. Faust E, Jansson E, André C, et al. Not that clean: Aquaculture-mediated translocation of cleaner fish has led to hybridization on the northern edge of the species' range. *Evol Appl*. 2021;14(6):1572-1587.
134. Dempster T, Overton K, Bui S, et al. Farmed salmonids drive the abundance, ecology and evolution of parasitic salmon lice in Norway. *Aquacult Environ Interact*. 2021;13:237-248.
135. Rae GH. Sea louse control in Scotland, past and present. *Pest Manag Sci*. 2002;58(6):515-520.
136. Heuch PA, Karlsen E. Detection of infrasonic water oscillations by copepodids of *Lepeophtheirus salmonis* (Copepoda Caligida). *J Plankton Res*. 1997;19(6):735-747.
137. Bailey RJE, Birkett MA, Ingvarsdóttir A, et al. The role of semiochemicals in host location and non-host avoidance by salmon louse (*Lepeophtheirus salmonis*) copepodids. *Can J Fish Aquat Sci*. 2006;63(2):448-456. <https://doi.org/10.1139/f05-231>
138. Tully O, Whelan KF. Production of nauplii of *Lepeophtheirus salmonis* (Krøyer) (Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (*Salmo trutta* L.) off the west coast of Ireland in 1991. *Fish Res*. 1993;17(1):187-200. [https://doi.org/10.1016/0165-7836\(93\)90018-3](https://doi.org/10.1016/0165-7836(93)90018-3)
139. Costello MJ. Ecology of sea lice parasitic on farmed and wild fish. *Trends Parasitol*. 2006;22(10):475-483.
140. 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. <https://doi.org/10.1080/07924259.1992.9672261>
141. Hemmingsen W, MacKenzie K, Sagerup K, Remen M, Bloch-Hansen K, Imsland AKD. *Caligus elongatus* and other sea lice of the genus *Caligus* as parasites of farmed salmonids: a review. *Aquaculture*. 2020;522:735160.
142. Samsing F, Oppedal F, Dalvin S, Johnsen I, Vågseth T, Dempster T. Salmon lice (*Lepeophtheirus salmonis*) development times, body size, and reproductive outputs follow universal models of temperature dependence. *Can J Fish Aquat Sci*. 2016;73(12):1841-1851.
143. Heuch PA, Parsons A, Boxaspen K. Diel vertical migration: A possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? *Can J Fish Aquat Sci*. 1995;52(4):681-689. <https://doi.org/10.1139/f95-069>

144. Oppedal F, Samsing F, Dempster T, Wright DW, Bui S, Stien LH. Sea lice infestation levels decrease with deeper 'snorkel' barriers in Atlantic salmon sea-cages. *Pest Manag Sci.* 2017;73(9):1935-1943.
145. 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.
146. Morton A, Routledge R, Peet C, Ladwig A. Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada. *Can J Fish Aquat Sci.* 2004;61(2):147-157. <https://doi.org/10.1139/f04-016>
147. Hamre LA, Bui S, Oppedal F, Skern-Mauritzen R, Dalvin S. Development of the salmon louse *Lepeophtheirus salmonis* parasitic stages in temperatures ranging from 3 to 24 C. *Aquacult Environ Interact.* 2019;11:429-443.
148. Penston MJ, McKibben M, Hay DW, Gillibrand PA. Observations of sea lice distributions in Loch Shieldaig, Western Scotland. 2002. ICES CM, CM2002/T:09.
149. Nelson EJ, Robinson SMC, Feindel N, Sterling A, Byrne A, Pee AK. Horizontal and vertical distribution of sea lice larvae (*Lepeophtheirus salmonis*) in and around salmon farms in the Bay of Fundy, Canada. *J Fish Dis.* 2018;41(6):885-899.
150. Pike AW, Wadsworth SL. Sealice on salmonids: their biology and control. In: Baker, JR, Muller, R & Rollinson, D (Eds.), *Advances in Parasitology.* USA: Academic Press; 1999:233-337.
151. Kabata Z. Parasitic copepoda of British fishes. *Ray Society, London.* 1979;152:1-468.
152. Rittenhouse MA, Revie CW, Hurford A. A model for sea lice (*Lepeophtheirus salmonis*) dynamics in a seasonally changing environment. *Epidemics.* 2016;16:8-16.
153. Tucker CS, Sommerville C, Wootten R. The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon, *Salmo salar* L. *J Fish Dis.* 2000;23(5):309-320. <https://doi.org/10.1046/j.1365-2761.2000.00219.x>
154. Skern-Mauritzen R, Sissener NH, Sandvik AD, et al. Parasite development affect dispersal dynamics; infectivity, activity and energetic status in cohorts of salmon louse copepodids. *J Exp Mar Biol Ecol.* 2020;530:151429.
155. Dalvin S, Are Hamre L, Skern-Mauritzen R, et al. The effect of temperature on ability of *Lepeophtheirus salmonis* to infect and persist on Atlantic salmon. *J Fish Dis.* 2020;43(12):1519-1529.
156. Bricknell IR, Dalesman SJ, O'Shea B, Pert CC, Luntz AJM. Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. *Dis Aquat Organ.* 2006;71(3):201-212.
157. Groner ML, Laurin E, Stormoen M, Sanchez J, Fast MD, Revie CW. Evaluating the potential for sea lice to evolve freshwater tolerance as a consequence of freshwater treatments in salmon aquaculture. *Aquacult Environ Interact.* 2019;11:507-519.
158. Fish Farming Expert. Sea lice 'were expected' at offshore farm. Accessed Magazine Article. <https://www.fishfarmingexpert.com/article/sea-lice-were-expected-at-offshore-farm/>
159. Scottish Salmon Producers' Organisation. Scottish salmon sea lice reporting. <https://www.scottishsalmon.co.uk>
160. Scottish Government. Scotland's aquaculture. <https://www.aquaculture.scotland.gov.uk>
161. Burrows MT, Harvey R, Robb L. Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Mar Ecol Prog Ser.* 2008;353:1-12.
162. Garcia HE, Boyer TP, Locarnini RA, et al. World ocean atlas 2013. Volume 3, Dissolved oxygen, apparent oxygen utilization, and oxygen saturation. 2013.
163. Locarnini M, Mishonov AV, Baranova OK, et al. World ocean atlas 2018, volume 1: Temperature. 2018.
164. Zweng MM, Seidov D, Boyer T, et al. World ocean atlas 2018, volume 2: Salinity. 2019.
165. Kragestein TJ, Simonsen K, Visser AW, Andersen KH. Identifying salmon lice transmission characteristics between Faroese salmon farms. *Aquacult Environ Interact.* 2018;10:49-60.
166. Revie CW, Gettinby G, Wallace C. Identifying epidemiological factors affecting sea lice *Lepeophtheirus salmonis* abundance on Scottish salmon farms using general linear models. *Dis Aquat Organ.* 2003;57(1-2):85-95.
167. Samsing F, Solstorm D, Oppedal F, Solstorm F, Dempster T. Gone with the flow: current velocities mediate parasitic infestation of an aquatic host. *Int J Parasitol.* 2015;45(8):559-565.
168. Adams MB, Nowak BF. Amoebic gill disease: sequential pathology in cultured Atlantic salmon, *Salmo salar* L. *J Fish Dis.* 2003;26(10):601-614.
169. Oldham T, Rodger H, Nowak BF. Incidence and distribution of amoebic gill disease (AGD)—an epidemiological review. *Aquaculture.* 2016;457:35-42.
170. Lima PC, Taylor RS, Cook M. Pseudocyst formation in the marine parasitic amoeba *Neoparamoeba perurans*: a short-term survival strategy to abrupt salinity variation. *J Fish Dis.* 2017;40(8):1109-1113.
171. Walochnik J. 15 Amoebae. In: Florin-Christensen, M & Schnittger L (Eds.), *Parasitic Protozoa of Farm Animals and Pets.* USA: Springer; 2018;389.
172. Tanifuji G, Cenci U, Moog D, et al. Genome sequencing reveals metabolic and cellular interdependence in an amoeba-kinetoplastid symbiosis. *Sci Rep.* 2017;7(1):1-13.
173. Powell MD, Nowak BF, Adams MB. Cardiac morphology in relation to amoebic gill disease history in Atlantic salmon, *Salmo salar* L. *J Fish Dis.* 2002;25(4):209-215.
174. Rodger HD. Amoebic gill disease (AGD) in farmed salmon (*Salmo salar*) in Europe. *Fish Vet J.* 2014;14:16-27.
175. Hvas M, Karlsbakk E, Mæhle S, Wright DW, Oppedal F. The gill parasite *Paramoeba perurans* compromises aerobic scope, swimming capacity and ion balance in Atlantic salmon. *Conserv Physiol.* 2017;5(1):cox066.
176. Steinum T, Kvellestad A, Rønneberg LB, et al. First cases of amoebic gill disease (AGD) in Norwegian seawater farmed Atlantic salmon, *Salmo salar* L., and phylogeny of the causative amoeba using 18S cDNA sequences. *J Fish Dis.* 2008;31(3):205-214.
177. Powell MD, Fisk D, Nowak BF. Effects of graded hypoxia on Atlantic salmon infected with amoebic gill disease. *J Fish Biol.* 2000;57(4):1047-1057.
178. Fisk DM, Powell MD, Nowak BF. The effect of amoebic gill disease and hypoxia on survival and metabolic rate of Atlantic salmon (*Salmo salar*). *Bull Eur Assoc Fish Pathol.* 2002;22(3):190-194.
179. Powell MD. *Physiological and Clinical Pathology.* Scotian Press. 2006;336-356.
180. Leef MJ, Harris JO, Powell MD. Metabolic effects of amoebic gill disease (AGD) and chloramine-T exposure in seawater-acclimated Atlantic salmon *Salmo salar*. *Dis Aquat Organ.* 2007;78(1):37-44.
181. Chalmers L, Taylor JF, Roy W, Preston AC, Migaud H, Adams A. A comparison of disease susceptibility and innate immune response between diploid and triploid Atlantic salmon (*Salmo salar*) siblings following experimental infection with *Neoparamoeba perurans*, causative agent of amoebic gill disease. *Parasitology.* 2017;144(9):1229-1242.
182. Chang YC, Hamlin-Wright H, Monaghan S, et al. Changes in distribution, morphology and ultrastructure of chloride cell in Atlantic salmon during an AGD infection. *J Fish Dis.* 2019;42(10):1433-1446.
183. Gowen RJ, Tett P, Bresnan E, Davidson K, McKinney A. Anthropogenic nutrient enrichment and blooms of harmful phytoplankton. *Oceanogr Marine Biol.* 2012;50:65-126.
184. Berdalet E, Fleming LE, Gowen R, et al. Marine harmful algal blooms, human health and wellbeing: challenges and opportunities in the 21st century. *J Mar Biol Assoc UK.* 2016;96(1):61-91.

185. Davidson K, Jardine SL, Martino S, et al. 6 *The Economic Impacts of Harmful Algal Blooms on Salmon Cage Aquaculture*. GlobalHAB: *Evaluating, Reducing and Mitigating the Cost of Harmful Algal Blooms: A Compendium of Case Studies*. PICES Press. 2020;84.
186. Trainer VL, Davidson K, Wakita K, et al. *GlobalHAB: Evaluating, Reducing and Mitigating the Cost of Harmful Algal Blooms: A Compendium of Case Studies*. PICES Press. 2020;28(1):30-32.
187. Okaichi T. Red tides in the Seto inland Sea. In: Okaichi, T & Yanagi, T (Eds.), *Sustainable Development in the Seto Inland Sea, Japan-From the Viewpoint of Fisheries*; Finland: Terra Scientific Publishing; 1997.
188. Anderson DM, Rensel J, Forster J, Hart S. Harmful Algae Blooms: assessing Chile's historic HAB events of 2016. Global Aquaculture Alliance Report. 2016. www.aquaculturealliance.org/wp-content/uploads/2017/05/Final-Chile-report.pdf
189. Davidson K, Tett P, Gowen R. Harmful algal blooms. In: Hester, RE, *Marine Pollution and Human Health*; 2011:UK: Royal Society of Chemistry, 95-127.
190. Bell GR. Penetration of spines from a marine diatom into the gill tissue of lingcod (*Ophiodon elongatus*). *Nature*. 1961;192(4799):279-280.
191. Shilo M. Toxins of chrysophyceae. *Microbial Toxins*. 1971;3:67-103.
192. Clément A. Phytoplankton monitoring program in the fish farming region of South Chile. In: Smayda, TJ & Shimizu, Y (Eds.), *Toxic Phytoplankton Blooms in the Sea*. USA: Developements en Marine Biology; 1993;223-228.
193. Kent ML, Whyte JNC, LaTrace C. Gill lesions and mortality in seawater pen-reared Atlantic salmon *Salmo salar* associated with a dense bloom of *Skeletonema costatum* and *Thalassiosira* species. *Dis Aquat Organ*. 1995;22(1):77-81.
194. Bruno DW, Dear G, Seaton DD. Mortality associated with phytoplankton blooms among farmed Atlantic salmon, *Salmo salar* L., in Scotland. *Aquaculture*. 1989;78(3-4):217-222.
195. Treasurer JW, Hannah F, Cox D. Impact of a phytoplankton bloom on mortalities and feeding response of farmed Atlantic salmon, *Salmo salar*, in west Scotland. *Aquaculture*. 2003;218(1-4):103-113.
196. Bresnan E, Arévalo F, Belin C, et al. Diversity and regional distribution of harmful algal events along the Atlantic margin of Europe. *Harmful Algae*. 2021;102:101976.
197. Davidson K, Bresnan E. Shellfish toxicity in UK waters: a threat to human health? *Environmental Health*. 2009;8(S1):S12.
198. Bates SS, Bird CJ, Freitas ASWd, et al. Pennate diatom *Nitzschia pungens* as the primary source of domoic acid, a toxin in shellfish from eastern Prince Edward Island, Canada. *Can J Fish Aquat Sci*. 1989;46(7):1203-1215.
199. Fehling J, Davidson K, Bolch CJ, Bates SS. Growth and domoic acid production by *Pseudo-nitzschia seriata* (bacillariophyceae) under phosphate and silicate limitation. *J Phycol*. 2004;40(4):674-683.
200. Trainer VL, Bates SS, Lundholm N, et al. *Pseudo-nitzschia* physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health. *Harmful Algae*. 2012;14:271-300.
201. Lefebvre K, Silver M, Coale S, Tjeerdema R. Domoic acid in planktivorous fish in relation to toxic *Pseudo-nitzschia* cell densities. *Mar Biol*. 2002;140(3):625-631.
202. Lefebvre KA, Frame ER, Kendrick PS. Domoic acid and fish behavior: a review. *Harmful Algae*. 2012;13:126-130.
203. McCabe RM, Hickey BM, Kudela RM, et al. An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. *Geophys Res Lett*. 2016;43(19):10366-10376.
204. Thronson A, Quigg A. Fifty-five years of fish kills in coastal Texas. *Estuaries Coasts*. 2008;31(4):802-813.
205. Kudela RM, Gobler CJ. Harmful dinoflagellate blooms caused by *Cochlodinium* sp.: global expansion and ecological strategies facilitating bloom formation. *Harmful Algae*. 2012;14:71-86.
206. Brand LE, Campbell L, Bresnan E. *Karenia*: the biology and ecology of a toxic genus. *Harmful Algae*. 2012;14:156-178.
207. Tangen K. Blooms of *Gyrodinium aureolum* (Dinophyceae) in North European waters, accompanied by mortality in marine organisms. *Sarsia*. 1977;63(2):123-133.
208. Davidson K, Miller P, Wilding TA, et al. A large and prolonged bloom of *Karenia mikimotoi* in Scottish waters in 2006. *Harmful Algae*. 2009;8(2):349-361.
209. Baptie M, Swan SC. A red tide event associated with the dinoflagellate *Karenia mikimotoi* in the Firth of Clyde, Scotland. *Harmful Algae News*. 2017;58:6-7.
210. Smayda TJ. *Harmful Algal Bloom Communities in Scottish Coastal Waters: Relationship to Fish Farming and Regional Comparisons: A Review*. Scottish Executive, Rural Group; 2006.
211. Robinson M. Algae bloom decimates two BC fish farms. *Vancouver Sun* (Website). 2018.
212. Tett P. *Phytoplankton and the Fish Kills in Loch Striven*. Scottish Marine Biological Association, Internal Reports; 1980:25.
213. Gowen RJ, Lewis J, Bullock AM. *A Flagellate Bloom and Associated Mortalities of Farmed Salmon and Trout in Upper Loch Fyne*. Scottish Marine Biological Association; 1982.
214. Ayres PA, Seaton DD, Tett PB. Plankton blooms of economic importance to fisheries in UK waters 1968-1982. *ICES CM*. 1982;50:38.
215. Gowen RJ, Bradbury NB. The ecological impact of salmonid farming in coastal waters: a review. *Oceanogr Marine Biol*. 1987;25:563-575.
216. McGillicuddy DJ Jr, Signell RP, Stock CA, et al. A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine. *J Plankton Res*. 2003;25(9):1131-1138.
217. Davidson K, Anderson DM, Mateus M, et al. Forecasting the risk of harmful algal blooms. *Harmful Algae*. 2016;53:1-7.
218. Farrell H, Gentien P, Fernand L, et al. Scales characterising a high density thin layer of *Dinophysis acuta* Ehrenberg and its transport within a coastal jet. *Harmful Algae*. 2012;15:36-46.
219. Whyte C, Swan S, Davidson K. Changing wind patterns linked to unusually high *Dinophysis* blooms around the Shetland Islands, Scotland. *Harmful Algae*. 2014;39:365-373.
220. Kurekin AA, Miller PI, Van der Woerd HJ. Satellite discrimination of *Karenia mikimotoi* and *Phaeocystis* harmful algal blooms in European coastal waters: merged classification of ocean colour data. *Harmful Algae*. 2014;31:163-176.
221. Paterson RF, McNeill S, Mitchell E, et al. Environmental control of harmful dinoflagellates and diatoms in a fjordic system. *Harmful Algae*. 2017;69:1-17.
222. Hallegraeff GM. Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge. *J Phycol*. 2010;46(2):220-235.
223. Moore SK, Mantua NJ, Salathé EP Jr. Past trends and future scenarios for environmental conditions favoring the accumulation of paralytic shellfish toxins in Puget Sound shellfish. *Harmful Algae*. 2011;10(5):521-529.
224. Wells ML, Karlson B, Wulff A, et al. Future HAB science: directions and challenges in a changing climate. *Harmful Algae*. 2020;91:101632.
225. Callaway R, Shinn AP, Grenfell SE, et al. Review of climate change impacts on marine aquaculture in the UK and Ireland. *Aquat Conserv*. 2012;22(3):389-421.
226. Clinton M, Ferrier DEK, Martin SAM, Brierley AS. Impacts of jellyfish on marine cage aquaculture: an overview of existing knowledge and the challenges to finfish health. *ICES J Mar Sci*. 2021;78(5):1557-1573.
227. Kingsford MJ, Schlaefer JA, Morrissey SJ. Population structures and levels of connectivity for Scyphozoan and Cubozoan jellyfish. *Diversity*. 2021;13(4):174.
228. Vodopivec M, Peliz AJ, Malej A. Offshore marine constructions as propagators of moon jellyfish dispersal. *Environ Res Lett*. 2017;12(8):084003.

229. Bosch-Belmar M, Azzurro E, Pulis K, et al. Jellyfish blooms perception in Mediterranean finfish aquaculture. *Mar Policy*. 2017;76:1-7.
230. BBC. Nearly 50,000 salmon escaped from storm- damaged fish farm. 2020.
231. The Seattle Times. Atlantic salmon net pen's Puget Sound collapse wasn't first problem at fish farm. <https://www.seattletimes.com/seattle-news/environment/atlantic-salmon-net-pens-collapse-followed-earlier-breakdown/>
232. Farmer Fish. Salmar faces Ocean Farm escape probe. <https://www.fishfarmermagazine.com/news/salmar-faces-ocean-farm-escape-probe/>
233. DNV-GL. RU-OU-0503: Rules for Classification of Offshore fish farming units and installations. <http://www.rules.dnv.com/docs/pdf/DNV/ru-ou/2017-07/DNVGL-RU-OU-0503.pdf>
234. Bruset M. *Dynamic Analysis of a Floating Fish Cage with Feeding Systems*. University of Stavanger; 2019.
235. Lerøy Seafood Group. Preline. www.leroyseafood.com
236. Innovasea. Submersible aquaculture systems. www.innovasea.com/open-ocean-aquaculture/submersible-aquaculture-systems/
237. IMechE. Fish farming offers second life for unwanted oil rigs. www.imeche.org/news/news-article/fish-farming-offers-second-life-for-unwanted-oil-rigs
238. The Fish Site. Atlantis stocked with second deep diving cohort. 2020. www.thefishsite.com/articles/atlantis-stocked-with-second-deep-diving-cohort
239. Tsukrov II, Ozbay M, Swift MR, Celikkol B, Fredriksson DW, Baldwin K. Open ocean aquaculture engineering: numerical modeling. *Mar Technol Soc J*. 2000;34(1):29-40.
240. Cifuentes CA. *Dynamic Analysis of Cage Systems Under Waves and Current for Offshore Aquaculture*. Texas A&M University; 2016.
241. Fish Farming Expert. Promising results from Atlantis Subsea cage trials. <https://www.fishfarmingexpert.com/article/salmon-behaving-normally-in-atlantis-subsea-cage/>
242. Chu YI, Wang CM. Hydrodynamic response analysis of combined spar wind turbine and fish cage for offshore fish farms. *Int J Struct Stab Dyn*. 2020;20(8):2050104.
243. Kristiansen T, Faltinsen OM. Modelling of current loads on aquaculture net cages. *J Fluids Struct*. 2012;34:218-235.
244. Cifuentes C, Kim MH. Hydrodynamic response of a cage system under waves and currents using a Morison-force model. *Ocean Eng*. 2017;141:283-294.
245. Orcina. OrcaFlex Software. <http://www.orcina.com>
246. Kristiansen T, Faltinsen OM. Experimental and numerical study of an aquaculture net cage with floater in waves and current. *J Fluids Struct*. 2015;54:1-26.
247. AKVA Group. Cage farming aquaculture. www.akvagroup.com
248. Gjuka A. *Dynamic Analysis of Feed Pipes for Fish Farming in Open Sea*. University of Stavanger; 2017. <http://www.uis.brage.unit.no/uis-xmlui/handle/11250/2460089>
249. Kankainen M, Mikalsen R. Offshore fish farm investment and competitiveness in the Baltic Sea. *Rep Aquabest Project*. 2014;2:2014.
250. Gordelier T, Parish D, Thies PR, Johanning L. A novel mooring tether for highly-dynamic offshore applications; mitigating peak and fatigue loads via selectable axial stiffness. *J Mar Sci Eng*. 2015;3(4):1287-1310.
251. Harrold MJ, Thies PR, Newsam D, Ferreira CB, Johanning L. Large-scale testing of a hydraulic non-linear mooring system for floating offshore wind turbines. *Ocean Eng*. 2020;206:107386.
252. Chu YI, Wang CM, Park JC, Lader PF. Review of cage and containment tank designs for offshore fish farming. *Aquaculture*. 2020;519:734928.
253. Wu Y, Chaffey J, Law B, et al. A three-dimensional hydrodynamic model for aquaculture: a case study in the Bay of Fundy. *Aquacult Environ Interact*. 2014;5(3):235-248. <https://doi.org/10.3354/aei00108>
254. Mykssvoll MS, Sandvik AD, Albretsen J, et al. Evaluation of a national operational salmon lice monitoring system—From physics to fish. *PLoS One*. 2018;13(7):e0201338. <https://doi.org/10.1371/journal.pone.0201338>
255. Fletcher R. Why invest in offshore aquaculture production? <https://thefishsite.com/articles/why-invest-in-offshore-aquaculture-production>
256. Hassan W, Føre M, Ulvund JB, Alfredsen JA. Internet of Fish: Integration of acoustic telemetry with LPWAN for efficient real-time monitoring of fish in marine farms. *Comput Electron Agricult*. 2019;163:104850.
257. Føre M, Frank K, Norton T, et al. Precision fish farming: A new framework to improve production in aquaculture. *Biosys Eng*. 2018;173:176-193.
258. Li D, Wang Z, Wu S, Miao Z, Du L, Duan Y. Automatic recognition methods of fish feeding behavior in aquaculture: a review. *Aquaculture*. 2020;528:735508.
259. O'Donncha F, Stockwell CL, Planellas SR, et al. Data driven insight into fish behaviour and their use for precision aquaculture. *Front Anim Sci*. 2021;2:695054. <https://doi.org/10.3389/fanim.2021.695054>
260. Su B, Kelasidi E, Frank K, Haugen J, Føre M, Pedersen MO. An integrated approach for monitoring structural deformation of aquaculture net cages. *Ocean Eng*. 2021;219:108424.
261. O'Donncha F, Grant J. Precision aquaculture. *IEEE Internet Things Magazine*. 2019;2(4):26-30.
262. Xu G, Shi Y, Sun X, Shen W. Internet of things in marine environment monitoring: a review. *Sensors*. 2019;19(7):1711.
263. Rocha Aponte F, Tveterås S. On the drivers of cost changes in the Norwegian salmon aquaculture sector: a decomposition of a flexible cost function from 2001 to 2014. *Aquacult Econ Manage*. 2019;23(3):276-291.
264. Hvas M, Stien LH, Oppedal F. The metabolic rate response to feed withdrawal in Atlantic salmon post-smolts. *Aquaculture*. 2020;529:735690. <https://doi.org/10.1016/j.aquaculture.2020.735690>
265. Hvas M, Stien LH, Oppedal F. The effect of fasting period on swimming performance, blood parameters and stress recovery in Atlantic salmon post smolts. *Comp Biochem Physiol A: Mol Integr Physiol*. 2021;255:110913.
266. Balseiro P, Moe Ø, Gamlem I, et al. Comparison between Atlantic salmon *Salmo salar* post-smolts reared in open sea cages and in the Preline raceway semi-closed containment aquaculture system. *J Fish Biol*. 2018;93(3):567-579.
267. Morro B, Balseiro Vigo P, Albalat A, et al. Effects of temperature and photoperiod on rainbow trout (*Oncorhynchus mykiss*) smoltification and haematopoiesis. *Aquaculture*. 2019;519:734711.
268. Reimers E, Kjørrefjord AG, Stavøstrand SM. Compensatory growth and reduced maturation in second sea winter farmed Atlantic salmon following starvation in February and March. *J Fish Biol*. 1993;43(5):805-810.
269. Bloecher N, Floerl O. Towards cost-effective biofouling management in salmon aquaculture: a strategic outlook. *Rev Aquacult*. 2021;13(2):783-795.
270. Mohammad M-BM. Relationship between biofouling and growth of the pearl oyster *Pinctada fucata* (Gould) in Kuwait, Arabian Gulf. *Hydrobiologia*. 1976;51(2):129-138.
271. Mohammed S. On the epifouling of pearl oyster (*Pinctada radiata*) in Qatari water Arabian Gulf and its influence on the flesh growth. *Egypt J Aquat Biol Fish*. 1998;2(2):73-85.
272. Field B. Marine biofouling and its control: history and state-of-the-art review. *IEEE*. 1981;542-544.
273. Almeida LP, Coolen JWP. Modelling thickness variations of macrofouling communities on offshore platforms in the Dutch North Sea. *J Sea Res*. 2020;156:101836.

274. Greene JK, Grizzle RE. Successional development of fouling communities on open ocean aquaculture fish cages in the western Gulf of Maine, USA. *Aquaculture*. 2007;262(2-4):289-301.
275. Atalah J, Fletcher LM, Hopkins GA, Heasman K, Woods CMC, Forrest BM. Preliminary assessment of biofouling on offshore mussel farms. *J World Aquaculture Soc*. 2016;47(3):376-386.
276. Broch OJ, Daae RL, Ellingsen IH, et al. Spatiotemporal dispersal and deposition of fish farm wastes: a model study from central Norway. *Front Mar Sci*. 2017;4:199.
277. Jansen HM, Broch OJ, Bannister R, et al. Spatio-temporal dynamics in the dissolved nutrient waste plume from Norwegian salmon cage aquaculture. *Aquacult Environ Interact*. 2018;10:385-399.
278. Roberts C, Telfer T, Johnson I, et al. Impact of salmonid pen aquaculture on hard substrates. SARF090 Report, R2127 Scottish Aquaculture Research Forum (SARF). 2014.
279. Salvo F, Mersereau J, Hamoutene D, Belley R, Dufour SC. Spatial and temporal changes in epibenthic communities at deep, hard bottom aquaculture sites in Newfoundland. *Ecol Ind*. 2017;76:207-218.
280. Taranger GL, Karlsen Ø, Bannister RJ, et al. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *ICES J Mar Sci*. 2015;72(3):997-1021.
281. Hamoutene D, Salvo F, Donnet S, Dufour SC. The usage of visual indicators in regulatory monitoring at hard-bottom finfish aquaculture sites in Newfoundland (Canada). *Mar Pollut Bull*. 2016;108(1-2):232-241.
282. Sutherland TF, Sterling AM, Ou M. Influence of salmonid aquaculture activities on a rock-cliff epifaunal community in Jervis Inlet, British Columbia. *Mar Pollut Bull*. 2018;127:297-309.
283. Verhoeven JTP, Salvo F, Knight R, Hamoutene D, Dufour SC. Temporal bacterial surveillance of salmon aquaculture sites indicates a long lasting benthic impact with minimal recovery. *Front Microbiol*. 2018;9:3054.
284. He X, Sutherland TF, Pawlowski J, Abbott CL. Responses of foraminifera communities to aquaculture-derived organic enrichment as revealed by environmental DNA metabarcoding. *Mol Ecol*. 2019;28(5):1138-1153.
285. Watson L, Falconer L, Dale T, Telfer T, Watson Lauren, Falconer Lynne, Dale Trine & Telfer Trevor C. (2022) 'Offshore' salmon aquaculture and identifying the needs for environmental regulation. *Aquaculture*, 546, 737342.
286. Jansen HM, Reid GK, Bannister RJ, et al. Discrete water quality sampling at open-water aquaculture sites: limitations and strategies. *Aquacult Environ Interact*. 2016;8:463-480.
287. Corbin JS, Holmyard J, Lindell S. Regulation and permitting of standalone and co-located open ocean aquaculture facilities. In: Buck, BH & Langan, R (Eds.), *Aquaculture Perspective of Multi-Use Sites in the Open Ocean*. USA: Springer; 2017;187-229.
288. Mekonnen AD, Gorsevski PV. A web-based participatory GIS (PGIS) for offshore wind farm suitability within Lake Erie, Ohio. *Renew Sustain Energy Rev*. 2015;41:162-177.
289. Krause G, Billing S-L, Dennis J, et al. Visualizing the social in aquaculture: How social dimension components illustrate the effects of aquaculture across geographic scales. *Mar Policy*. 2020;118:103985.
290. Buck BH, Krause G, Rosenthal H. Extensive open ocean aquaculture development within wind farms in Germany: the prospect of offshore co-management and legal constraints. *Ocean Coast Manag*. 2004;47(3-4):95-122.
291. Jensen Ø, Dempster T, Thorstad EB, Uglem I, Fredheim A. Escapes of fishes from Norwegian sea-cage aquaculture: causes, consequences and prevention. *Aquacult Environ Interact*. 2010;1(1):71-83.
292. Callier MD, Byron CJ, Bengtson DA, et al. Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. *Rev Aquacult*. 2018;10(4):924-949.
293. Sanchez-Jerez P, Karakassis I, Massa F, et al. Aquaculture's struggle for space: the need for coastal spatial planning and the potential benefits of Allocated Zones for Aquaculture (AZAs) to avoid conflict and promote sustainability. *Aquacult Environ Interact*. 2016;8:41-54.
294. Gimpel A, Stelzenmüller V, Grote B, et al. A GIS modelling framework to evaluate marine spatial planning scenarios: Co-location of offshore wind farms and aquaculture in the German EEZ. *Mar Policy*. 2015;55:102-115.
295. Christie N, Smyth K, Barnes R, Elliott M. Co-location of activities and designations: a means of solving or creating problems in marine spatial planning? *Mar Policy*. 2014;43:254-261.
296. Di Tullio GR, Mariani P, Benassai G, Di Luccio D, Grieco L. Sustainable use of marine resources through offshore wind and mussel farm co-location. *Ecol Model*. 2018;367:34-41.
297. Van den Burg SWK, Kamermans P, Blanch M, et al. Business case for mussel aquaculture in offshore wind farms in the North Sea. *Mar Policy*. 2017;85:1-7.
298. Van den Burg SWK, Röckmann C, Banach JL, van Hoof L. Governing risks of multi-use: seaweed aquaculture at offshore wind farms. *Front Mar Sci*. 2020;7:60.
299. Belton B, Little DC, Zhang W, Edwards P, Skladany M, Thilsted SH. Farming fish in the sea will not nourish the world. *Nat Commun*. 2020;11(1):1-8.
300. Wilford A. *Effects of Offshore Farming on Welfare of Atlantic Salmon* (*Salmo salar*). University of Stirling; 2019.

How to cite this article: Morro B, Davidson K, Adams TP, et al. Offshore aquaculture of finfish: Big expectations at sea. *Rev Aquac*. 2022;14:791-815. <https://doi.org/10.1111/raq.12625>