A Review of Factors Affecting Farmed Atlantic Salmon (*Salmo salar*) Welfare in Australia and Beyond

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Abstract

With the increasingly global scale and scope of aquaculture, the need to match this development with improvements in fish welfare is a central societal and industry goal. We provide a comprehensive assessment of the farmed Atlantic salmon (*Salmo salar*) literature with targeted examples focusing on Atlantic salmon farmed in Tasmania, Australia. We synthesise insights from both small- and industry-scale perspectives, highlighting other reviews that provide discussions of particular sub-areas of farmed salmon research. We focus on recent advances and improved methods for farmed Atlantic salmon handling and management, behaviour, health issues and breeding. We also address wildlife interactions resulting from fish farming, as well as future research directions and system development. This review can serve as the basis for the development of aquaculture management guidelines that place individual fish welfare as a primary goal.

1. Introduction

There is evidence that fish are sentient and experience pain and suffering. Fish behaviour is known to be highly flexible, with a level of behavioural and cognitive sophistication that is equivalent to other classes of vertebrates and, in many cases, exceeds them (Bshary and Schaffer 2002, Bshary and Brown 2014, Pouca and Brown 2018, Vila Pouca and Brown 2018). For all human interactions with fish, the ethical and respectful treatment of these animals should be kept to the highest standards, which is especially true in the aquaculture industry. With the increasingly global scale and scope of aquaculture, the need to match this development with improvements in fish welfare should remain at the forefront of scientific and industrial advances (Cooper et al. 2023). This viewpoint is also reflected in growing public pressure on the aquaculture industry to minimise compromises to the welfare of individual fish.

The growth of this consensus is visible in welfare legislation and can be seen through formal recognition of animal sentience in the European Union, New Zealand and Australia in the Australian Capital Territory (ACT). The Animal Welfare Legislation Amendment Bill was passed in September 2019 making the ACT the first jurisdiction to recognise animal sentience in Australia. The main objects of this Act recognise that animals are sentient beings, have intrinsic value and that people have a duty of care for their mental and physical welfare. The objects are to be achieved in several ways, providing humane treatment and management of animals and preventing their abuse or neglect. Importantly, the absence of or freedom from suffering is not the only target. Within the Five Domains model, there is a strong focus on positive experiences and mental well-being (Mellor and Reid 1994, Colditz 2023). Research equips humans with the knowledge of how to provide positive welfare experiences and create opportunities for improving the mental states of a group or individual animals in particular situations.

Globally, the aquaculture industry is embracing welfare standards and there is growing recognition that happy, healthy fish produce a higher quality product, improving efficiency through increased health and feed conversion ratios among other benefits. In Australia, the status of fish under wider state and territory legislation is dependent upon their inclusion in the definition of the terms ‘animal’ and ‘vertebrate’. In terms of seafood production, the Tasmanian salmon industry is Australia’s highest-value seafood sector. Legislation does not yet mention sentience; however, fish are included in the definition of ‘animal’ under the Tasmanian Animal Welfare Act 1993.

Here we provide a comprehensive assessment of the farmed Atlantic salmon (*Salmo salar*) literature (through January 2024) with targeted examples relevant to aquaculture systems in Tasmania, Australia. Focal areas include handling and management, behaviour, health issues, wildlife interactions, and breeding. Specific information is provided in each of these areas that can be used as the basis to optimize aquaculture designs and conditions to ensure the welfare of salmon.

2. Handling and Management

2.1. Stocking Density

Density-dependence is a fundamental principle in ecology, i.e., that organism densities are a determinant of individual- or population-level traits or responses. This has direct management implications, including for salmonid populations (Grossman and Simon 2020, Matte et al. 2020). Herein, stocking density (also termed 'biodensity') is the salmon biomass per unit volume of water (often expressed in units of kg/m^3). It is one of the most fundamental variables to account for in salmon farming as it may lead to multiple density-dependent responses. In this context, we note juveniles typically are reared in land-based systems (of various types and designs referred to in this review) whereas adults are reared in marine pens. Such system-specific contexts in terms of facilities and fish life stages must be considered when seeking generalities regarding stocking density.

Studies typically assess response variables across stocking densities, within extremes of 8 and 125 kg/m^3, with most focusing on densities in the 10–40 kg/m^3 range. Response variables can be considered in general categories, such as mortality, growth-related factors and physiological effects. Since these variables are sensitive to many external and internal variables (see subsequent sections), at least an annual (preferably more frequent) review of stocking density is commonly suggested. Turnbull et al. (2008) provide a general overview and conceptual frameworks for the study of stocking density and here we highlight some more recent empirical studies since that review.

Salmon stocked in experimental tanks at a density of 30 kg/m^3 showed high levels of fin-biting and damage (Jones et al. 2011). Calabrese (2017) found that densities above 75 kg/m^3 compromised salmon post-smolt performance and welfare in flow-through seawater tanks. No negative effects of stocking density were noted at densities up to 86 kg/m^3 if water flow rate, water quality and food allocation were kept within recommended standards in experimental tanks (Berg et al. 1996). Although Jones et al. (2011) found salmon fin damage in experimental tanks was higher with high salmon densities, fish in low-density treatment groups had lower final weights, body lengths and condition. Thorarensen and Farrell (2011) indicate that stocking densities up to 80 kg/m^3 does not affect growth or survival, providing water quality is maintained, which is the main challenge at high densities, i.e., stocking density may affect salmon physiology (and thus growth) through indirect pathways. For example, high stocking densities of post-smolts in experimental saltwater tanks led to lower dissolved oxygen levels, increased CO_2 and ammonia, and decreased pH, which result in feedbacks affecting salmon physiology (Sundh et al. 2019). Therefore, there is a trade-off between stocking at higher densities with careful attention and control of water quality parameters vs. stocking at a lower density when there is high potential variability and less control of water quality parameters. Facilities with stocking densities set too high are more prone to unpredictable events realised through changes in water quality parameters, such as oxygen, temperature, or sulphur, as well as being more susceptible to disease spread.

Stocking density in recirculating aquaculture systems (RAS) (Mugwanya et al. 2022b) is a particular welfare concern because of the limited space inherent to the design of the systems. These systems are independent of natural environmental conditions and replace natural currents or circulation with water filtration and circulation systems. This greatly reduces water demand (up to a 99% reduction) compared to flow-through systems (Also see Section 7.1 and Minich et al. 2020). Wang et al. (2019) show several parameters (e.g., specific growth rate, final weight, feed conversion rate, hormone activities) are sensitive to stocking density and suggested the maximum density is 30 kg/m^3 for preferred yield outcomes in RAS.

Lower stocking densities (values not reported as kg/m^3) in RAS resulted in preferred concentrations of ammonium, nitrate and organic load, which supported a robust population of nitrifying bacteria (Dronen et al. 2021). Liu et al. (2015) found high stocking density (30–61 kg/m^3) had significant negative effects on growth and blood serum parameters. Liu et al. (2017) suggest that various growth and physiological factors are affected at densities >50 kg/m^3 in RAS, thus providing a specific maximum density recommendation for farming Atlantic salmon in these facilities.

There is less information for commercial marine pens. Jensen (2020) found a close link between density and mortality in commercial marine farms, although specific densities were not reported in the study. The RSPCA Australia Standard is 15 kg/m^3 in marine pens (RSPCA Australia 2020), which is at the low end of the spectrum compared to densities in land-based facilities. The intuitive thought is that negative density dependence should be common in all aquaculture farming stages but some studies do not find evidence for this (Delfosse et al. 2021). A foundational study suggested that density is one component of salmon welfare in marine pens, but other variables must be included in models to fully assess its relevance (Turnbull et al. 2005). Caution also should be taken when extrapolating results from tanks or mesocosms (where many density or water quality experiments are conducted) to larger-scale production systems (Gaffney and Lavery 2022). Determining the "golden stocking density"—one that maximises stocking density, yield, and fish welfare, in the context of numerous influencing variables—is an elusive, although principled, goal (but see Saraiva et al. 2022). As such, assessments of salmon stocking density for individual farming facilities are warranted.

2.2. Water Parameters

Numerous water parameters are relevant to salmon farming, including temperature, dissolved oxygen, salinity, nitrogen-containing compounds, pH, flow velocity, sulphur, and oceanographic conditions for marine production stages (Toni et al. 2019, Hvas et al. 2021a). Perhaps the most important takeaway from the literature is that it is difficult to isolate a single variable driving fish mortality, growth-related factors, and physiological effects, as these variables have complex interactions and are highly variable (e.g., Kristensen et al. 2012, Toni et al. 2019), and their relevance varies substantially across systems (particularly land-based vs. open-ocean stages of rearing). As such, in this broad review, it is hard to make generalisations, and system-specific studies are warranted when working toward optimal rearing strategies. We divide this overview into land-based rearing and marine sea pen stages, seeking consistent threads of recommended conditions that emerge.

Water quality is particularly critical in RAS because of the limited space and sensitive parameter variation in the enclosed conditions. For example, long-term nitrite exposure of post-smolts maintained in RAS can lead to nitrogen accumulation in fish, with implications for their health (Mortensen et al. 2022); long-term sulfur exposure is also a concern (Nicolaysen et al. 2024). Perhaps the most comprehensive review of water quality parameter recommendations for optimal salmon performance and welfare is found in Thorarensen and Farrell (2011) and we refer to that source. They include recommendations for oxygen saturation (80–100%), NH_3 (≤0.012 mg/L) and water exchange (≥0.2–0.3 L/min/kg), among others. They also recommend the use of a thermal growth coefficient to estimate growth rates (see details of the calculation therein). Ytrestoyl et al. (2020) found that post-smolt growth rate and feed conversion rate in RAS were higher at a lower salinity (12 ppt vs. 22 and 32 ppt) and 12 ppt resulted in the best skin morphology and lowest erosion of the caudal fin. Higher salinities were linked to mortality, elevated plasma cortisol levels, higher incidence of cataracts and a higher expression of stress-induced genes in the skin. These are logical findings, as 12 ppt is close to the salt density in fish blood, thus necessitating the least energy required for osmoregulatory processes.

Water flow in land-based systems can impact other traits, e.g., stress and immune responses are higher in fish skin at low flow (Sveen et al. 2016). Higher water velocities are preferred (e.g., ≥0.2–0.3 L/min/kg; Thorarensen and Farrell 2011), as it increases aerobic capacity and the efficiency of energy and protein utilization (Ytrestoyl et al. 2020). Although elevated temperatures are often used to increase growth in smolts, this also causes them to mature earlier than may be optimal (Crouse et al. 2022, Martinez et al. 2022, Martinez et al. 2023). Temperature also affects other traits, such as wound healing (Jensen et al. 2015). As such, the choice of temperature regime will vary widely based on which traits one wants to optimise. Much like the 'golden stocking density', managers should carry out facility-specific studies to find the temperature range which provides the best balance of maximising desired traits while minimising negative welfare outcomes (but see Lambert et al. 2024).

There is less specific information regarding optimal water quality in marine pens. Fossmark et al. (2021) compared brackish (3 ppt) and seawater (28 ppt) in RAS, and fish from the latter when transferred to marine pens had higher weights but also higher mortality (an intermediate salinity was not assessed). Once in pens, effects on performance and welfare are mediated indirectly via water quality parameters. Salinity and temperature may affect ectoparasite abundance (see Section 4.2) and thus salmon health (Groner et al. 2016). Mortality has been found to vary seasonally in freshwater farms in Norway, which is related to changes in water quality parameters (Gasnes et al. 2021). Shifts toward more saline and nutrient-rich waters drove harmful algal blooms in fjord systems of Chile, resulting in mass mortality of farmed salmon (Leon-Munoz et al. 2018). Tides, water transparency, and sea temperatures affect the densities of two algae species in Chile, which, at high densities, affects the behaviour and ultimately mortality rate of salmon. Meng et al. (2022) show how ocean warming will differentially affect the suitability of farming in different regions of Tasmania (see Section 7.5). Assessing optimal water parameters in sea pens warrants more consideration in future studies.

2.3. Lighting Regimes

Light has three components—colour, intensity and duration—all of which can influence salmon performance and welfare in land-based systems (Gaffney and Lavery 2022). Manipulation of artificial lighting regimes (e.g., different day lengths vs. continuous lighting) influences various reproductive and growth factors (Moccia et al. 2020). Although results vary widely among studies, the most apparent consensus is that continuous light (or very long light cycles) has undesirable effects on salmon rearing (Shulgina et al. 2021b). Unwanted male post-smolt maturation is highest under continuous light regimes as compared to different light-dark cycles—early male puberty is often not desired because it reduces hypo-osmoregulatory abilities and constrains growth, thereby prolonging the time to reach an optimal reproductive state (Fraser et al. 2023). In freshwater RAS, Martinez et al. (2021) found shifting to a light:dark 12:12 cycle from a continuous light regime resulted in compensatory growth and positive effects on smoltification. For fish reared in freshwater and brackish RAS, continuous light-reared smolts had reduced performance (compared to 12:12-reared fish) after being transferred to the sea, with this effect being size-dependent (Ytrestoyl et al. 2022). Consistent lighting regulates gene expression related to muscle growth in salmon yearlings (Shulgina et al. 2021a). Continuous light conditions also alter lipid profiles in salmon fingerlings (fry) (Nemova et al. 2020, Nemova et al. 2021). Notably, the effects of continuous light conditions may not occur across all life history stages and may be dependent on the period of maturation the fish are in, such that only in reproductively 'critical periods' will negative effects of continuous light on reproductive parameters be apparent (Taranger et al. 1999).

However, some studies have come to different conclusions, e.g., continuous light was related to a higher growth rate of salmon fingerlings in experimental tanks by affecting the aerobic and anaerobic capacity in their muscles (Churova et al. 2020), and continuous light following seawater transfer has been shown to result in higher muscle growth (Johnston et al. 2004). Another study demonstrated that 14 °C for six weeks with a long-day photoperiod minimises negative effects on growth and mortality for juvenile Atlantic salmon (van Rijn et al. 2021). As we have pointed out in other places in this review, emergent effects on salmon are tied to the site- and system-specific characteristics that preclude broad generalizations, but the balance of information suggests light/dark cycles are preferred to continuous light. One area for future research is the importance of sleep for salmon in various lighting regimes.

2.4. Feeding Regimes

A complete assessment of diet *composition* would comprise a review in itself, especially because different diets are aimed at maximising different traits in salmon. We defer to various other studies on this issue (Gillund and Myhr 2010, Hixson et al. 2014, Davidson et al. 2016, Emery et al. 2016, Harvey et al. 2016, McMeans et al. 2017, Caballero-Solares et al. 2018, Neuman et al. 2018, Weihe et al. 2018, Foroutani et al. 2020, Lovmo et al. 2021, Gaffney and Lavery 2022, Goglio et al. 2022, Kousoulaki et al. 2022, Sundell et al. 2022).

Instead, we highlight other aspects of feeding regimes: feeding frequency, predictability of delivery schedules, feed restriction and withdrawal and feed distribution. These regimes have many far-reaching impacts on water quality, waste, and feed conversion ratios. It was suggested early in salmon aquaculture research that frequency of feeding (up to 80 times a day) does not affect growth rates or size variation in post-smolts (Thomassen and Fjaera 1996). Conversely, Sun (2016) found that doubling the frequency from 2 to 4 meals per day (with the same total food mass) increases growth rates and final body weights. Flood et al. (2012) demonstrated that a single meal per day following the freshwater-to-seawater transfer of smolts results in significantly lower feed intake than that of a higher feeding frequency, consequently, multiple daily feeds were recommended following introduction to seawater. Jones (2012) examined predictable and unpredictable feed delivery schedules on the behaviour and welfare of Atlantic salmon parr and fish were more aggressive under predictable feeding schedules. However, greater dorsal fin damage in the unpredictable treatments was evidence of poorer welfare status in fish due to an organised network where individual members attained hierarchical roles according to their aggressive behaviour. There is no current consensus regarding feeding frequency and predictability.

Feeding restrictions are utilised in many circumstances, implemented for reasons ranging from maintaining water quality to preparing fish for stressful procedures (such as vaccinations, size sorting, transportation and slaughter). For example, Shi et al. (2017) used recirculating tanks to compare fish that had free access to self-feeders to ones that received meals at dawn, midday and dusk. The results indicated that time-restricted self-feeding resulted in fin damage to Atlantic salmon but had little effect on growth. Periods of food restriction depend on the issue being addressed and the extent of the restriction, as well as external factors such as temperature, water quality, disease incidence, and stocking density, among many others. These complexities render it difficult to make generalisations about the effects on fish condition, physiology and overall welfare. However, it has been noted that Atlantic salmon post-smolts can persist for up to 4 weeks without food without apparent implications for their welfare (Hvas et al. 2020b). Food restriction and withdrawal are discussed in detail by Gaffney and Laverly (2022) and we encourage a review of that paper for further information. Some agencies have specific guidelines, e.g., the European Food Safety Authority suggests 2–3 days is the minimum to reduce metabolic rates before handling and transport, as well as allow for clearing of digestive tracts (Algers et al. 2009). The RSPCA Australia Standard indicates any food restriction may not exceed 72 hours (RSPCA Australia 2020). A consensus for such recommendations remains unclear.

Food distribution is a key consideration in marine pens, which often takes the form of feed being distributed on the water surface by a pneumatic conveying system. This results in uneven pellet distribution but can be mediated by spreader airspeed and equipment angle/tilting, e.g., higher airspeeds have been shown to result in a more even spread of feed (Oehme et al. 2012). Alternative approaches, e.g., spreaders releasing pellets at different ballistic angles and equipment to increase throw length, provide promise for improved feed distribution (Skoien et al. 2018). Other studies emphasise that the hydraulic properties of feed pellets (e.g., sinking rates) need to be considered along with distribution patterns. Drones are being used to assess distribution patterns and inform spreader settings (Skoien et al. 2016, Lien et al. 2019), and the rapid technological advances in drone technology suggest tracking the fine-scale distribution of feed is within reach. Models have been developed on growth rates of Atlantic salmon in aquaculture production units, including the distribution of feed pellets, behaviour and energetics of the fish, and the abiotic conditions in the water column (Føre et al. 2016). Such models can be used to develop hypotheses on optimal pellet type and distribution regime. Adjustments to traditional systems may increase feed distribution efficiency and reduce wasted feed, e.g., by using echo sound to monitor fish biomass at feeding areas (Folkedal et al. 2022).

2.5. Direct Handling

Several procedures in the production pipeline require the handling of fish, including vaccination, transport, harvest and slaughter. Reducing stress during fish handling is a step toward a more sustainable industry that places welfare at its forefront. Fish face high stress when smolts are transported from freshwater systems to marine pens (Iversen et al. 2005, Nomura et al. 2009), as such, we frame most of this section on fish handling in the context of transport. Erikson et al. (2022) and Wedemeyer (1996) provide an overview of previous research on fish transport, including closed vs. open transport systems. One theme that emerges is that physical loading is more stressful than transport and that crowding (the process of reducing the available swimming area in an enclosure to facilitate removal)—even for the relatively short transport period—is problematic. As an empirical example, Erikson et al. (2022), in experimental tanks, simulated a 5 h open-boat transport (flow-through system) to closed transport (aerated system with no flow-through). They found more stress in the closed system and recommended that such a system is only viable if the transport duration is <2 hours—otherwise extensive water treatment is required. This is consistent with the results of Gatica et al. (2010a) who evaluated stress based on variables such as blood cortisol and osmolality. Another study, based on blood concentrations of cortisol, glucose, lactate, sodium, chloride and osmolality, found the most stressful stage was during pumping from resting pens to the processing plant, i.e., the last step of the process is least humane (Gatica et al. 2010b). The season in which smolts are transferred may also affect welfare (Myklatun et al. 2023). Yet, data are mixed on the stress incurred by introducing smolt to marine pens, with some studies showing less severe effects than others (Arnesen et al. 1998).

Other aspects of handling deserve more attention. For example, studies have explored the effects of simple handling, e.g., simply removing smolts from seawater tanks with nets and holding them out of water for just 15 seconds. Even in this limited handling situation, smolts showed significantly higher plasma cortisol levels and more attached copepodids than control salmon (Delfosse et al. 2021). Anaesthetics are a critical part of fish handling, specifically to alleviate stress, and have been well-reviewed elsewhere (Zahl et al. 2012, Chance et al. 2018, Priborsky and Velisek 2018, Martins et al. 2019). Studies have evaluated anaesthetics in the context of transport to sea (Sandodden et al. 2001), e.g., AQUI-S (5.0 mg/L) reduced mortality from 11.5% in unsedated fish to 2.5% in sedated individuals (Iversen and Eliassen 2009) and clove oil (4.0 mg/L) reduced mortality by 10% (Iversen et al. 2009). Other approaches include providing protection from microbial stressors, such as from the microalga *Heterosigma akashiwo* (Goncalves et al. 2022).

2.6. Humane Slaughter

Euthanasia and slaughter in salmonids were thoroughly reviewed by Gaffney and Laverly (2022) and we highlight some of their takeaway points. Gaffney and Laverly (2022) define a humane death as one that is quick, causes minimal stress and pain, and results in a rapid loss of consciousness followed by death without the ability to regain consciousness. Humane approaches for slaughtering salmon are both an explicit and tacit desire in salmon farming and society as a whole.

First, stunning and slaughter techniques are diverse, and optimal approaches will vary based on species, body size, prior holding conditions, density, personnel skill level, and various other internal (physiological) and external (environmental) variables. Despite such variation, percussive and electrical stunning have emerged as preferred methods, sometimes used in conjunction, i.e., electrical stunning followed by a percussion blow. Electronarcosis causes loss of consciousness much faster than ice immersion in rainbow trout (Bermejo-Poza et al. 2021). In general, ice immersion is considered to be an inhumane method of stunning and slaughter (Barkerud 2021). Likewise, water saturated with CO_2 triggers prolonged struggling (several minutes) suggesting unnecessary harm to fish, whereas fish are immobilised almost instantly when exposed to an electric current (Grans et al. 2016). Studies have yet to definitively identify the exact cause of death following percussive and electrical stunning, limiting our ability to fully assess the positives and negatives of these methods for slaughter. Bleeding out following electrical or percussive stunning is well-studied in mammals and birds (e.g., Aghwan et al. 2016, Saxmose et al. 2019), and this is commonly done by gill slitting in fish (Borderias and Sanchez-Alonso 2011). There are many studies regarding slaughter methods on fillet quality (Lerfall et al. 2015, Imsland et al. 2019, Skjold et al. 2020, Rotabakk et al. 2022), but less information is published on how variation in methods and conditions (e.g., variables such as crowding conditions and pumping system) affect fish welfare.

Focusing specifically on the choice between percussive and electrical stunning, the information is somewhat ambiguous. For a review of these approaches, see Lambooij et al. (2010). The authors indicate that both approaches can be humane if carried out correctly, although they note that visual verification of consciousness is not reliable. As such, they suggest the use of electroencephalography (EEG) to infer fish welfare, as do general animal welfare reviews (Kumar et al. 2022). Yet, using seizures and visually-evoked responses may not reflect the actual conscious state (e.g., Hjelmstedt et al. 2022) and using EEG to more reliably assess consciousness is not viable at an industrial scale. Further research is needed using EEG data to link to specific behavioural indicators that can then be used to assess the most humane methods.

For electrical stunning, Lambooij et al. (2010) suggest combined AC and DC results in stunning to unconsciousness within 5 seconds. Other studies have further investigated optimal currency ranges for stunning (Grimsbo et al. 2014, Grimsbo et al. 2016). Lines et al. (2003) mention, that for the trout industry, individual percussion and bleeding by hand is uneconomic, yet high-speed machinery to bleed fish automatically would be complex and expensive. Thus, an industrial benefit of electrical stunning is that it does not require individual handling of fish (Robb and Roth 2003); conversely, individual handling during percussive stunning allows for faster stunning speed and the best chance at visual unconsciousness verification. Although both percussive and electrical approaches are preferred methods to alternatives, there is less information directly comparing these two and specifics of using them in combination are not detailed.

2.7. Genetic Considerations

The rapid development of genetic methodologies has provided new insights into aquaculture strategies. For example, transcriptome analysis has been used to characterise gene expression patterns involved in immune responses to microbial infections, e.g., detecting pilchard orthomyxovirus, a virus of vital concern in Tasmania (Samsing et al. 2022). Such approaches can be used to examine physiological responses to abiotic and biotic stressors (Alipio et al. 2022, Gervais et al. 2022), determine optimal rearing conditions for promoting immunocompetence (Ellison et al. 2020), help reduce disease outbreaks, (Ajasa et al. 2024) and develop more efficacious vaccines against infection (Fu et al. 2022). Genetic techniques also have demonstrated that quantifying hormone expression can guide the determination of optimal stocking densities, by using peptide hormones as biomarkers to analyse the physiological response of Atlantic salmon to population densities (Alvarez et al. 2022). Intestinal health variation across different diets (e.g., proportions of saturated vs. unsaturated fat) can be revealed by gene expression patterns, as can physiological stress-coping mechanisms (Lovmo et al. 2020, Lazado et al. 2022b). Advanced genetic techniques also empower genetic selection regimes (Naeve et al. 2022) and gene editing (Blix and Myhr 2023) for optimising salmon production. Efforts are moving toward commercial scales, such as in the selective breeding program of the Australian Salmon Enterprises of Tasmania (SALTAS) (Verbyla et al. 2022). These approaches may facilitate rapid trait selection (e.g., personality traits) that are better suited to aquaculture conditions.

3. Behaviour

Behaviour is a key, non-invasive, welfare indicator that is highly plastic and reflects changes in internal and external factors affecting salmon (Barreto et al. 2022). A first-level analysis of farmed Atlantic salmon behaviour is to point out the obvious, i.e., the behaviour of farmed fish is significantly different from that of wild fish (Huntingford 2004, Naslund 2021). Differences from wild environments include the confined space, lack of migratory behaviour, high-quality food always made available, protection from predators (for the most part), and the fact that diseases can be treated. Other challenges remain, e.g., high densities can result in more aggressive intraspecific interactions and higher incidence and spread of parasites and disease. The direct handling of fish by humans, including transport and associated crowding and pumping, is a stressor not faced by wild salmon. The potential for genetic interventions, including selective breeding and gene editing, can speed evolution toward desired traits much faster than happens in wild populations.

There are general reviews (i.e., across species and farming systems) linking fish behaviour and their welfare (Ellis et al. 2012, Martins et al. 2012, Segner et al. 2012, Macaulay et al. 2021a, Rey et al. 2021, Barreto et al. 2022). Changes in foraging, aggression, swimming mode, sociality, and physiologically related behavioural traits (such as ventilation rate) have been linked with acute and chronic stressors in production systems and are considered indicators of welfare. Martins et al. (2012) write that “welfare indicators that are relevant for inclusion in an operational welfare assessment system should be science-based, should measure welfare over extended periods, should be measurable on a commercial farm within a realistic framework and should be relevant as a decision support system for the farmer.” We use this definition to frame our discussion herein.

In this section, we provide information that can be used to work toward operational welfare indicators (OWIs) for salmon based on observational and experimental scientific evidence (Kristiansen et al. 2020). We organise around three topical areas—environmental drivers of behaviour, cognition and effects on behaviour following environmental enrichment. We then discuss practical issues regarding monitoring systems and equipment, as well as welfare modelling.

3.1. Environmental Drivers

A foundational study reviewed the effects of numerous environmental variables on Atlantic salmon behaviour (Oppedal et al. 2011, see Table 1 in particular), and we do not repeat their findings and references here. Briefly, the authors address influences on fish behaviour from light regimes, temperature, salinity, dissolved oxygen, water current velocity, and sea lice treatments (as well as combinations of these environmental drivers), providing robust guidelines for environmental variable target levels. We highlight more recent studies, with a focus on conditions relevant to welfare in marine pens based on current velocity, waves, temperature, oxygen, and surface air access.

3.1.1. Currents and Wave Action

With the greatly expanding scale and scope of salmonid coastal farms (McIntosh et al. 2022a), and with finite sheltered areas for farms, exposed offshore sites are increasingly being considered (Gentry et al. 2017, Hvas et al. 2021a, Føre et al. 2022, Morro et al. 2022). In this context, it is critical to understand the effects on behaviour due to currents and wave action, as well as interactions between the two (Johannesen et al. 2020). Other environmental variables, such as temperature, can further interact with wave energy to affect the condition of salmon (Szewczyk et al. 2024). It can be argued that conditions that force the fish to swim at speeds dictated by the environment rather than at their preferred cruising speed will result in poor welfare since they violate the freedom to express normal behaviour that they would express in the wild (Johansson et al. 2014, Hvas et al. 2021a).

At high current velocities, salmon switch from a circular, polarised group structure assumed at lower velocities (Føre et al. 2009, Johansson et al. 2014, Hvas et al. 2017b) to a formation where fish keep orientations at fixed positions swimming against currents (Johansson et al. 2014). Yet, salmon do tend to move to portions of pens with lower currents when velocities are too extreme (Johannesen et al. 2022). More concerning is when currents are so strong they push the fish to the down-current side of the pen, resulting in various unwanted physiological effects and even mortality (Hvas et al. 2021a). Hvas et al. (2021b) found individual smolts were able to sustain continuous swimming for more than 72 h without becoming fatigued, but fish swimming above >85% critical swimming speed (i.e., the fastest pace a fish can maintain an aerobic swimming threshold continuously without exhaustion) reached fatigue within a few hours. They suggest a current threshold of ≤2.3 body lengths/sec allows fish to maintain swimming performance for long periods, perhaps enhancing their fitness. Solstorm et al. (2016b) observed behaviour and fin erosion on post-smolt salmon stocked at 39 kg/m^3 in raceways at water current velocities of 1.5, 0.8, and 0.2 body lengths/sec, and found that moderate velocities are best from a welfare perspective. At slower velocities, between-individual interactions could be stressful for the fish; at faster velocities, fish collide with obstacles and exhibit fin erosion. For farms on the Norwegian coast, Jonsdottir et al. (2019) found that only 1 of 5 exposed sites had any currents that exceeded critical swimming speeds. In sum, as a welfare guideline (Hvas et al. 2021a), chronic current conditions at exposed sites should not exceed 60% of the critical swimming speed.

An ocean wave is defined as a periodic surface movement constrained to the uppermost layer of the water column (Hvas et al. 2021a). Waves interact in idiosyncratic ways with currents to influence fish behaviour. For example, Johannesen et al. (2020) found in weak currents, fish moved further down in pens under larger wave scenarios; stronger currents caused fish to move up in pens regardless of wave conditions. Hydrologic conditions had more of an effect on fish behaviour during the day than at night. In extreme scenarios (heights up to 2.9 m), waves affect the bottom of pens, eliminating the bottom as a refuge from wave stress. In general, waves drive fish to the more sheltered side of pens, decreasing utilised space (Johannesen et al. 2022). Research in an M.S. thesis suggested shoaling behaviour breaks down in wave patterns with heights of 2–2.5 m (Dam 2015). Little other information is available and thus wave effects on behaviour and welfare warrant further study as offshore aquaculture sites expand.

3.1.2. Temperature

For temperature, the transfer of smolts is one of the most stressful periods in the production process. Tang et al. (2022) simulated transfer from a lab-rearing preferred temperature (13 °C) to a series of lower temperatures. Based on measurements of plasma cortisol and expression of key genes involved in telencephalic regulation, which are linked to emergent behavioural patterns to cope with stress, they suggested exposing post-smolts at 13 °C to temperature reductions of 6 degrees °C or greater should be avoided in transfers to minimise fish stress. Salmon in Newfoundland, Canada, marine pens were found to move to areas of the pen with a temperature of 14–18 °C, which translated to distributions in deeper pens during summer (Gamperl et al. 2021). Breau et al. (2011) measured behaviour (feeding and stress responses) and physiological variables in wild 0+ (less than one year) and 2+ (2-year-old) wild Atlantic salmon acclimated to water temperatures between 16 and 28 °C. Their results showed that 2+ year Atlantic salmon employ behavioural responses (e.g., movement to cool-water sites) at higher temperatures, thereby mitigating physiological imbalances.

In experiments conducted in Macquarie Harbour, Tasmania, salmon preferred temperatures 16.5 °C to 17.5 °C, yet this could be overridden by avoidance of areas with low oxygen saturation (<35%); salmon also avoided the warmest surface waters (>20.1 °C, Stehfest et al. 2017). Combined, these factors led to significantly reduced space utilisation in the pens and high localised fish densities. As such, water parameters can intensify negative density dependence (see Section 2.1) thereby affecting welfare. Temperature also influences swimming behaviour, as swimming capacity decreases at both high (above 18 °C) and low (below 14 °C) extremes (Hvas et al. 2017a). Most behavioural and physiological traits follow this response curve. Land-based experimental results need to be placed in the context of ocean warming, especially in cold water areas such as Tasmania and Norway (Calado et al. 2021, Meng et al. 2022), to predict the regional areas that will be more or less suitable for aquaculture into the future.

3.1.3. Oxygen

Atlantic salmon become stressed and exhibit a reduced appetite at oxygen levels below 4–6 mg L-1 (Burke et al. 2021), and this can be mediated by temperature and currents among other factors. Metabolic rates of salmon have been found to decrease linearly below 27% saturation (Hvas and Oppedal 2019). Oldham et al. (2017) used tarps wrapped around marine pens to reduce oxygen saturation. Salmon swam 1.5 to 2.7 times slower than individuals in control pens, and they swam above or below the most hypoxic layer. Yet, temperature and salinity explained more of the variance in fish distribution, suggesting oxygen is a secondary, although non-trivial, factor affecting fish behaviour. Hypoxic conditions can accelerate the spread of diseases, such as amoebic gill disease, with oxygen saturation at 40–60% compared to >90% of control conditions (Oldham et al. 2020). Oxygen is considered to be of less importance in exposed open marine pen sites because conditions are typically within ranges that do not affect swimming capacity. As such, studies on how oxygen (and how it is mediated by temperatures) affects behaviour and welfare should be prioritised for sheltered farms where oxygen levels are more likely to fall below acceptable levels.

3.1.4. Surface Access

Behaviour is related to buoyancy regulation, as salmon have a physostomous swim bladder that they fill by gulping air from the surface (Sievers et al. 2018, Macaulay et al. 2020). Glaropoulos et al. (2019) showed that fish swam fast and had tight schools when pens were submerged for days. But when pens were lifted to the surface allowing air access, increased jumping and rolling behaviour indicated the salmon had previously been negatively buoyant. They suggest at least weekly surface access is a desired schedule to promote salmon welfare. Pens can also be fitted with air domes to mimic surface access (Warren-Myers et al. 2022).

3.1.5. Pen Design and Maintenance

Pen size and design affect environmental variables, such as dissolved oxygen (Alver et al. 2023), thus indirectly influencing fish behaviour and welfare. Cleaning of marine nets releases biofouling debris that can contribute to thrombi/subacute vascular lesions in the gills, although such effects may be limited to a small proportion of fish over short periods (Ostevik et al. 2021). Early studies suggested biofouling communities may support microbial communities that lead to amoebic gill disease outbreaks (Tan et al. 2002), but a more recent study suggests that is not the case (Jevne et al. 2020). It appears net cleaning may be an important management procedure that can impact welfare by improving water flow or removing harmful organisms. Yet, the mechanical process of net cleaning itself can be stressful for fish and more research is needed to determine the optimal frequency and methods to ensure fish welfare.

3.2. Cognition

Fish cognition has been well-reviewed elsewhere (Allen 2013, Braithwaite et al. 2013, Bshary et al. 2014, Lucon-Xiccato and Bisazza 2017), so we focus on salmonid-specific studies. First, affective states are defined as the state reflecting the valence, positive or negative, of emotions over time, reflecting cognitive abilities (Mendl et al. 2010). Salmon can display behavioural reactions indicative of the affective state of frustration in response to the omission of an expected reward (OER) (Vindas et al. 2012). Vindas et al. (2012) conditioned fish to associate a flashing light (a conditioned stimulus, CS) with feeding opportunities. Conditioning led to a shift from aversion to a positive response to the CS. Fish were then subjected to an OER, in which the food was delayed for 30 min for two of three daily meals. The OER fish (compared to controls) displayed higher levels of aggression and a more pronounced social hierarchy, demonstrating behavioural flexibility based on affective states (Vindas et al. 2012). Vindas et al. (2014b) extended their earlier study to show the neural plasticity of a frustrating non-reward, representing a foothold for the study of the links among cognition, behaviour, and welfare. Bratland et al. (2010) demonstrated habituation and associative learning in salmon exposed to what was, at first, aversive stimuli. Rainbow trout (*Oncorhynchus mykiss*) are capable of discriminating between cues during judgement bias tests, demonstrating an affective state in responding to positive rewards (Anderson et al. 2022). Behaviours also can feedback to influence neurology, e.g., swimming exercise has been linked to increased telencephalic neurogenesis and neural plasticity in salmon (Mes et al. 2020). These are intriguing directions with implications for feeding regimes in farmed systems and more research is needed to provide clarity on links between behaviours and welfare.

Animal personality is another perspective, i.e., examining individual-level repeatability and significant correlations between suites of behaviours (Sih et al. 2015, Axling et al. 2023). One such variation in traits has been termed ‘coping styles’, i.e., a consistent set of behavioural and physiological responses to stress at the individual level (Koolhaas et al. 1999, Berlinghieri et al. 2021). Vaz-Serrano et al. (2011) studied behavioural traits of farmed salmon fry, comparing individuals with an early or late time to emerge. Behavioural stress coping styles were consistent for individuals 2 and 5 months after emergence reflecting unique individual personalities were maintained. In other words, even in relatively homogeneous and stable conditions in a rearing environment, individual-level variation was notable. Individual variation in stress responsiveness is reflected in the visual appearance of salmon (Kittilsen et al. 2009). Individuals with more spots show reduced physiological and behavioural responses to stress, thus a visual indicator to assess individual-level fish behaviour. Damsgard et al. (2019) demonstrated a link between proactive behavioural coping to hypoxia stress and high growth rates. Also, individuals that are the fastest to arrive at feeding areas may have an advantage in procuring the resource (Harwood et al. 2003). Vindas et al. (2017) showed differences in forebrain neural and endocrine responses in proactive vs. reactive fish. These studies introduce the importance of individual-level-based fish welfare studies, as ‘mean’ population traits may mask variation in behaviour and welfare among individuals in aquaculture systems

(Schraml et al. 2021, Torgerson-White and Sanchez-Suarez 2022). Selecting for personality traits, such as for specific coping styles, may be beneficial in shaping the behaviour of fishes to be better suited for aquaculture conditions.

3.3. Environmental Enrichment

Environmental enrichment is a deliberate increase in environmental complexity to reduce maladaptive and aberrant traits in fish reared in otherwise stimuli-deprived environments (Naslund and Johnsson 2016). In aquaculture, it refers to providing new environmental stimuli (such as structure) to help captive fish meet their physiological, behavioural, and psychological needs (Arechavala-Lopez et al. 2022, Kleiber et al. 2023, Zhang et al. 2023). For example, adding complexity in a rearing environment promotes cognitive abilities and improves brain plasticity (Salvanes et al. 2013). Alnes et al. (2021), using structure manipulations in tanks, show that Atlantic salmon are sensitive to structural stimuli when they are parr, but not fry. Parr deprived of enrichment are less likely to explore mazes and often remain still, indicating stress. Exposure to enrichment can also impact other behavioural traits including laterality and personality (Brown & Bibost 2014) which can have welfare implications (Berlinghieri et al. 2021). For rainbow trout, weight gain, feed conversion ratio, individual fish length and fish weight are significantly higher in structurally complex tanks compared to unenriched controls (Crank et al. 2019). Simple air bubbles have been used to condition trout responses to feeding, and feeding predictability following bubbling resulted in fewer pre-feeding agonistic behaviours (Kleiber et al. 2022). Also for trout, frustrative reward omission increases aggression in fishes inferior in the social hierarchy (Vindas et al. 2014a).

Even though aquaculture fish are not released into the wild as are fish from hatchery stocking programmes, hatchery-based studies are informative about the cognitive and physiological benefits of enrichment. Naslund et al. (2013) and Cogliati (2022) demonstrate that structural complexity can influence exploration behaviour in Atlantic salmon and Chinook salmon (*Oncorhynchus tshawytscha*). Naslund et al. (2013) examined pre-smolt Atlantic salmon from three different environmental treatments: barren environment, plastic tube enrichment, and plastic shredding enrichment. Blood cortisol levels and fin deterioration were higher in barren treatments, reflecting aggressive behaviours and higher stress levels. Bergendahl (2016) demonstrated that salmon reared in enriched conditions had enhanced spatial learning abilities. Mes et al. (2019) showed the presence of rocks and artificial plants affects forebrain gene expression which translated into higher survival of fish in the wild. Reiser et al. (2021) show, in rainbow trout, that enrichment can even mediate epigenetic patterns, including DNA-methylation, indicating improved brain function when fish are reared in more structurally complex environments. For more examples, enrichments in captive environments are summarised in Naslund and Johnsson (2016), Naslund (2021), and Johnsson (2014).

Although not a common practice in either land-based facilities or marine pens, the fact that the simple addition of structure can mediate fish behaviour provides important insights into salmonid cognitive abilities and cognitive links to the environment. Jones et al. (2021) point out that many aspects of enrichment are poorly detailed in studies and they highlight those that could be quantified using their DETAILS approach: dimensions, ecological rationale, timing, amount, inputs, lighting, and social environment. There is not one type of enrichment approach that is common across studies, so specific recommendations are not available (but for a general overview see Arechavala-Lopez et al. 2022). That being stated, designing tanks or pens with almost any type of structure seems to improve salmon welfare by inducing brain activity and behavioural shifts.

3.4. Monitoring Systems and Equipment

A review by Macaulay et al. (2021b) is the best source for details on biotelemetry tagging to study fish behaviour (with most studies in the review focusing on salmonids). For example, Stehfest et al. (2017) used VEMCO acoustic telemetry tags to log temperature and dissolved oxygen conditions and fish distributions. Hassan et al. (2022) coupled telemetry tagging with a Doppler computation algorithm to quantify swimming speeds and movement patterns. Star-Oddi milli-HRT ACT and Milli-TD data loggers were used to monitor the welfare of salmon in aquaculture facilities in Newfoundland, including 3D acceleration (i.e., activity/behaviour), electrocardiograms (heart rate and heart rate variability), depth, and temperature (Gamperl et al. 2021). Kolarevic et al. (2021) and Calduch-Giner et al. (2022) employed the miniaturised biosensor AEFishBIT, a tri-axial accelerometer with a sampling frequency of 50–100 Hz, to track measurements of physical activities, respiratory rates, and metabolic activities. Heart rate (HR) bio-loggers have been used to monitor fish physiology, which can be used to infer fish activity levels (Hvas et al. 2020a).

One study showed untagged conspecifics had significantly higher weights, fork lengths and condition factors than tagged fish, suggesting a negative effect on fish welfare (Hvas et al. 2020a). This is consistent with reductions in growth rates following transplantation of heart rate biologgers as shown by Warren-Myers et al. (2021). Macaulay et al. (2021b) quantified mortality of tagged fish was ~10 times higher in sea pens than in tanks and the mortality of tagged fish was higher in longer trials (from 4% in single-day trials to 36% after 100 days). Further, electronic tags have been shown to increase mortality via effects on fish buoyancy (Wright et al. 2019). Higher mortality and reduced performance rates for tagged fish, coupled with unknown sublethal effects on behaviour, must be considered when interpreting tagging study results (Macaulay et al. 2021b), and these authors provide an extensive list of recommendations for quantifying the effects of tags on fish welfare (see Table 3 therein). Although providing valuable and otherwise unobtainable information (Brijs et al. 2021), tagging data should be qualified accordingly, inferences made with appropriate caution, and fish welfare incorporated into decision-making on the pros and cons of employing tagging studies (Virtanen et al. 2023).

3.5. Welfare Models

Models for assessing fish welfare are another tool to ensure that desired rearing conditions are met in commercial operations. The Salmon Welfare Index Model (SWIM 1.0) provides a tool for aquaculture facility managers to apply a standardised system using specific welfare indicators (Stien et al. 2013). It compiles all of the available welfare proxies and environmental variables (such as those discussed in this paper) into a single model, termed a ‘semantic’ model by the authors. It focuses on rigorous science-backed metrics, with the qualification that they can be readily measured by managers on a farm. The input indicators included are water temperature, salinity, oxygen saturation, water current, stocking density, lighting, disturbance, daily mortality rate, appetite, sea lice infestation ratio, condition factor, emaciation state, vertebral deformation, maturation stage, smoltification state, fin condition and skin condition (Stien et al. 2013). The SWIM model does not include behaviour as a key indicator or positive welfare states, perhaps because it is too subjective to assess across systems. SWIM 2.0 (Pettersen et al. 2014), targeted for fish health veterinarians/inspectors, extended the original model to include metrics based on eyes, cardiac condition, abdominal organs, gills, opercula, skeletal muscles, vaccine-related pathology, aberrant fish, necropsy of dead fish, and active euthanasia. We could only find one example of the application of these models published in a refereed journal. Folkedal et al. (2016) studied ten farms on the Norwegian coast and found the evaluations were relatively quick and produced welfare index scores that largely agreed with farmers’ rankings of their pens—the authors proffer that the SWIM model is a promising avenue to assess salmon in sea pens. It is unclear why SWIM models have not been applied more broadly. More recently, a Qualitative Behavioral Assessment model was proposed based on fish behaviour, e.g., using descriptors reflecting relaxation, agitation, lethargy, or confidence (Jarvis et al. 2021)—it has since found some support as a welfare indicator (Wiese et al. 2023). Digital techniques to analyse external morphological traits have also been introduced (Lindberg et al. 2023).

4. Health Issues

4.1. Disease

Diseases of most concern vary among countries, a complete survey of which is beyond the scope of this review. We take Tasmanian salmon farming as a case study which can be used as a guide for issues related to the incidence, physiopathology, environmental drivers, and treatment for diseases. Amoebic gill disease (AGD) was first described in Tasmania, in the 1980s and it is now found in most salmon-producing regions globally. It is caused by the free-living, facultative, protozoan ectoparasite *Neoparamoeba perurans*—see Oldham et al. (2016) for a detailed review of its biology. In short, *N. perurans* colonises gills, leading to the expansion of the lamellar epithelium and generating surplus gill mucus. The disease tends to spread more readily in warmer months and decreases the tolerance of salmon to environmental stressors, resulting in increases in basal energy requirements and a reduction in hypoxia tolerance (Bowden et al. 2022). Fish affected are characterised by lethargy, anorexia and increased ventilation rates (Oldham et al. 2016). Extreme incidence led to mortality greater than 80% in Norway in 2006 (Steinum et al. 2008) and has been estimated to increase the cost of rearing salmon by 20% in Tasmania (Kube et al. 2012).

Recent studies highlight factors that may affect the incidence of amoebic gill disease. Cyclic hypoxia exposure, which may be found in diel patterns of aquaculture pens, accelerates the progression of AGD in post-smolts (Oldham et al. 2020). Large Atlantic salmon have significantly lower gill parasite burdens and reduced AGD-related pathologies compared to small fishes (Smith et al. 2022). Intense fish crowding in narrow depth bands can lead to increased AGD risk (Wright et al. 2017). Marcos-Lopez and Rodger (2020) provide the most recent review of host responses to this disease, with foci including pathophysiology, immune responses, mucus characterisation, and oxidative stress patterns, and we defer to their study for extensive detail. Since the biology of AGD is covered in depth by other reviews (Oldham et al. 2016, Marcos-Lopez and Rodger 2020), we focus on recent disease treatment aspects that are relevant to salmon welfare.

Table 3 in Oldham et al. (2016) summarises the commonly used treatment approaches, including variations of two commercially utilised treatments, freshwater or hydrogen peroxide bathing, as well as some oral treatments. The efficacy of the approaches varies widely, depending on the specifics of the treatment regime and the system in which it is employed. Of the limitations identified, they point out two points regarding future treatments: (1) the development of a vaccine will continue to be a significant challenge in the near future and (2) there is a clear need for research on novel treatments. As for the first point, Hudson and Nowak (2021) update the limited progress that has been made toward vaccines based on a discussion of the design of challenge experiments and endpoints in experimental trials. They also suggest effective vaccines for AGD do not seem imminent (but we note vaccines are more widely used for other diseases) (Bakke et al. 2021, Avendano-Herrera et al. 2022).

As for the second point in Oldham et al. (2016), a common thread in the literature is that alternative treatment approaches have not proved promising. Hudson et al. (2022) showed that although salmon exposed to low temperatures had reduced attachment of *N. perurans*, a 15-minute, cold water bath treatment was not more effective at reducing AGD than the common commercial 2 h bath. Taylor (2021a) examined a sodium percarbonate (SPC) treatment in freshwater and indicated that a 30-minute exposure is not a suitable alternative to existing freshwater treatment regimes. Lazado et al. (2022b) treated AGD-affected fish with peracetic acid either by exposing them to 5 ppm for 30 min or 10 ppm for 15 min. With these protocols, there was no clear treatment effect for AGD, although it did clarify aspects of the host-parasite interactions. Taylor et al. (2021b) caution that *N. perurans* are likely to return to seawater following commercial freshwater treatments and that problem should be reduced by longer bathwater holding times (≥4 hours).

Another potential treatment direction is diet manipulations. Mullins et al. (2020) showed the inclusion of arginine, micro-additives, and vitamins C and E improved salmon survival, with arginine an important driver of pathogen protection. Talbot et al. (2022) showed a customised feed (the composition of which is too lengthy to include here) could delay the onset of clinical symptoms associated with AGD and enhance the expression of genes promoting mucosal defence. Other studies employ genetic tools, e.g., a transcriptomic study provided molecular insights into the pathology of AGD (Botwright et al. 2021). Also, AGD resistance in Norwegian Atlantic salmon was improved by selective breeding (Lillehammer et al. 2019).

Additionally, infections with oomycetes of the genus *Saprolegnia* are among the main parasitic diseases affecting freshwater-famed salmonids and are a major health problem (Tedesco et al. 2021, 2022). Infections by mycotic agents are generally considered a result of chronic stress and poor water quality. Tedesco et al. (2022) found that lower water temperature and handling procedures increased *Saprolegnia* prevalence in trout and Atlantic salmon farming in Italian, Spanish and Scottish farms, with temperature and water quality being the main factors influencing prevalence in Atlantic salmon farms.

As is true for other salmon-farming countries, multiple diseases are concerning in Tasmania. Pilchard orthomyxovirus (POMV) was isolated from wild pilchards in southern Australia in 1998 and is likely transmitted from wild fish to farmed Atlantic salmon (Godwin et al. 2020, Mohr et al. 2020, Samsing et al. 2022). In experimental trials, the development of the disease is rapid, including mortality within 5 d of direct exposure to POMV (Godwin et al. 2020). Samsing et al. (2022) used a reverse transcriptase real-time PCR (RT-qPCR) assay to study a Tasmanian Rickettsia-like organism (TRLO)—a facultative, intracellular bacterium, that triggers Tasmanian salmonid rickettsiosis (Morrison et al. 2016). TRLO has been implicated in sporadic outbreaks of disease, typically coinciding with annual peaks in water temperature. The disease is characterised by a high morbidity rate and affected fish are commonly co-infected with the Tasmanian Atlantic salmon reovirus (TSRV) during outbreaks; however, it is not known whether the presence of the virus is incidental or causal in the disease (Morrison et al. 2016). Different strains of RLO have been linked to mortalities of salmonids in other countries. For New Zealand Chinook salmon, NZ-RLO was strongly associated with fish presenting with skin ulcers (Brosnahan et al. 2019). However, it is not known whether NZ-RLO is the cause of skin ulcers or whether the presence of ulcers lowers the resistance of individuals to NZ-RLO. The authors also found that NZ-RLO was only associated with skin ulcers in the sites with the highest seawater temperatures and that there was a higher prevalence of NZ-RLO at sites with higher water temperatures. This further highlights the association between elevated water temperatures and increased risk of disease. Multiple diseases affecting salmon suggest that a single disease treatment approach is unlikely to address all pathological challenges in salmon farming.

Over recent decades, the use of anti-microbials including antibiotics has increased due to production pressure and is currently commonly used for prevention and treatment of bacterial disease (Miranda et al. 2018). The widespread use of antibiotics in aquaculture has resulted in significant concerns regarding both the development of bacterial resistance and environmental impacts. For a general review of the types of antibiotics used in salmon aquaculture, see Burridge et al. 2010. Although it may be necessary in some cases to use antibiotics as therapeutic agents in the treatment of infections, in general, the need to use large quantities of antibiotics is the result of shortcomings in rearing methods and environmental conditions that promote stress and susceptibility to diseases (Burridge et al. 2010).

One of the most comprehensive reviews of anti-microbials for disease treatment is for the Chilean farming industry, particularly in addressing *Piscirickettsia salmonis*, a facultative intracellular bacterium (Avendano-Herrera et al. 2022). A contrast with Norway provides insight into the range of antimicrobial use across countries. Levels administered are quite high in Chile, 727,812 tons in 2016 and up to 985,958 tons in 2021—compared with just 222 kg in 2019 in Norway. Florfenicol is a broad-spectrum, semi-synthetic antimicrobial compound, and is currently the most frequently used in Chilean salmon farming. In Norway, 115 kg of florfenicol, 107 kg of oxolinic acid and 1 kg of oxytetracycline were employed country-wide in 2020. In experimental tanks in Norway, after florfenicol and oxolinic acid were applied in feed, the composition and abundance of the dominant intestinal bacterial phyla shifted significantly (Gupta et al. 2019). The nexus of antibiotics, microbial communities, and disease incidence and behaviour will likely shape future research directions in this area.

Disease influences on salmon welfare vary widely, necessitating region-specific approaches to disease management. In Norway, haemorrhagic smolt syndrome (Krasnov et al. 2020, Gasnes et al. 2021), salmon gill poxvirus (Tartor et al. 2022), pancreas disease, nephrocalcinosis (Gasnes et al. 2021, Klykken et al. 2022a, Klykken et al. 2022b), and *Moritella viscosa* (Ramberg et al. 2022, Tingbo et al. 2024) are well-studied. In Chile, *Piscirickettsia salmonis* is of the most concern and Canadian studies have addressed how *Piscine orthoreovirus* affects the cardiorespiratory capabilities of Atlantic salmon.

Finally, biosecurity management is a critical aspect of minimising the risk of the introduction and spread of disease within a commercial population and the spread of disease between sites, other farms and susceptible wild populations. Practices such as the separation of year classes, mandatory fallowing periods, zoning, coordination between farmers within zones, and careful planning of site locations can be used to ensure biosecurity management (Midtlyng et al. 2011).

4.2. Ectoparasites

The ectoparasitic salmon louse (*Lepeophtheirus salmonis*, Kroyer 1836) is threatening salmon farming operations globally. However, since sea lice infections are less problematic in Tasmania than elsewhere in the world (Torrissen et al. 2013), we only briefly address the issues here, although we caution this may become a more important consideration in the future. Sea lice feed on mucus and blood leading to decreased fish condition and lower disease resistance. The degree of threat is related to multiple factors. Stocking density and temperature (Montes et al. 2022) and salinity (Sievers et al. 2019) are key, with regional climate driving open-sea dynamics, as mediated by temperature changes (Hurford et al. 2019). It is generally assumed higher fish densities result in higher sea lice infections (Jansen et al. 2012), but this relationship may be more complex than seems apparent (van Walraven et al. 2021). Artificial light in open-pen salmon aquaculture may attract sea lice and increase infestations (Nordtug et al. 2021). Conversely, ultraviolet light has been shown to suppress the reproduction of sea lice, albeit to the detriment of salmon health (Barrett et al. 2020a). Temperature mediates salmon-parasite relationships, with lower ambient temperatures perhaps affecting sea lice more than salmon (Ugelvik et al. 2022). The most obvious negative temperature effects on fish welfare are found following delousing at high temperatures, e.g., ≥28 °C (Nilsson et al. 2019), suggesting such parasite control approaches need to be re-evaluated in the context of welfare (Nilsson et al. 2023).

The issue of balancing lice removal with salmon health is at the forefront of these management applications (Walde et al. 2021). For example, thermal delousing and hydrogen peroxide bathing, although potentially effective in reducing sea lice incidence, has been found to harm salmon in other ways

(Oliveira et al. 2021, Bui et al. 2022, Thompson et al. 2023), and thus remains debated. Temperature also mediates the efficacy of hydrogen peroxide baths, namely, moving fish from warmer ambient temperatures to colder baths reduces salmon mortality while retaining lice removal efficacy (Overton et al. 2018). For medicinal treatments to reduce lice infestation, more research is needed on the evolving resistance to drugs employed (Aaen et al. 2015). In addition to effects on fish welfare, economic considerations often relate to treatment program decisions (Walde et al. 2023). For a thorough assessment of treatment methods, see Aldrin et al. (2023).

Tens of millions of cleaner fish are used each year in salmon farming facilities, and they have been found, under certain conditions, to be effective feeders on sea lice. Yet evidence remains mixed—although cleaner fish consume sea lice, reduction in sea lice loads on salmon may be minimal or non-existent (Barrett et al. 2020b, Gentry et al. 2021). Concerns have been repeatedly raised over cleaner fish welfare, as they differ in biology and nutritional needs compared with Atlantic salmon, and their mortality in salmon cages is often unacceptably high (Geitung et al. 2020, Garcia de Leaniz et al. 2022). Further challenges to effective sea lice application include properly rearing cleaner fish to be successful in reducing sea lice loads (e.g., acclimatising them with sea-lice-infested salmon) and maintaining desired welfare standards in the process of cleaner fish rearing (Gentry et al. 2021).

4.3. Bone health and skeletal deformities

A review by Baeverfjord et al. (2019) outlines the key issues regarding bone health in salmonids, with an emphasis on mineral nutrition. They point out that the emphasis in bone health research is on dietary phosphorus (P) and the levels of that nutrient needed to minimise skeletal deformities. Table 1 is especially of note in this paper, providing a comprehensive account of the studies that have described skeletal deficiencies due to low P intake. They draw on other studies to show negative correlations between available P (diet %) and the proportion of deformed fish (both diploid and triploid, albeit not statistically significant for the former), with 1.2% dietary P resulting in the lowest level of skeletal deformities. Cost-benefit analyses for individual farms are warranted, as higher P diets are more costly, and they have environmental impacts via effluent released from facilities. Baeverfjord et al. (2019) also review research on other essential nutrients, such as calcium, magnesium, and zinc, but studies on these are less common than for P.

Other studies have since extended research reviewed by Baeverfjord et al. (2019). Drabikova (2022) fed salmon parr with low (6.8 g/kg), medium (10.0), or high (13.0) P diets. They found vertebrae compression-related deformities at the low P diet, but these recovered once the fish were transferred to seawater. The frequency of other types of deformities was not significantly different for salmon with different dietary P. As such, high or low dietary P in freshwater rearing ultimately had no overall effect on the prevalence of deformities at harvest. This followed a previous study from their research team that showed a low P diet with a continuous feeding regime can maintain growth rates such that salmon have well-developed vertebral bodies (Drabikova et al. 2021). Consistent with these studies, vertebral malformations were not more common in salmon subjected to 16 weeks of a 50% reduced P diet (Witten et al. 2019). Fraser et al. (2019) showed a low phosphorus diet reduced bone mineralization and increased the incidence of vertebral deformities, compared to medium and high phosphorus diets; however, the prevalence of severely deformed fish at harvest was reduced by switching from the low to higher P diet for 4 months after moving the fish to seawater. Together, these studies suggest although a high P diet may improve some bone health issues to a degree, it is not solely responsible for proper skeletal development in salmon parr and smolts. Other risk factors that can affect skeletal development include temperature, photoperiod, vaccinations, mechanical load, exercise and genetics (Fjelldal et al.

2012, Witten and Hall 2015, Solstorm et al. 2016a). For further information regarding skeletal anomalies and causative factors, see recent reviews (Boglione et al. 2013a, Boglione et al. 2013b).

4.4. Heart morphology and health

A first consideration is whether heart morphology differs between wild and domesticated individuals, yet we found only two studies address this issue for Atlantic salmon. An early study showed heart morphology does differ, i.e., hearts of farmed fish are rounder and that the angle between the ventricular axis and the axis of the bulbus arteriosus is more acute in wild fish. Notably, a strong positive correlation has been established between the more acute shape in wild fish and optimum cardiac output and function (Poppe et al. 2003). However, Perry et al. (2020), in a common garden experiment, found no evidence for domestication-driven divergence in heart or liver morphology. Results of the latter study run counter to many other traits that are selected for in domesticated salmon, notably increased growth rate (Glover et al. 2017).

Frisk et al. (2020) demonstrated a link between a faster pace of growth at early rearing stages and cardiac deformities later in life. These deformities were associated with cardiac rupture in individuals during delousing, thus suggesting a slower pace of smolt production improves cardiac health and reduces the risk of mortality. AGD can also affect heart morphology, e.g., fishes from sea pens that were highly or lightly affected with AGD were compared in a study in Tasmania (Powell et al. 2002). The authors found that high-AGD-exposed fish had higher ratios of ventricle axis length and width and axis length and height, suggesting compromises for energy losses due to AGD.

A consistent thread of evidence indicates the importance of aerobic exercise for cardiovascular health in farmed Atlantic salmon. Balseiro et al. (2018) employed a floating raceway system in marine pens that provided a continuous flow of water in the semi-closed containment environment. The forced aerobic activity resulted in better cardiac health and muscle development, consistent with the results of other studies (Zhang et al. 2016, Robinson et al. 2017). As for temperature, one study showed no effect of different feed levels or rearing temperatures (15 °C vs. 19 °C) on heart shape and bulbus alignment of Tasmanian farmed salmon (Foddai et al. 2022). Muir et al. (2022) examined the cardiac plasticity of juvenile salmon reared under control (7 °C) or elevated (11 °C) conditions using a non-invasive Doppler echocardiograph system. Ventricular roundness and relative ventricle size did not differ, although the proportion of compact myocardium in the ventricular wall was greater for the higher temperature-reared fish (many other responses were measured as well). This study revealed how assessment of cardiac health under different environmental conditions can be complex, and thus conclusions may vary based on the specific response variables. Many such studies note that examinations of cardiac plasticity are especially relevant for salmon farming in the context of ocean warming (also see Calado et al. 2021).

Cardiomyopathy syndrome (CMS), caused by piscine myocarditisvirus (Su et al. 2021), is an infectious disease in farmed Atlantic salmon and is one of the most common causes of mortality during production (Fritsvold et al. 2021). Little is known about the disease and its potential treatment. Kavaliauskiene et al. (2022) found L-plastin expression is elevated in cardiac tissue thus providing a potential biomarker to target the disease. Other biomarkers for salmon CMS include proteins that are identified with cardiac disease in humans (Costa et al. 2021). Fritsvold et al. (2022) describe an RNAscope hybridisation method that had better diagnostic performance than traditional immunohistochemistry approaches and thus may be a promising tool. CMS may be an increasingly important factor affecting salmon welfare in future years.

4.5. Cataracts

Cataracts are opacities of the eye caused by changes in the epithelial tissues surrounding the lens fibres resulting in clouded, or loss of, vision. Incidence can be high in some salmon farming operations, e.g., 90% of salmon were found to be affected in a commercial-scale experiment in Norway in late summer (Hamre et al. 2022). Potential underlying causes are many (Remo et al. 2014). For example, fluctuation in water temperature may increase growth rate, but also cataract development (Bjerkas et al. 2001). The same study also noted cataract development initiated in the freshwater-rearing phase continues after transfer to marine pens. One mediator of the prevalence of cataracts is prominent—histidine, an essential amino acid. Waagbo et al. (2010) found that cataract development (one year after the transfer of salmon smolts from freshwater to seawater) can be minimised with histidine supplementation just before or during the early phases of that development. In a tank experiment in Norway, cataract prevalence and severity were negatively correlated with dietary histidine concentration—to minimise the risk of cataract development the authors suggested feeding with 14.4 g His/kg (Remo et al. 2014). Studies since Remo et al. (2014) have not provided different recommendations for specific histidine levels in feed. More information regarding cataracts is found in Section 6.1 based on comparisons of diploid and triploid fish.

5. Wildlife Interactions

Marine aquaculture facilities have the potential to attract wildlife, including pinnipeds (seals), porpoises, and seabirds, serving as a potential food source or for rest or shelter, (Bath et al. 2023). Non-target fish and other marine species can also infiltrate marine pens and threaten biosecurity and fish welfare. A new Tasmanian Salmon Industry Plan (Department of Natural Resources and Environment Tasmania 2022) proposes the development of a Wildlife Interaction Standards to replace the existing Seal Management Framework and Minimum Requirements for Wildlife Exclusion Measures.

5.1. Pinnipeds and Porpoises

In economic terms, it is estimated that pinniped predation of salmon farms causes losses of up to 12% of gross production costs, which is greater than typical losses due to fish mortality or sea louse infestation (Heredia-Azuaje et al. 2022), although the reported losses are lower in Australia than in other salmon-producing countries. Most pinniped attacks occur at night which presents a particular challenge for detection and management (Sepulveda and Oliva 2005). There is some evidence that predators induce stress that may affect growth, disease susceptibility and survival (Heredia-Azuaje et al. 2022). As highlighted in a recent Tasmanian study, there is also concern that seals may pose a biosecurity risk to farmed Atlantic salmon by introducing potential fish pathogens (D'Agnese et al. 2020).

Aquaculture operations in Tasmania experience significant interactions with wild Australian fur seals (*Arctocephalus pusillus doriferus*) and long-nosed fur seals (*Arctocephalus forsteri*), whose populations have rebounded in recent years from near extinction (D'Agnese et al. 2020, McIntosh et al. 2022b). Today, seal welfare is a particularly sensitive public relations issue for Tasmanian aquaculture and has attracted worldwide media attention. In 2022, *The Guardian* reported on seal deaths resulting from the use of ‘seal crackers’, i.e., underwater explosive devices intended to scare the animals away from sea pens (Burton 2022). The 2021 book, *Toxic: The Rotting Underbelly of the Tasmanian Salmon Industry*, asserted that these devices blow up seals (Flanagan 2021). A small number of these explosive deterrents did result in seal fatalities, possibly due to injury. It is also important to consider the effects of noise pollution on non-target species in addition to the fish themselves, especially harbour porpoises and other acoustically sensitive marine mammals (Simonis et al. 2020). The limited available evidence shows that salmonids may not react significantly to these explosions (Thompson et al. 2021), which may reflect that captive salmon can become habituated to higher levels of ambient noise (Erbe et al. 2022). Due to limited evidence of their potential effects, further research is required on explosive deterrents.

As alternatives to underwater explosive devices, the aquaculture industry employs acoustic deterrent devices (ADDs) and acoustic harassment devices (AHDs). ADDs produce omnidirectional pings oscillating between 5–160 kHz at 150 dB, whereas AHDs use pulsed frequency sweeps or tone pulses at 205 dB within the same frequency range (Stevens et al. 2021). Existing studies on ADDs characterise them as either ineffective (or only partially effective) and the use of these devices is not permitted in Tasmania (Wildlife Management Branch 2018). Like with seal crackers—which proved to be ineffective in California (Thompson et al. 2021)—predators can quickly learn that these sounds pose no real danger, and they may even come to associate ADDs with a source of food, inadvertently creating a 'dinner-bell' effect (Würsig and Gailey 2002).

In western Scotland, ADDs were routinely used because of the abundance of harbour seals. The farmed salmon are reportedly not affected by these devices as they only respond to lower frequencies (<4 kHz) (Āboltiņš et al. 2020), and aquaculture farms reported active ADDs for 88% of stocked days from 2014 to 2019 (Scottish Government 2021). A recent study of the associated welfare impacts on wild seals (Findlay et al. 2022) identified a low risk of auditory impairment but acoustic modelling suggests the animals are exposed to audible ADD noise (i.e., above ambient background noise levels). Similar concerns have been expressed about the impact on other non-target species, especially cetaceans (Díaz López 2020, Stevens et al. 2021, Thompson et al. 2021). Findlay et al. (2021) identified a risk of ADD-associated auditory impairment for harbour porpoises up to 30 km from aquaculture facilities, with the potential for ADD noise to remain high at distances exceeding 50 km. Hiley et al. (2021) observed significant avoidance behaviour of the species and suggested that ADDs may cause hearing damage. Another study found that AHD sounds affected harbour porpoises but not harbour seals (Mikkelsen et al. 2017).

Scottish Atlantic salmon farms have reduced their usage of ADDs since 2020, e.g., by activating systems only when seals are in the vicinity (Wildlife Management Branch 2018). Reiterating the apparent ineffectiveness of such devices, Findlay et al. (2022) encouraged the adoption of alternative measures, e.g., anti-predator nets and stiffer net materials (Thompson et al. 2021). Anti-predator nets surrounding the main sea pen are not always effective since seals can slowly push the outer net towards the inner pen net to get close enough to bite the latter (which also leads to fish escapes). This sometimes leads to the entanglement of the predators, although the extent of the problem is unknown (Heredia-Azuaje et al. 2022). Seals can also access pens by climbing over net walls, using walkways, or exploiting gaps where netting has loosened (Thompson et al. 2021). Using rigid anti-predator nets can improve farming structures. Other effective non-acoustic deterrents include the regular removal of dead fish from sea pens, keeping the water free of debris, and maintaining proper tension in nets and ropes. Non-lethal methods such as these are generally preferred in the United States (Zajicek et al. 2023).

In Tasmanian finfish aquaculture, there has been an emphasis on predator-excluding infrastructure, with other deterrents or targeted destruction viewed only as complementary control measures (Cummings et al. 2019). Consistent with this, the Australian aquaculture industry has recently invested AUD 100 million in the development of double-netted 'fortress pens' (Fløysand et al. 2021). These were introduced to cope with the rough offshore conditions in the Storm Bay area and also to deter predators through design features that include an outer anti-predator net maintained at high tension (Aquaculture 2022). Such systems led to a significant drop in seal incursions (Breen 2019).

A newer generation of devices, known as acoustic startle deterrents or targeted acoustic startle technology (TAST), is intended to elicit mammalian startle responses that cannot be habituated to (Cummings et al. 2019). These devices can reduce effects on non-target wildlife based on inter-species differences in hearing (Götz and Janik 2016). Trials in Scotland showed promising results (Heredia-Azuaje et al. 2022). Although the welfare impacts on non-target species may be reduced (Thompson et al. 2021), more systematic evaluation is warranted. Detrimental effects on non-target species might also be mitigated by using seal tracking systems based on video monitoring, which can be used to ensure that deterrent devices are triggered when seals are in the vicinity. One such system was shown to be effective even at night (Anwary et al. 2022). Another approach used a conditioned aversion method: 'electric fish' placed among dead fish at the bottom of pens (Thompson et al. 2021)—designed to mimic dead salmon but deliver an electric shock upon contact. Taste aversion, using emetic-laced bait fish, is another approach (Schakner and Blumstein 2021). Grey and harbour seals show an aversive response to camphor, suggesting olfactory deterrents may be useful (Campagna et al. 2022).

5.2. Seabirds

Potential interactions with seabirds include predation of fish, the spread of disease and entanglement in farm structures. But one recent analysis noted a 'near total absence of current observational data on seabird behaviour around fish farms in Scotland and elsewhere' (Benjamins et al. 2020, p. 14). A report by the US National Oceanic and Atmospheric Administration (NOAA) concluded that aquaculture farm infrastructure poses a slight risk of entanglement for seabirds (Price and Morris Jr. 2013). In New Zealand, recent best practice guidelines developed for the offshore aquaculture industry mention that seabird interactions are occasionally reported for inshore farms (Gaskin et al. 2021). New Zealand guidelines for offshore aquaculture recommend a mesh size of 6 cm to avoid seabird entanglement (Gaskin et al. 2021). Montevecchi (2023) asserted that seabirds encroaching upon aquaculture sites are often shot. The spread of diseases by seabirds is little studied and warrants more attention.

The majority of studies on seabird entanglement relate to bycatch in fishing gear, particularly gillnets and demersal longlines, which are estimated to kill over one million seabirds each year (Melvin et al. 2023). The relationship between mesh size and risk of entanglement is not particularly well-defined (Bellebaum et al. 2013, Heswall et al. 2021). 'Bird-scaring lines' of various designs have proven effective in reducing bycatch (Bull 2007), as have LED lights on gillnets (Bielli et al. 2020, Lucas and Berggren 2022). For the latter, the impact on farmed fish requires further attention as varied behavioural responses to artificial light sources were observed for Chinook salmon (Yochum et al. 2022). An alternative visual cue for seabird bycatch mitigation is a 'looming eyes buoy', a floating device mimicking large eyespots and looming eye movement (Rouxel et al. 2021). There appears to be only a single study of acoustic deterrents for seabirds (Northridge et al. 2017)—given the concerns raised for mammals this seems unlikely to be a productive research direction.

5.3. Other Non-Target Species

Chemotherapeutic agents used in salmon farming, especially for the control of sea lice, can have detrimental impacts on non-target species in the surrounding area. These include the thiophosphate insecticide azamethiphos, hydrogen peroxide, and the pyrethroid insecticides deltamethrin and cypermethrin, which are typically released into the marine environment after use. There is evidence that these substances have the potential to harm non-target species, particularly crustaceans and bivalves, at concentrations that have been found in the vicinity of salmon farming pens (Bechmann et al. 2019, Urbina et al. 2019, Parsons et al. 2020, Strachan and Kennedy 2021). Extensive use of these agents has also driven drug resistance which sometimes results in treatment failure (Guragain et al. 2021). The chitin synthesis inhibitor diflubenzuron is added to salmon feed to help control sea lice but this can inadvertently affect non-target crustaceans such as shrimp (Moe et al. 2019). Given this, non-pharmacological interventions are preferable for disease management in terms of both animal welfare and sustainability (Lieke et al. 2020). For example, nano-filtered, hyposaline water is effective against sea lice and AGD, demonstrating the feasibility of more sustainable and welfare-friendly treatments (Mc Dermott et al. 2021).

6. Breeding

6.1. Triploid Salmon

For reproductive systems, the predominant issues are trade-offs regarding diploid vs. triploid fish. Triploidy is induced in Atlantic salmon, producing sterile fish to hinder early sexual maturation and to avoid genetic interactions with wild salmon. Triploid salmon are typically induced by exposing fertilised eggs to hydrostatic pressure, resulting in triploid eggs with two sets of chromosomes from the female and one from the male (Benfey 2016). There is a history of triploidy in salmon aquaculture research, and here we focus on the most recent developments (2018–present) that can guide management. There is abundant data on the positive and negative aspects of using triploid fish but a lack of consensus on the appropriate uses in salmon aquaculture. Choices regarding the rearing of triploid fishes will depend on the aspects of welfare and performance that are targeted by farmers or regulatory agencies. We first highlight studies that do not find differences in welfare or performance between diploids and triploids and then counter with those that demonstrate non-desired traits.

In a Norwegian tank experiment (Bortoletti et al. 2022), diploid and triploid fish were raised from fry to smolt stages. Real-time PCR and radioimmunoassays were used to assess growth, stress (e.g., cortisol concentrations) and oxidative stress biomarkers of lipids (MDA) and proteins (AOPP). Changes in the biomarkers were related to sampling time rather than being associated with diet or ploidy. The authors suggest triploid individuals have similar welfare as diploids and thus triploidy could be beneficial for the salmon farming industry. In another study, digestive tract histomorphology, proteolytic enzyme activities, digestibility, and amino bioavailability did not differ substantially between ploidies (Martinez-Llorens et al. 2021). For the parr and smolt stages, the biological processes enriched for down-regulated genes were closely aligned in diploid and triploid fish, reflecting a similar liver morphology and level of vacuolisation (Odei et al. 2020). Benhaim et al. (2020) showed triploid and diploid fish had similar swimming activity, boldness traits and gut microbiome composition, including higher survival for triploids when raised at 8 °C.

Evidence suggests triploid fish grow faster, as has been shown for European salmon strains (Crouse et al. 2021). Ignaz et al. (2022) exposed triploid Atlantic salmon to incremental temperature increases that mimicked natural ocean temperature trends. The data showed that $\leq 5\%$ of female triploid Atlantic salmon in experimental tanks died before temperatures reached 22 °C, suggesting a desirable high-temperature tolerance. Bowden et al. (2018) showed that triploidy does not translate to reduced thermal tolerance or differences in the metabolic rate of juvenile salmon in freshwater environments. Fonseka et al. (2022) found ploidy had transient effects on plasma biochemistry but no effect on vertebral deformities (but triploids had a higher prevalence of cataracts). The gill microbiome of triploids can be more resistant to pathogens than diploids (Brown et al. 2021). Triploids also have been shown to respond well to vaccination (Chalmers et al. 2020).

Yet, other studies since 2018 have found distinct differences between diploids and triploids. Prominent among them is a study by Madaro et al. (2022) who studied fish from four Norwegian aquaculture companies. Overall, triploid salmon exhibited reduced survival, a higher incidence of emaciated fish, and a lower quality rating during primary processing. Contrary to the studies cited above, disease incidence may be higher in triploids—infectious salmon anaemia was 9.4 times more likely in triploid fish than diploid fish at a commercial-site level (Aunsmo et al. 2022). In this study, at some sites, anaemia outbreaks were only in pens with triploid fish suggesting, at a minimum, triploid fishes should be kept in separate pens from diploids. Other experiments demonstrate that even when induction of triploidy is successful, chromosome aberrations are present that may affect gene expression (Glover et al. 2020). Triploids appear to require a lower incubation temperature than the current industry standard of 8 °C (Clarkson et al. 2021), thus temperature control is one way to minimise otherwise emergent deformities in triploids. Large triploid Atlantic salmon have been shown to perform better at colder water temperatures compared to diploids (Sambraus et al. 2018).

Higher susceptibility to oxidative stress in triploid lenses is linked to the prevalence of cataracts (Olsvik et al. 2020). Likewise, Sambraus et al. (2018) found a higher incidence of cataracts in triploids. Specific diets may be required for the normal development of the triploid Atlantic salmon alevins (Wu et al. 2020). Peruzzi (2018) showed the incidence of vertebral abnormalities was higher in triploids in tank experiments in Iceland. Sambraus et al.(2020) found triploid Atlantic salmon have a higher dietary P requirement for bone mineralisation during early development. Triploids fed low P diets have increased skeletal deficiencies, suggesting early P supplementation is crucial for development (Peruzzi et al. 2018, Smedley et al. 2018, Baeverfjord et al. 2019). In sum, triploid performance and welfare may be improved and be similar to (or better) than that of diploids with rearing at relatively low temperatures and high P diets.

Another consideration is hybridisation with other species and, consistent with the theme above, data are mixed. Fraser et al. (2022) assessed the growth of smolts in Norway for diploid and triploid Atlantic salmon × brown trout (*Salmo trutta*) hybrids compared to diploid and triploid salmon. Compared to diploid salmon, triploids were significantly heavier at the end of the trial and triploid hybrids were heavier than diploids. However, both triploid groups had a higher incidence of deformed vertebrae and more severe cataracts. They concluded triploid hybrids have no growth advantage over triploid salmon and suffer from similar welfare issues. This followed previous studies from this research team that found triploids and triploid hybrids have better freshwater and early seawater growth than diploid counterparts (Fraser et al. 2021) but with vertebral deformities higher (likely because of rapid growth). We reiterate the conclusion offered at the opening of this section—the differing evidence on the performance and welfare of diploids vs. triploids (and hybrids) renders singular recommendations regarding their farming challenging. Farming decisions will be based on which welfare metrics are targeted and the performance outcomes desired.

A final note on producing sterile adult salmon relates to germ-free individuals, i.e., blocking the ability to reproduce by inhibiting the function of proteins that are necessary for germ cell development and/or survival. One approach is to knock out dead-end gene *dnd* to produce germ-free individuals (Guralp et al. 2020, Kleppe et al. 2022). The resulting sterile broodfish can pass the sterility trait to the next generation. Almeida et al. (2022) identified another target, the protein Piwil1, which affects the survival of primordial germ cells. Such approaches are likely to progress rapidly concomitant with technological advances.

6.2. Selective Breeding

The primary target in the selective breeding of aquaculture species is faster growth with an emphasis on feed intake and utilisation (Thodesen et al. 1999, Thorland et al. 2020). Faster growth also promotes fish welfare by shortening rearing periods and thus lessens the risk from disease agents and parasites. This reduces the need for physical or chemical treatments, as well as reducing facility operation costs and freeing money to target other aspects of maintaining fish welfare. However, faster growth may also produce risk factors, such as poor skeletal health.

Studies provide different lines of evidence to support that selective breeding can promote fish welfare and yields. A notable example is the Australian Salmon Enterprises of Tasmania Pty Ltd (SALTAS) selective breeding program, which was implemented in 2018 (Verbyla et al. 2022). The goal is to use genomic selection as a means to increase genetic gain using family-level selection, maximising primary traits (e.g., harvest weight) without undesirable effects on other traits. An optimised genotyping scheme was used in which all individuals in each year class were genotyped. A 19% genetic gain in total weight was established with a 54% increased rate for AGD resistance. When translated to the commercial scale with selected males, there was a net 5.7% increase in production yield.

For salmon in European breeding programs, Janssen et al. (2017) found after 10 selected generations there was a cumulative genetic gain of about +200% in harvest weight, a reduction in the rearing period to 2–3 years from egg to harvest, and an increase in harvest weight to ~5 kg. Naeve et al. (2022), in a common garden experiment, used contemporary farmed Atlantic salmon (generation 11) eggs fertilised with cryo-preserved milt from previous generations. The resulting difference in average body weight between generation 0 and half-sibs from present-day salmon was 1.5 kg. Many genes are involved in regulating growth, providing a broad scope of genetic targets for selective breeding (Thorland et al. 2020). Genotype imputation can provide a cost-effective method for generating robust genetic information for large numbers of fish (Tsai et al. 2017).

Selective breeding targets other than those focused on growth include disease resistance and temperature tolerance. Kjoglum et al. (2008) show selective breeding has the potential to increase the resistance of Atlantic salmon to furunculosis, infectious salmon anaemia, and infectious pancreatic necrosis. Candidate genes for resistance to AGD have been identified that could be targeted for selection (Aslam et al. 2020, Robledo et al. 2020, Botwright et al. 2021), and enhanced AGD resistance in Norwegian Atlantic salmon has been demonstrated via selective breeding (Lillehammer et al. 2019). Host resistance to sea lice in farmed Atlantic salmon has a significant genetic component and thus has received much attention (Jones et al. 2002, Kolstad et al. 2005, Gharbi et al. 2015, Tsai et al. 2016) and there remains untapped potential in this research (Rosendal and Olesen 2022). Especially in the context of ocean warming, thermo-tolerance is critical in selective breeding programs (Calado et al. 2021). There are also instances of unintentional selection, e.g., the evolutionary emergence of compensatory mechanisms to a diet low in essential long-chain polyunsaturated fatty acids in domesticated environments (Jin et al. 2020).

6.3. Emerging genetic selection approaches

Long generation times in Atlantic salmon render selective breeding a slow (generational) process but novel genetic approaches are emerging to provide more rapid means towards desired genetic traits. D'Agaro et al. (2021), Houston et al. (2020) and Houston and Macqueen (2019) provide reviews of how genomics is being applied at multiple stages of the domestication process to optimise selective breeding, emphasising biotechnological innovations such as genome editing and surrogate broodfish technologies. Genome editing can target DNA changes to single nucleotide replacements allowing for efficient inclusion of favourable alleles (Straume et al. 2021, Yanez et al. 2022, Raudstein et al. 2024). CRISPR/Cas9-induced homology-directed repair is a powerful tool towards this end (Roy et al. 2022)—albeit one with technical, regulatory and ethical considerations (Okoli et al. 2022). Applications include genetic modifications for disease resistance, sterility, and enhanced growth, with particular optimism for addressing sea lice infestations (Robinson et al. 2022). Another example is the causative gene underlying resistance to infectious pancreatic necrosis virus, as shown by combining high-throughput genomics with targeted genome editing (Pavelin et al. 2021).

6.4. Other Spawning Issues

In salmon farming, sexual maturation and spawning can be manipulated to enable a supply of eggs and smolt throughout the year. Reproduction is induced through hormonal stimulation and spawning can be achieved through changing light, temperature and feeding regimes, and stripping of eggs and sperm. The welfare of broodfish may thus be impaired directly by these procedures and also indirectly by the associated handling (Saravia et al. 2019). However, further research on the welfare implications of spawning practices in salmon farming is needed. Skjærven et al. (2022) showed that alteration in spawning time by adjusting abiotic factors influences the nutrient status of the next generation of Atlantic salmon via nutritional and metabolic programming. Zepeda et al. (2020) investigated the effects of treatment with gonadotropin-releasing hormone analogue (GnRHa) on Atlantic Salmon broodfish. They found that the use of the hormone reduces the effect of endocrine disruptors, does not affect fertilization rate and has positive effects on embryonic development and the larval stage of offspring by reducing the number of morphological deformities.

Broodfish are typically reared for a longer period than the production fish raised for consumption. This makes them particularly vulnerable and necessitates specific welfare requirements. The process of sexual maturation is energetically costly and involves trade-offs with other fitness components such as growth and survival (Mobley et al. 2021). It is common for broodfish, as with wild salmonids, to go off feed before spawning which results in a reduced body condition. Additionally, broodfish are subjected to frequent handling events, including tagging for identification, fin clipping for genotyping, maturation checks and stripping, and are therefore susceptible to increased handling stress.

For some salmonid species reproductive events are terminal (i.e., semelparous species) and are therefore humanely euthanised before stripping. Atlantic salmon (an iteroparous species) are commonly used for multiple spawning events and are anaesthetised before stripping. Broodfish should be fed a specially formulated diet to meet their nutritional requirements and must be encouraged back on feed after spawning events if being used for further events. However, one could question the ethics of keeping broodfish for repeat spawning events considering the significant risks to the welfare of this particular group of production fish face.

Other studies are relevant to Atlantic salmon breeding that warrant mention but lack sufficient information to develop further herein. Ultrasound technology is a quick and noninvasive method that could reduce the number of stressful handlings and unwanted sacrifice of broodfish required for maturation monitoring in Atlantic salmon (Naeve et al. 2018). Environmental factors in broodfish husbandry influence the nutrient status of the next generation via nutritional and metabolic programming (Skjaerven et al. 2022). Another study documented the great plasticity in the timing of salmon puberty—maturation as rapid as 6 months after hatching—which could have important implications for farming programs (Ciani et al. 2021). Subsequently, more evidence has linked early onset puberty to high-rearing temperatures (Martinez et al. 2022, Martinez et al. 2023). Lopez et al. (2019) note that genetic drift may mask artificial selection which indicates a different genetic basis for similar traits in different farmed strains.

7. Future Research Directions

7.1. Recirculating aquaculture systems and the microbiome

Modern recirculating aquaculture systems (RAS) were originally pioneered in the 1970s in Germany and Denmark and were subsequently implemented for commercial use in several European countries (Ahmed and Turchini 2021). The recirculated water is purified by sequential processes, including filtration and sterilisation, and water reuse in current systems can be as high as 99% (Shitu et al. 2022). Technology and adoption of RAS have increased, especially in the context of a climate adaptation strategy (Mortensen et al. 2022, Mota et al. 2022). With RAS, the industry has achieved production of Atlantic salmon to full market size in land-based facilities without the need for marine pens (Crouse et al. 2021). In other cases, the time spent in marine pens can be reduced by producing larger post-smolts in onshore RAS before transfer. However, knowledge of post-smolt biological and welfare requirements in close containment systems is limited (Ytrestoyl et al. 2020). Real-time monitoring and machine learning approaches are being developed for parameters such as water quality management, feeding control and disease detection (Brijs et al. 2021, Chen et al. 2021). The Tasmanian aquaculture industry has adopted RAS and the largest such system in the southern hemisphere was opened in the state in 2019 (Fløysand et al. 2021).

The rise of ‘omics’ technologies has brought a growing understanding of commensal microbiomes and their impact on human health and disease. Similar investigations have been undertaken in fish, where a healthy microbiome, particularly in gills and skin (Lorgen-Ritchie et al. 2022), is thought to protect against infection and disease (Dahle et al. 2023). Microbial communities in RAS are recognised as important mediators of fish health and welfare (Rud et al. 2017, Drønen et al. 2022). This may, at least partially, explain why gradual salinity changes before transfer to seawater reduce mortality of smolts since it also allows for adaptations in the host microbiome (Fossmark et al. 2021, Morales-Rivera et al. 2023).

The microbiomes in recirculating water systems contain various beneficial species (e.g., nitrifying and probiotic populations), as well as pathogenic bacteria. Bacterial biofilms are particularly problematic since they harbour fish pathogens (Schoina et al. 2022). Sampling of tank water and fish skin are appropriate screening measures for early warning of disease (Drønen et al. 2022). Careful management of the bacterial communities present in RAS biofilters is essential since they influence water microbiota. Dahle et al. (2022) identified post-biofilter UV treatment as a promising sterilisation strategy to protect against pathogens without compromising the tank water microbiome. Ozone has also been explored as a disinfection strategy in post-smolt RAS, which improves water quality without any apparent detrimental impact on animal welfare, as assessed on 14 physical and physiological welfare indicators (Lazado et al. 2021).

7.2. Offshore Aquaculture

Most marine production facilities are located close to shore but there is a growing interest in offshore systems for industry expansion and climate change adaptation (López Mengual et al. 2021, Johannesen et al. 2022). There are reservations because of a lack of data on welfare in offshore systems, although existing evidence is promising (Aryai et al. 2021). One survey of salmon industry stakeholders revealed no perceived differences in fish welfare (Watson et al. 2022). A shift to offshore sites may be preferable to reduce the risk of sea louse infestation since salmon lice occur at their highest density close to shore (McIntosh et al. 2022a). Nevertheless, the harsher environmental conditions experienced farther from shore present various engineering and production challenges for aquaculture installations, as well as raising additional welfare concerns. In this context, emerging technologies of tagging and video monitoring systems may be especially advantageous.

Various spatial planning approaches can be used to find the most favourable locations for offshore salmon farms (Aryai et al. 2021). Existing siting models combine remotely sensed environmental data (e.g., temperature, salinity and current speed) with species-specific knowledge to identify suitable areas (Jossart et al. 2020, Yu et al. 2022). Long-term ocean current data is desirable for choosing locations to ensure that farmed fish will not be forced to swim above their critical swimming speed (Jonsdottir et al. 2019). After smoltification, Atlantic salmon are strong swimmers that seem well suited to offshore aquaculture without any impact on their welfare—if chronic currents remain within 60% of U_{crit} (Hvas et al. 2021a). In Norway, several offshore areas meet such conditions, with the temperature dependence of U_{crit} being an additional factor to consider (Mugwanya et al. 2022a). Offshore expansion of the aquaculture industry is also hindered by a lack of regulatory and policy preparedness (Galparsoro et al. 2020, McPhail and McDonald 2021, Watson et al. 2022).

7.3. Management with Artificial Intelligence

'Smart aquaculture' or 'precision aquaculture' can increase productivity and sustainability (Føre et al. 2018, Vo et al. 2021, Gladju et al. 2022) and they also hold promise for well-being (Lazado et al. 2022a). One focal point is real-time monitoring driven by increased automation and the use of AI-based tools. Biosensors can collect real-time data on individual animals, including parameters such as heart rate, acceleration, depth and position (Brijs et al. 2021). For example, analysis of behavioural patterns and feeding activity has been used to optimise feeding protocols, including for Atlantic salmon (Liu et al. 2014, Brijs et al. 2021, Vo et al. 2021). This information can be combined with AI-based feeding systems (Lloyd et al. 2020, Behrend et al. 2022) to optimise resource use and improve welfare (e.g., avoid the competitive and aggressive behaviour associated with underfeeding).

Non-invasive methods are preferable for detecting abnormal behaviour or physiological stress (Li et al. 2022). Using images or video captured by underwater cameras, machine vision algorithms have been applied for counting, sizing and early disease detection of farmed fish (Vo et al. 2021, Ahmed et al. 2022). Accurate counting of Atlantic salmon in sea pens has been achieved using video monitoring (Zhang et al. 2020) and acoustic monitoring of marine pens has been used to characterise feeding behaviour (Rosten et al. 2023). Underwater drones are another strategy for fish recognition and water quality measurement (Meng et al. 2018, Lloyd et al. 2020). Although the welfare implications of interaction with these devices are not yet clear, an 'animal-friendly' robot design may be able to sufficiently minimise avoidance responses (Kruusmaa et al. 2020). In addition, aerial drones are capable of monitoring feeding behaviour (Ubina and Cheng 2022). This approach has enabled fish counting and sizing from the air, offering a more economical alternative to underwater equipment (Ubina et al. 2021).

Despite concerns with sensor and tagging studies (Section 3.4), welfare studies of handling or treatment interventions can benefit from these devices as they are capable of tracking physiological stress markers (Brijs et al. 2021). They can also provide information on the effects of overcrowding, interactions with other species, and environmental conditions that can vary temporally and spatially within RAS or marine pens (Vo et al. 2021, Yadav et al. 2023). For example, intelligent variable-flow machine learning models can optimise water quality in RAS (Chen et al. 2021). Deepwater tidal meters (Sosa and Montiel-Nelson 2022) can guide siting and welfare management for offshore aquaculture facilities by determining the most appropriate stocking density based on long-term monitoring of local currents.

It may be possible to reduce welfare impacts and economic losses due to disease through AI-based methods. Machine learning has been applied to provide early warning of sea louse outbreaks by combining real-time observations with historical time series (O'Donncha and Grant 2019). A related application of remote sensing technologies is in jellyfish detection. Already a significant source of losses in commercial open-pen aquaculture (Boerlage et al. 2020), jellyfish blooms are increasing, including in

Tasmania (Carr and Minshull 2020). In some cases, these occurrences can cause mass mortality events (Clinton et al. 2021). One jellyfish early warning system uses machine learning methods for real-time analysis in combination with video monitoring (Martin-Abadal et al. 2020).

7.4. Salmonid Nutrition

Aquatic animals have particularly high protein requirements, so alternative protein sources have been a focus in salmonid nutrition research. It is increasingly necessary to replace the fish oil and fish meal used in commercial salmon feed to minimise costs and increase sustainability. Both of these ingredients are derived from small, wild-caught pelagics whose numbers are not unlimited (Jia et al. 2022). There are poor welfare outcomes for these food fishes as well. The shift to plant-based feeds exposes farmed salmon to components not present in their natural diet and concerns have been expressed over possible health impacts, including stress, immune health and liver function (Krøvel et al. 2010, Caballero-Solares et al. 2020). These feeds may be contaminated with agricultural pesticides, such as the broad-spectrum insecticide endosulfan, which has long been suspected of negative physiological effects in salmonids (Krøvel et al. 2010). A recent toxicological study in Atlantic salmon of pirimiphos-methyl, an organophosphate pesticide, concluded that the concentrations found in some commercial salmon feed exceed safe levels (Berntssen et al. 2021). There is also evidence of hepatotoxicity with the herbicide glyphosate (Søfteland and Olsvik 2022), which might be found in soy products.

Soybean meal is commonly used as a protein source and fish meal replacement in commercial aquaculture feedstocks—the Global Salmon Initiative has promoted responsible sourcing among its members (Global Salmon Initiative 2023). However, high levels of soybean meal in the diet of Atlantic salmon can cause reduced feed intake and weight gain, distal intestinal inflammation and compromised overall health (Krogdahl et al. 2020, Hossain et al. 2023). As potentially superior alternatives to soy, diets including microalgae, macroalgae, insect-based meal, or single-cell proteins (e.g., from bacteria or yeasts) have been tested in Atlantic salmon with promising results (Nagappan et al. 2021, Yue and Shen 2022, Zatti et al. 2023). In terms of food quality for human consumption, fish oil replacement with microalgae can also maintain the natural omega-3 fatty acid content and growth of farmed salmon (Cottrell et al. 2020, Carr et al. 2023, Santigosa et al. 2023). Yet, in addition to economic factors and sustainability, fish welfare needs to be prioritised when developing new feed formulations. The impact on gut microbiota has been identified as a significant animal health issue (Napier et al. 2020), including salmon (e.g., Dhanasiri et al. 2023).

7.5. Welfare and Climate Change

The entire aquaculture production chain is vulnerable to climate change (Ahmed and Turchini 2021, Austin et al. 2022), and impacts on the industry have received considerable attention (Khalid 2022). As a cold-water species, Atlantic salmon may be particularly vulnerable to sea surface temperature increases (and other related changes) in areas where open marine pens are used for production (Mugwanya et al. 2022a). Detrimental effects on health and welfare begin above 16 °C, becoming more pronounced above 18 °C, including slower growth along with increased stress and mortality (Falconer et al. 2020, Meng et al. 2022). Long-term environmental monitoring data, especially if shared among nearby farms, can be used to identify trends and anticipate future consequences of climate change, including more frequent and stronger storms (Bell et al. 2022).

Compared with other salmon-producing countries, such as Scotland and Norway, the warmer waters around Tasmania traditionally gave the region an advantage in terms of faster growth and reduced time-to-harvest (Meng et al. 2022). However, the state's recent experience as a 'hot spot' of rapid ocean warming now threatens its aquaculture sector. Northwest Bay and Bruny Island are forecast to become unsuitable for Atlantic salmon aquaculture within the next decade (Meng et al. 2022). By contrast, Icelandic waters are expected to be amenable to these operations until at least 2050 (Bannan et al. 2022), and suitable areas in Norway are projected to increase by mid-century (Oyinlola et al. 2022).

As suggested by the previously mentioned Tasmanian study (Meng et al. 2022), ocean warming conditions may drive marine aquaculture operations farther offshore in the future (McPhail and McDonald 2021). This shift is already driven by social and environmental factors following the public backlash over increased Macquarie Harbour production and its negative ecological impacts (Lindfors 2022). Higher-than-average temperatures have caused significant production losses for Norwegian salmon farms (Islam et al. 2022), and similar trends have been experienced in Tasmania, Iceland and North America. Salmon may congregate in a certain area of a marine pen depending on variations in temperature and oxygen (Falconer et al. 2022), such that stocking density may need to be adjusted to avoid overcrowding. Increased storm surges may also elevate the risk of damage to coastal aquaculture infrastructure (Maulu et al. 2021). As such, climate change may also lead to increased reliance on land-based facilities, such as RAS (Ahmed and Turchini 2021). RAS may replace inland freshwater aquaculture in areas affected by significant temperature extremes or droughts, as well as avoid the frequent flooding that leads to escape events and water contamination (Reid et al. 2019). Sea level rise may ultimately necessitate relocation or closure of inland freshwater aquaculture facilities due to salinisation and could also damage the coastal ecosystems that support the feedstock for aquaculture operations (Maulu et al. 2021).

The increasing acidity of the world's oceans is also problematic (Henson et al. 2017). The impact of acidification on salmon welfare is not yet well understood, and further research is needed (Falconer et al. 2022). Marine CO_2 removal technologies for aquaculture are currently at an early stage of development but they hold promise for future mitigation of seawater acidification (Myers and Subban 2022). Current predictions indicate changing temperatures cause increased spread and incidence of zoonotic diseases (Khalid 2022, Mugwanya et al. 2022a). Finfish are predicted to be susceptible to these effects, with sea louse infestation identified as a major concern for farmed salmon (Bannan et al. 2022). As noted above, the gut microbiome of salmonids influences their disease susceptibility and is known to be strongly dependent on their environment and thus climate changes (de Bruijn et al. 2017). In the warmer and more acidic waters anticipated, bacterial pathogens, such as *Vibrio* spp., proliferate and are associated with disease in Atlantic salmon (Bruno et al. 1998, Zhang and Austin 2000, Ji et al. 2020). Conversely, it is acknowledged that the incidence of some cold-water diseases of Atlantic salmon may decrease (Maulu et al. 2021).

Recent decades have also seen an apparent increase in marine harmful algal blooms (HABs) (Maulu et al. 2021). The toxins released during these events can cause widespread fish mortality and pose a threat to human health through the consumption of contaminated seafood. The Chilean salmon industry has experienced particularly large losses due to HABs (Soto et al. 2021), and these events recently were identified as severe threats among aquaculture industry stakeholders (Soto et al. 2019). This level of concern appears to be justified by a significant range expansion for two of the key responsible species over the past 20 years (Trainer et al. 2020). Eutrophication is another factor driving HABs—which the aquaculture industry may contribute to (Soto et al. 2021). Tasmania also has experienced a marked increase in HABs over the past decade, with climate change thought to be the driver. Although they have mostly affected shellfish aquaculture, remote monitoring of such blooms seems advisable as the industry moves offshore. Behavioural monitoring of farmed salmon may also identify early warning signs of HAB-related toxicity (Boerlage et al. 2020) and help to ensure that losses are minimised in future events.

Conflicts may arise between climate impacts and animal welfare. Through case studies, Macaulay et al. (2022) suggested that early identification and evidence-based decision-making should be adopted to enable optimal tradeoffs. Animal welfare should remain a high priority in future sustainability frameworks (Stentiford et al. 2020), and various climate mitigation strategies are possible without negatively affecting fish health and welfare. Although RAS are regarded as a sustainable innovation and their tightly controlled environments make them appealing for climate adaptation, associated greenhouse gas (GHG) emissions are high relative to other aquaculture systems (Ahmed and Turchini 2021, Jones et al. 2022). The emerging technology of 'aquaponics' offers potential solutions, combining aquaculture with hydroponics to use wastewater from fish tanks to grow vegetables (Taha et al. 2022). For offshore aquaculture sites, co-location and integration with marine power sources (wind and/or wave energy) are being explored (Weiss et al. 2020, Aryai et al. 2021).

7.6. Other Recent Advances

• Advances in biochemistry provide insights into various health and dietary issues. For example, Phosphorus-31 NMR spectroscopy, which uses nuclear magnetic resonance (NMR) to study chemical compounds that contain phosphorus, can be used to explore factors that affect skeletal muscle tissue (Totland et al. 2022).

• Semi-closed containment systems (S-CCS) are approaches with cultured fish separated from the natural environment by a physical barrier, reducing the time fish spend in open marine pens (Nilsen et al. 2020). For example, a study using a Preline Fishfarming S-CCS resulted in higher salmon growth rate, final weight, and survival, as well as lower sea lice infestations, suggesting such a system has advantages over entirely open systems (Ovrebo et al. 2022).

• Elucidating the relationship between epigenetics, phenotypic variation and fitness can inform salmonid breeding and rearing practices (Koch et al. 2022).

• Commercially available, real-time dissolved oxygen and temperature sensors can be distributed throughout pens to track salmon distribution and behaviour based on the spatial and temporal variability of water parameters (Burke et al. 2021).

• Automated passive acoustic monitoring has been used to monitor the condition of entire sea pens (Rosten et al. 2023). Such use of the soundscape can depict a 'hungry' vs. 'satiated' population based on relative sound frequencies, providing information on optimal times to feed fish, thus minimising wasted feed and improving fish welfare.

• An EchoBERT (echo bidirectional encoder representation transformer) has been proposed for behavioural assessments using spatiotemporal properties from echograms, e.g., pancreas disease detection purely from abnormal behaviour patterns in the echogram data (Maloy 2020).

• Deep learning approaches are emerging to analyse fish behaviour (Alshdaifat et al. 2020, Iqbal et al. 2022). A dual-stream deep learning recurrent network shows the ability to capture swimming dynamics and provide for feeding action recognition (Maloy et al. 2019). Machine learning has been used to detect disease (Ahmed et al. 2022) and model dissolved oxygen profiles (Palaiokostas 2021, Chatziantoniou et al. 2022). Image-based machine-learning techniques can be used to detect wounds or lice prevalence (Gupta et al. 2022). A review of such applications can be found in Vasquez-Quispesivana et al. (2022).

• Advanced video and vision systems are used in many ways to assess behaviour in aquaculture systems (Saberioon et al. 2017), both in tanks (Okarma et al. 2022) and marine pen settings (e.g., Johannesen et al. 2020). Image-based machine-learning techniques can be used to detect wounds or lice prevalence (Gupta et al. 2022).

- We have focused on the directional relationship between the environment to salmon welfare. We acknowledge that another focal research area is the opposite—how salmon ocean aquaculture affects aspects of the surrounding ecosystem (Macaulay et al. 2022, Rector et al. 2022) or carbon cycles (Ziegler et al. 2024). This is beyond the scope of this review, but we note that studies that examine the effects of salmon aquaculture on environmental quality are diverse and impactful, e.g., studies on environmental DNA leakage (Shea et al.) and nutrient flow facilitating adjacent mussel aquaculture programs (Camelo-Guarin et al. 2021).

8. Conclusion

Improved fish welfare benefits individual animals and the industry as a whole. Although there are numerous avenues to further our understanding of fish welfare, this review identifies current opportunities for improving the welfare of farmed Atlantic salmon. Improved sustainability of farming practices, including fish welfare, is essential for desired industry growth and future food security. As is outlined in this document, technological progress opens many new trajectories to improve aquaculture system design with the welfare of individual fish as a central goal. Gene editing approaches and artificial intelligence will likely relate to many of the emerging opportunities. These will provide avenues for ensuring fish welfare and increasing the sustainability of aquaculture as a whole.

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