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REVIEW

REVIEWS IN Aquaculture

Fasting and its implications for fish welfare in Atlantic salmon aquaculture

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Abstract

Periods of fasting occur for a multitude of reasons in Atlantic salmon aquaculture. Feed withdrawal is widely used prior to transport, parasite treatments, preslaughter and for depuration purposes in recirculating aquaculture systems. Voluntary fasting is a coping response when fish have poor health or are exposed to poor farm environments. Owing to increased attention to animal welfare in aquaculture, concerns have been raised regarding ethical issues when farmed fish are subjected to fasting. However, thorough science-based recommendations for fasting and feed-withdrawal regimes have been lacking. The purpose of this review is to provide a synthesis of the various causes for fasting in Atlantic salmon aquaculture and evaluate their associated welfare implications so that guidelines for appropriate practices can be formulated. To interpret impacts, we describe biological responses and tolerance limits to fasting in Atlantic salmon and consider adaptations in the wild. Fry and parr are highly sensitive to feed withdrawal. However, post-smolts and adults are well-adapted to endure prolonged fasting without experiencing compromised functionality or health. Here, short periods of feed withdrawal prior to operations should therefore not constitute significant welfare concerns. Serious concerns are instead associated with voluntary fasting that may continue for weeks. We emphasize that environmental extremes that exceed appetite impairing thresholds must be avoided. Additionally, farmed fish should not be subjected to practices that lead to chronic stress that induce cessation of appetite. Diseases or parasites that impair appetite should also be mitigated. Fasting is here a symptom rather than a cause for poor welfare.

KEYWORDS
compensatory growth, feed withdrawal, recirculating aquaculture system, restricted feeding, starvation

1 | INTRODUCTION

The goal in commercial aquaculture is to maximize growth and feed conversion rates of the species being cultured to facilitate the highest profit margins. This is particularly true for Atlantic salmon (*Salmo salar*), the most widely farmed global marine finfish species for over two decades,[1] where economic motivations have led to substantial research efforts into improving production performances. Key research topics include nutritional requirements and how feed composition can be engineered and adapted to improve growth.[2–5] The effects of environmental factors such as temperature, oxygen levels, salinity, light regimes and flow conditions on production performance have also been studied extensively.[6–11] Furthermore, Atlantic salmon have been artificially selected for growth traits since the initiation of breeding programs in the 1970's.[12–14] This has led to substantially higher growth rates in domesticated genotypes compared to counterparts of wild genetic origin when subjected to intensive farm conditions.[15,16]

Owing to a strict focus on growth optimization in Atlantic salmon aquaculture, fish farmers are afraid to underfeed their fish and overfeeding is commonly observed, coarsely estimated at 3%–5%.[17] Overfeeding in traditional flow-through hatcheries can lead to increased nutrient waste discharge, in particular nitrogen and phosphorous, leading to the eutrophication of the recipient water bodies.[18–20] In recirculating aquaculture systems (RAS) hatcheries, overfeeding and the use of feeds with suboptimal water stability can increase organic load and concentration of suspended particles resulting in deteriorated water quality and potentially increased bacterial carrying capacity of the systems.[21] In addition, increased feed waste will lead to increased amounts of sludge production and increased operational costs of RAS. In open sea-cage production systems that are extensively used in the grow out phase, overfeeding causes high amounts of uneaten food pellets to spread into the adjacent aquatic environment.[17,22] Local wild fish can therefore aggregate around salmon cages as they have learned to take advantage of these abundances of easy high energy meals.[23,24] At the same time, fish feed is by far the largest expense in the production of farmed Atlantic salmon with a total cost share of over 50% during the marine on-growing phase.[25,26] There is therefore a great economic incentive to minimize feed waste and maximize feed conversion ratio, for instance by implementation of more sophisticated feeding systems to feed responsive rations at optimal quantities based on changes in the daily observed appetite of the fish.[27–29] However, the perceived risks of underfeeding as well as any occurrences of periods where the fish cannot be fed or are reluctant to eat remains a major concern because it is firmly believed to cause significant economic losses owing to forgone growth potential.[30]

Irrespective of the farmers caution for growth loss, fasting and feeding restriction periods do occasionally occur for a number of reasons in Atlantic salmon aquaculture. The type of fasting can either be voluntary or involuntary. Voluntary fasting may occur when the fish are subjected to suboptimal environmental conditions, suffers from stress, injury, or from certain prevailing pathogens. In worst case scenarios, voluntary fasting periods may last for weeks or even months and significantly impair production. Common environmental factors that induce voluntary fasting are hypoxia and thermal extremes during summer heatwaves[31–33] or cold winters.[34] Common diseases that lead to anorectic farmed salmon include pancreas disease (PD),[35–37] infectious pancreatic necrosis (IPN),[38] and amoebic gill disease.[38] In addition to disease, farmed salmon risk being deloused several times during a production cycle in sea cages.[39] It has been shown that the most commonly used methods, mechanical and thermal delousing, which require the fish to first be crowded, then pumped into a treatment unit, then subjected to mechanical or thermal delousing, before being returned to the sea cage, are associated with lowered appetite at the group level, which may involve some individuals stopping to eat altogether due to stress and injury.[40–42]

Involuntary fasting occurs during periods of feed withdrawal that are used as a tool by the farmers to empty the gut of the fish before major operations. These operations can involve crowding, pumping, and transportation, for instance before delousing, other health related treatments, or pre-slaughter.[43,44] Fish can be subjected to feed withdrawal for hygiene reasons, to reduce risks of poor water quality from waste products, and to reduce the oxygen demand of the fish which may increase their tolerance to acute stress.[44,45] As opposed to voluntary fasting, feed withdrawal practices to empty the gut are of much shorter durations and typically of 48–72 h.[46]

Differing production systems or farming approaches may also present distinct characteristics or situations where the fish must be subjected to periods where feed withdrawal is necessary. These situations can occur in exposed offshore aquaculture, where prevailing bad weather conditions can periodically make normal feeding management impossible.[47] The production of differing life stages of Atlantic salmon in RAS may also necessitate system-specific periods of feed withdrawal. For example, it is sometimes necessary to fast the fish, or limit feeding, if the nitrification capacity in the biofilter is reduced and concentrations of potentially toxic ammonia and nitrite increases in the rearing water.[48,49] In addition, when farming Atlantic salmon in RAS to slaughter size they may accumulate geosmin and 2-methylisoborneol in the flesh which gives an undesirable muddy taste. To purge the fish prior to slaughter they are therefore subjected to several days of fasting in odour-free water tanks.[50–52]

While any fasting period, voluntary or involuntary, is an economic concern for the fish farmer, another important aspect to consider are its underlying effects upon animal welfare and health. As vertebrates, fish are considered sentient beings with sophisticated cognitive functions and the capacity to experience distress.[53–56] In commercial animal productions such as Atlantic salmon aquaculture, there is therefore an inherent ethical obligation to treat the fish with respect, and to avoid or at least minimize suffering if it cannot be avoided.[46,57] There are also legal obligations such as various national and international animal welfare acts that cover terrestrial and aquatic animal production.[58]

When discussing animal welfare 'the five freedoms' are often used as a starting reference, where one of these freedoms is the freedom from hunger and thirst.[59–61] Nutritional state is also considered in further welfare conceptual frameworks including the five domains model.[62] As such, fasting in aquaculture can violate the fundamental ethics of animal welfare if the periods last long enough to cause hunger, distress and potentially even malnourishment. Fortunately, good animal welfare in aquaculture is generally associated with excellent growth performance and low mortalities, and it is therefore also in the interest of the fish farmer to strive for good welfare. The industry will also benefit from a better reputation among the general public by prioritizing ethical issues such as the welfare of fish.

In practice it can, however, be difficult to define exactly when fish welfare is compromised and to quantify the severity of distress. This is partly because fish are very different from humans in how they perceive the world and in their ways of expression.[63] Attempts to project our empathy unto them in a meaningful way are therefore not as intuitively straightforward as compared to mammalian species.[64] Hence, how farmed Atlantic salmon experience hunger is an esoteric topic where it is difficult to provide scientific evidence for when welfare is compromised following extended fasting periods.[45] Moreover, when interpreting welfare implications of fasting a distinction between feed withdrawal periods and voluntary fasting is necessary. For instance, since farmed Atlantic salmon have been conditioned all their life to being fed excessively daily and normally show a great desire to feed, sudden occurrences of feed withdrawal could therefore be perceived as particularly stressful by the fish. On the other hand, if the fish voluntarily start fasting owing to health issues or a poor farm environment, one could argue the freedom from hunger is not being violated as the fish evidently are not hungry. Yet the underlying causes for lack of normal appetite clearly suggest that the welfare is not satisfactory. Presently the Atlantic salmon aquaculture industry does not have proper science-based recommendations for responsible fasting periods based on fish welfare considerations.

The purpose of this review is to summarize available knowledge relevant to feed withdrawal and feed restriction practices as well as the occurrences of prolonged voluntary fasting periods in Atlantic salmon aquaculture with regards to impacts on fish welfare. The aim is then to provide context-dependent guidelines for fasting based on these fish welfare considerations.

This review is structured into several sections. First, existing fish welfare legislations and guidelines on fasting practices in aquaculture are summarized. Second, the lifecycle of wild Atlantic salmon with an emphasis on naturally occurring fasting periods are described. Our present knowledge of the fundamental physiological responses and tolerance limits to fasting in Atlantic salmon are thereafter introduced. This is followed by sections on feed withdrawal practices prior to various operations as well as the implications of fasting in emerging farm concepts, particularly in RAS. Then occurrences of voluntary fasting owing to extreme environmental conditions or poor health are considered. This is followed by discussions on how Atlantic salmon interpret hunger, the potential benefits from strategic fasting or feed restriction, and the subsequent capacity for compensatory growth. Finally, the review concludes with our proposed guidelines for context-depending fasting periods in Atlantic salmon aquaculture.

2 | EXISTING LEGISLATIONS AND GUIDELINES FOR FEEDING AND FASTING IN AQUACULTURE

Many countries now have animal welfare legislations to help facilitate better care and respect for animals. However, the details with regards to species and context can vary substantially between countries. For finfish aquaculture species such as the Atlantic salmon, the specifics in official welfare legislations tend to be vague and overly general with broad statements such as ‘protecting animals from danger and unnecessary stress and strains’.[58] This can be ascribed to the fact that fish species only recently started to be considered as sentient beings with an intrinsic value, irrespective of the value they may have to humans. Hence, attention to fish welfare in aquaculture is a fairly new phenomenon when compared to domesticated terrestrial animals.[57,65,66] As such, broadly defined obligations to ensure good fish welfare mean existing legislations can be interpreted in various ways, and their value may therefore be mostly symbolic and overridden by economical concerns or other legislations with more specific demands.[67] However, issues with formulating detailed and robust welfare guidelines for different cultured fish species in diverse contexts can partly be excused from lack of concrete systematic knowledge in a rapidly evolving industry. Fortunately, fish welfare has become a growing area of research in recent years, and as more knowledge is gathered, better science-based and more specific welfare guidelines can be developed and implemented. An overview of fish welfare legislations and guidelines with regards to feeding and fasting in some of the major salmon producing countries are provided in the following sections.

In Norway, the largest producer of cultured Atlantic salmon, legal obligations for the care of farm animals are described in the animal welfare act.[68] This act broadly states that feed to animals should be of good quality, satisfy nutritional needs and stimulate good health and welfare. Additionally, Norway has a specific legislation for aquaculture management regulations[69] that provides more details on animal welfare requirements in aquaculture. Here it is similarly stated that the quantity of feed should be adequate, and that feed should be composed in a way that promotes good health and welfare. Moreover, the feed should be adjusted to species, age, developmental stage, size and other physiological and behavioural needs. Of particular interest to this review, it is further stated that fish normally should be fed *daily* unless this is inappropriate for a particular species or developmental stage. Also, it is stated that fish should not be fed in situations where feeding practices are considered harmful to the welfare of the fish, hygiene or their quality. However, such periods without feeding must be kept as short as possible. The legislations in Norway therefore does not provide specific statements on appropriate context-dependent fasting periods in aquaculture species, except that fish generally should be fed daily. This leaves considerable room for professional judgement with regards to what it means to ensure good welfare and avoiding unnecessary stress and strains.

Scotland is another significant producer of farmed Atlantic salmon and has an animal health and welfare act and an accompanying guidance document[70,71] that afford fish a basic level of protection and prevention of unnecessary suffering. Here it is stated that animals should be offered suitable diets that are adequate to maintain full health and vigour through every phase of life. However, as in Norway, statements on appropriate fasting periods are lacking. It must, however, be added that one of the reasons that there is relative sparse regulation of fish welfare in the United Kingdom may be due to circa 70% of the fish farmers being committed to following the RSPCA (Royal Society for the Prevention of Cruelty to Animals) welfare standards[72] (see below).

In the EU, a similar broad animal welfare legislation exists that formulate minimum standards for the protection of farm animals, including fish.[73] This legislation states that animals must be fed a wholesome diet which is appropriate to their age and species and is provided in sufficient quantity to maintain good health and satisfy nutritional needs. Also, all animals must have access to feed *at intervals* appropriate to their physiological needs. Furthermore, on their webpage, the European Food Safety Authority refer to external international organizations such as the World Organization for Animal Health that have issued more detailed recommendations and guidelines concerning the particulars of fish welfare.[74] Of interest to this review topic, these guidelines mention that fish should be starved to reduce metabolism and excretion of waste products before certain management practices, transport, slaughter or for administration of therapeutics. Furthermore, such periods of food deprivation should be appropriate to the species and consider environmental conditions, particular temperature, and be kept as short as possible.[75,76] However, specifics for what constitute appropriate fasting periods in various contexts are not provided in any of these recommendations and guidelines.

A similar approach is adopted by the Scottish Salmon Code of Good Practice[77–80] in the United Kingdom, that also has numerous sections regarding feed withdrawal and fasting but lacks specific concrete details on suitable fasting durations for both freshwater and seawater production as well as differing production systems. It also uses the same text for each life stage and system. The code states that: (i) subjecting fish to fasting in relation to gut evacuation must be temperature and species specific, (ii) fasting associated with vaccination should be 'for an appropriate period, in accordance with Data Sheet recommendations and fish welfare guidance', (iii) fasting shouldn't be used in order to condition fish before harvest, should be for the minimum period necessary for gut evacuation and 'should be withheld to reduce metabolic rate and the excretion of waste products, and to eliminate the presence of food and faecal material in the gut at harvest, thus minimizing the risk of microbiological contamination during processing', (iv) if undertaken in relation to health or environmental challenges, veterinary guidance should be pursued, and fasting protocols should be included in the Veterinary Health Plan and Biosecurity Plan where appropriate. Fasting recommendations are not made for broodstock fish. Further, the guidelines also state that any feed management plan should feed accurate amounts of feed 'over the correct period(s) of the day'.[77–80]

Global Animal Partnership's 5 Step Animal Welfare Standards for Farmed Atlantic salmon[81] also state salmon must be fed daily and that feed withdrawal must be (i) less than 24 h for smolt transfer to seawater, crowding, pumping, handling, treatment or vaccination purposes, (ii) less than 30 degrees days (temperature × days) prior to fish transport, unless seawater temperature is below 5°C for three or more days and a withdrawal period of no more than 15 degree days is then applied. Force majeure delays to transport are considered in relation to fasting out with these windows in the standard.[81]

In the Americas, Canada is a significant producer of farmed Atlantic salmon as well as other salmonid species. In 2021, a code of practice specifically concerned with farmed salmonids and their welfare was released along with a comprehensive companion report written by a committee of scientists.[82,83] Going forward, such initiatives should ideally be adopted by other countries as well and include other important cultured species. In the companion report, the authors review conditions that involve periods of voluntary or involuntary fasting. They reflect on the issues with identifying acceptable limits of starvation in farmed fish owing to the lack of empirical studies on how food deprivation affects stress physiology and behaviour. Moreover, they conclude that it is difficult to provide simple time durations of appropriate feed withdrawal practices, since welfare impacts likely will depend on temperature, body size and lipid reserves.[82] To provide some specific guidelines, they refer to the Farm Animal Welfare Council in the UK that previously recommended that Atlantic salmon could be fasted for up to 72 h prior to slaughter for food hygiene reason, and that fasting above 50-degree days should be avoided.[84,85] However, these numbers were neither explained nor supported by specific findings in the scientific literature and thus appear to be opinion based.

Similarly, RSPCA provide a comprehensive report on welfare standards for farmed Atlantic salmon.[86] While giving general statements on ensuring nutritional needs through adequate feeding, as found elsewhere, this report also has concrete guidelines for appropriate fasting times. The report states that for harvest, fasting should not exceed 72 h, and pre-transport fasting should not exceed 48 h, unless directed by the designated veterinary authority for fish welfare reasons. Additionally, this standard note that while Atlantic salmon may not feed for long periods in the wild, depriving farmed fish that previously were fed regularly usually will have an *adverse* effect on welfare. It is also stated that it is unacceptable to deprive salmon of food for perceived flesh quality reasons.[86] However, these recommendations and statements are not backed up by scientific studies and thus appear to reflect the opinion of the expert panel behind this report. Nevertheless, having concrete guidelines is arguably more useful for implementation of good standards compared to the vague statements found in most national animal welfare regulations. Although, if the guidelines become too specific and rigid this can lead to evasion of responsibility for the fish farmers, as any occurrences of substandard fish welfare then can be blamed on a strict set of regulations that merely was followed to avoid potential liability.[67]

A final important note here is that none of the existing guidelines and legislations consider voluntary fasting periods.

3 | NATURAL FASTING IN WILD ATLANTIC SALMON

3.1 | Juvenile freshwater phase

Wild Atlantic salmon juveniles can exhibit diverse life histories and are known to live 1–7 years in freshwater before undergoing the smolt migration to sea. Fish then spend between 1 and 6 years at sea before returning to the rivers to spawn.[87] In the course of the salmon' first summer in freshwater, prospective resident and migrating fish have differing size trajectories and by autumn they diverge into bimodal groupings with divergent life histories. The early migrants (upper modal group) have relatively high metabolic rates, good growth and will migrate to the sea the following spring. The delayed migrants (lower modal group) fish will defer smolt migration and remain in the freshwater environment for at least another year.[88] During overwintering, the fish seek shelter in the stream bed and do not feed, going into a natural, prolonged period of winter anorexia from autumn to spring, even when prey is readily available and temperatures are suitable for growth. The duration and severity of this anorexia is shaped by the lipid reserves of the fish.[89,90]

3.2 | Seawater growth phase

During the marine migration and feeding phase it is unknown how frequently Atlantic salmon typically eat in the wild since it is difficult to monitor the feeding behaviours of individual fish in the open ocean over long time periods. Further advancements in sophisticated bio-logging tag technologies may change this in the future.[91] Following smoltification and seaward migration, getting big as fast as possible greatly increases survival chances owing to lowered risks of predation.[92] The young salmon therefore have a great incentive to feed whenever the opportunity presents itself, and in optimal conditions they would presumably be feeding daily. Yet, resources in the marine environment are patchy and vary substantially between seasons and years, and wild Atlantic salmon will therefore experience periods where they struggle to find food resulting in late summer post-smolt condition factors approaching 0.8 in bad years as opposed to normal levels of 1.0–1.2 in other years.[93] Furthermore, tracking studies of wild Atlantic salmon in the open ocean have documented long-distance movements of several hundreds of kilometres.[94] This suggests that over time individual fish are actively moving between feeding grounds and are thereby presumably encountering various intermittent periods of fasting.

3.3 | Upriver migration and spawning

Once Atlantic salmon have matured and are ready to migrate back to their native river to spawn, they reduce feeding activity and eventually completely stop feeding as they become voluntarily anorexic[95,96] (Figure 1). The spawning migration of Atlantic salmon generally starts in spring whereafter they arrive in their native rivers during summer and spawn in late autumn. Since they are not feeding in the rivers, this implies a natural voluntary fasting period of 3–4 months where they rely on existing internal energy reserves.[97] It has been estimated that both male and female Atlantic salmon spend approximately 50% of their total energetic content on spawning.[98] In agreement with this, muscular lipid content was reduced by 50%–60% at the time of spawning.[96,99] In Atlantic salmon from the Baltic Sea, weight loss from entering the mouth of the rivers to spawning was approximately 10%.[100] This percentage weight loss is comparable to larger sized farmed

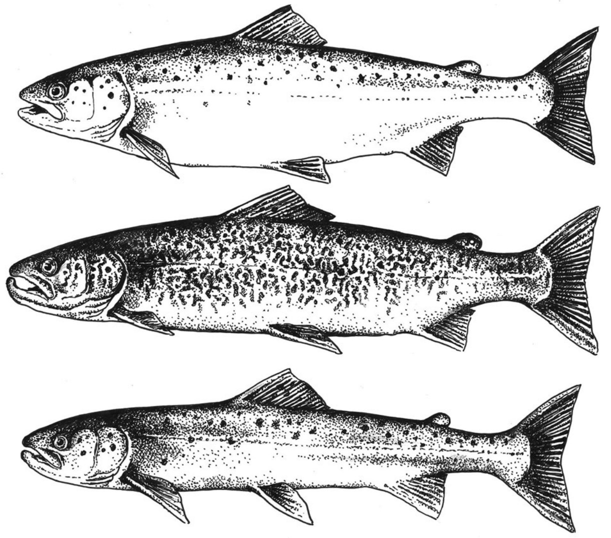

FIGURE 1 Illustrations of mature wild Atlantic salmon pre-spawning (top and mid) and post-spawning (bottom). Atlantic salmon may not feed for several months during the upriver spawning period. In some cases, they overwinter in the river before returning to sea, further prolonging voluntary fasting periods by several months. Such fish will have very low condition factors.

Atlantic salmon fasted for 11–12 weeks.[101–103] As opposed to pacific salmonids, Atlantic salmon are repeat spawners and will migrate back to the ocean to continue feeding. However, occasionally adult Atlantic salmon may spend the winter in the river and thereby drastically extend their fasting period further, which may put them in an emaciated state.[104,105] For instance, it has been documented that mature Atlantic salmon were able to endure 6–11 months of fasting in freshwater.[106]

3.4 | Summary of fasting in wild Atlantic salmon

The conditions for feeding opportunities and growth in nature are obviously very different from the daily ad libitum feeding practice experienced in aquaculture. Nevertheless, how wild Atlantic salmon live their lives provides context to the biological limits and adaptations of this species. This can aid us in interpreting animal welfare status in aquaculture settings. With regards to fasting, Atlantic salmon are naturally adapted to a feast and famine existence, where feeding and growth spurts may come in spatially and temporally divided intervals throughout different life cycles and seasons.

4 | RESPONSES AND TOLERANCE TO PROLONGED FASTING IN ATLANTIC SALMON

4.1 | The three metabolic phases in fasting animals

All animals need to eat periodically to maintain their energy balance. Growth, maturation and reproduction is not possible without a surplus of energy from ingested food. Ultimately, animals can die from starvation, but before reaching this dramatic endpoint a series of physiological, morphological and behavioural changes occur that can serve as indicators of nutritional status. A general phenomenon across vertebrate animal groups is that when a fasting period is initiated, three successive stages occur based on the primary energy source used for metabolism.[107–110] In the initial post-absorptive phase, the animal relies on glycogenolysis in the liver and the main energy source is glucose. As liver glycogen becomes depleted the second phase begins, and energy is supplied primarily from oxidation of fatty acids stored in adipose tissues. Once the majority of fat reserves have been metabolized, the third phase begins where energy is obtained from breaking down muscle protein. The third phase thereby represents severe starvation and will rapidly reduce an animal's physiological capacities resulting in serious weakness and eventual death. These responses to prolonged fasting have been extensively studied in endothermic mammals and birds, whilst the literature on ectothermic fish is more limited. However, existing studies suggests that fish also follow a similar three phase metabolic response when subjected to extended fasting, with the notable difference that each phase lasts longer because fish have lower metabolic rates than birds and mammals.[111–115]

4.2 | Fasting in ectothermic animals

As ectothermic animals have lower metabolic rates they generally show a much greater resilience to food deprivation in comparison to endothermic animals. As such, while small mammals and birds can starve to death within days,[116–118] reptiles, amphibians and fish can survive months or even years without food.[119,120] The European eel has for instance been reported to survive 4 years of fasting.[121]

In addition to the metabolic rate, additional factors such as ambient temperature, body size, and body composition are important factors for determining the resilience of animals to fasting. Specifically, basal metabolic requirements increase with temperature in fish and other ectotherms,[122–124] and the rate of weight loss is therefore higher when fasting at elevated temperatures.[125,126] Mass specific metabolic rates decrease with size,[127,128] and larger individuals at later life-stages can therefore endure longer fasting periods. Furthermore, if a fish has been eating well and has been able to store additional lipid reserves prior to a fasting period, it will cope better. Owing to these factors, the earliest life-stages are the least resilient to fasting. Fish larvae in particular are in real danger of starving to death following depletion of the yolk sac, and first feeding events are therefore crucial for survival.[129,130]

4.3 | Long-term fasting and weight loss in seawater adapted Atlantic salmon

In farmed Atlantic salmon, the effects of prolonged fasting periods have mostly been studied in seawater adapted post-smolts. Some of the longest reported experimental periods of enforced fasting have been 11–13 weeks during the winter months in larger sized Atlantic salmon of 2–5 kg.[101–103,131] These studies were performed in the 1990's at a time when prolonged fasting was used to control biomass in sea cages and to manipulate flesh quality. Today it is generally considered unethical to fast salmon for such purposes.[86] Nevertheless, valuable data on the resilience to fasting in Atlantic salmon were obtained. The fish lost 8%–11% of their body mass over 11–13 weeks, with weight loss being greater in the early periods of fasting. Weight loss was mainly caused by depletion of fat reserves, especially visceral fat in two studies,[101,131] while in another study both fat and protein in the muscles, viscera and liver were reported as important energy sources during fasting.[103] Interestingly, while the fish became progressively leaner with a reduced condition factor, the composition of the muscle tissue on a per weight basis changed little in fasted fish that instead showed a general shrinkage of the entire body.[103] This suggests that Atlantic salmon can adequately regulate muscle protein relative to fat content in the flesh during extended fasting periods. Thus, the three-phase metabolic response to fasting based on a primary energy source[109] may not necessarily be as straightforward to infer in Atlantic salmon. Further, farmed Atlantic salmon still had normal ranges of fat and protein in the muscle tissue after 12 weeks of fasting, suggesting they were not yet subjected to severe starvation.[132]

4.4 | Energy preservation and functional capacities in fasting Atlantic salmon

To adapt to prolonged periods of food shortage, Atlantic salmon can progressively downregulate their baseline metabolic requirements to save energy. As such, at a midrange temperature of 12°C the standard metabolic rate was reduced by 15% after 1 and 2 weeks of fasting, and by 23% after 3 and 4 weeks of fasting.[45] Moreover, following subsequent refeeding for 1-week, metabolic rates returned to normal pre-fasting levels, showing that this adaptive metabolic downregulation was readily reversable once food became available again.[45] Other species of fish may similarly downregulate their metabolism when fasting for longer periods.[133,134] However, preservation of energy becomes more difficult when fasting in warmer waters. In Atlantic salmon fasted for 4 weeks the oxygen uptake rates during routine swimming was reduced by 24% at 9°C, but only by 16% at 18°C when compared to fed control groups within the same temperature.[45] Since basal energetic requirements inevitably increase with temperature, resilience to prolonged fasting is therefore further reduced at higher temperatures. Fish welfare is closely linked to physiological functions such as swimming performance, aerobic capacity, immune defence, and the ability to respond and recover adequately from stressors.[63] Any biological or environmental factor encountered in aquaculture settings that compromise physiological functioning can therefore be considered a welfare issue.[135,136] With regards to prolonged fasting in Atlantic salmon post-smolts, it appears that key functions are maintained provided the fish remain in an energetic state where protein levels are within normal ranges. For instance, in smaller post-smolts of

≈250 g held at 12°C, the critical swimming speed was unaffected over a 4-week fasting period.[137] Similarly, in Atlantic salmon of ≈500 g critical and sustained swimming performances were unaffected by a 4-week fasting period at both 9 and 18°C.[126] However, prolonged fasting will eventually affect swimming performance negatively. This has been documented in Atlantic cod (*Gadus morhua*) that had a reduced critical swimming speed after a 12-week fasting period that concomitantly decreased the condition factor from 1.0 to 0.5.[138] In comparison, the condition factor in the Atlantic salmon swimming studies after 4 weeks of fasting were only reduced from 1.03 to 0.89 and 1.30 to 1.05, respectively[126,137] (Figure 2).

Preservation of swimming capacities following extended fasting is a strong indicator that maximum metabolic rates and associated cardio-vascular functioning are not yet negatively affected. Indeed, while oxygen uptake rates were reduced at lower activity levels, Atlantic salmon achieved similar peak oxygen uptake rates when approaching their critical swimming speed.[126] The difference between resting and maximum oxygen uptake rates is termed the aerobic scope and is widely used to infer adaptations in various environmental contexts.[124,139,140] A high aerobic scope implies good capacity to engage in energetically demanding activities such as intense swimming, immunological responses, digestion, growth, and reproduction. Since basal energetic requirements are downregulated while maximum capacities are preserved, the aerobic scope becomes higher in Atlantic salmon following prolonged fasting. In theory, an adequately fasted Atlantic salmon should therefore be better equipped to cope with acute stress such as experienced during crowding events and delousing operations in aquaculture.

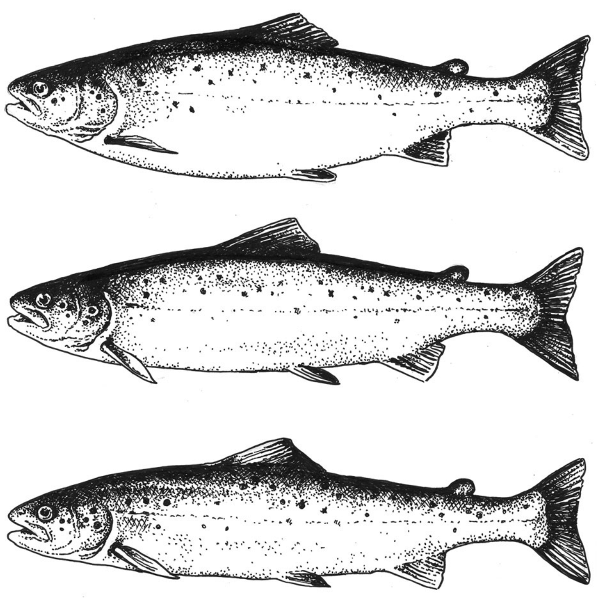

FIGURE 2 Illustrations of cultured Atlantic salmon post-smolts with different conditions factors. These illustrations represent condition factors of approximately 1.3 (top), 1.15 (mid), and 1.0 (bottom). Prolonged fasting or restricted feeding will gradually reduce condition factors. Low condition factors can also be a sign of chronic stress and poor health.

4.5 | Chronic and acute stress responses in fasting Atlantic salmon

Prolonged fasting does not appear to cause a state of chronic stress in Atlantic salmon of ≈250 g at 12°C as inferred from haematological parameters, as resting blood plasma levels of cortisol, lactate, major ions, osmolality as well as the haematocrit and haemoglobin concentration were unaffected over a 4-week fasting period.[137] In some fish species, fasting also did not affect haematological parameters,[141,142] while others may become progressively anaemic.[143] If Atlantic salmon were subjected to more extreme fasting periods than presently documented, haematological parameters would presumably change eventually to reflect an altered homeostasis. This could involve lower haematocrits, and elevated plasma cortisol and osmolality to reflect anaemia, chronic stress, and a less tightly regulated osmotic balance.

Acute stress responses have also been found to mostly be preserved over a prolonged fasting period in Atlantic salmon. In one study, the peak oxygen uptake rate measured following a period of acute confinement stress was unaffected between fed controls and fish fasted for up to 3 weeks. However, after 4 weeks of fasting, peak oxygen uptake rates were slightly reduced.[126] Another study found that prolonged fasting was associated with a slightly higher osmotic disturbance and reduced recruitment of red blood cells when Atlantic salmon were forced to swim until fatigue.[137] Moreover, this study also found that the cortisol response was repressed after 4 weeks of fasting. Overall, this suggests the onset of some impairment in alertness and capacity to react to stressors around week four of fasting in Atlantic salmon post-smolts at intermediate temperatures. A longer fasting period would presumably further reduce stress responsiveness as the fish becomes more lethargic.

Exhaustive exercise stress in seawater adapted salmonids is associated with massive physiological disturbances, particularly in acid–base and osmotic balances, and these take several hours to recover from.[144–146] However, the ability to reestablish baseline oxygen uptake rates and recover haematological parameters following acute stress or exhaustive swimming was unaffected by up to 4 weeks of fasting in Atlantic salmon.[45,137] An uncompromised recovery trajectory following intense stress should provide a strong indicator for that fasted fish still remain in good health.

4.6 | Immune response and disease resilience in fasting fish

Mobilization of an immune response is considered energetically expensive, although exact costs are difficult to quantify and may vary substantially in salmonids depending on contexts and type of infection.[147–150] Nevertheless, it may be hypothesized that prolonged fasting eventually would impair the ability of Atlantic salmon to protect themselves from pathogens owing to resource limitations. Few studies have investigated immune responses and disease resistance in Atlantic salmon or other fish species following extended fasting. In a study on small (≈55 g) Atlantic salmon in freshwater at 12°C, fish were fasted for 4 weeks and subjected to a bacterial infection.[151] Fasted fish had a decreased immune gene transcription and a reduced production of plasma protein genes. However, upon infection there was a large increase in acute phase response proteins in fasted fish, but at the cost of a further decrease in other plasma protein genes. Thus, while components of the immune system become depressed during fasting, Atlantic salmon would attempt to compensate for this by increasing the expression of key immune related genes to a greater extent than fed controls upon infection.[151] In other species of fish immune responses while fasting may vary, and partly owing to different experimental contexts. For instance, in a study on zebrafish (*Danio rerio*) 3 weeks of fasting increased the susceptibility to a bacterial infection, but at the same time innate immune parameters such as lysozyme activity were upregulated,[152] and in European sea bass (*Dicentrarchus labrax*) subjected to 31 days of fasting the mucus lysozyme content doubled.[141] However, in binni (*Mesopotamichthys sharpeyi*) fingerlings 16 days of fasting and refeeding did not affect lysosomes or total immunoglobulins.[153] Moreover, pacu (*Piaractus mesopotamicus*) subjected to a bacterial infection after 30 days of fasting were still able to mount an adequate immune response despite of this being an energetically expensive process.[154] Generally, it remains to be demonstrated whether prolonged fasting makes fish species in farm environments more vulnerable to diseases and parasites. Considering the preservation of other key performance traits in Atlantic salmon subjected to prolonged fasting,[137] this species will presumably still be capable of mounting an adequate immune response during similar fasting periods.

4.7 | Behavioural responses to fasting in farmed Atlantic salmon

Fish behaviour can be an important indicator of welfare status in Atlantic salmon aquaculture.[46,155] During periods of feed withdrawal, it could be hypothesized that farm conditioned fish would become aggressive towards each other, exemplified by fin biting and erratic swimming patterns. However, when video monitoring the behaviour of Atlantic salmon post-smolts in a controlled tank study at relevant fish densities over an 8-week fasting period, no aggressive behaviours were observed and behaviour was indistinguishable from fed control groups.[156] Nevertheless, behaviour can vary drastically between Atlantic salmon in the earlier freshwater phases and in seawater adapted post-smolts. In freshwater, the young salmon fry and parr can be territorial and aggressive which likely reflects adaptations to a river environment with limited space and feeding opportunities,[157] whereas smoltified salmon are more tolerant to conspecifics. Whilst there is limited information on the effects of fasting rather than feed restriction, upon the welfare of juvenile Atlantic salmon, increased dorsal fin damage has been reported in tank-held salmon parr up to circa 40 g when they were subjected to 3 days of feed withdrawal.[158] It is therefore particularly important to pay attention to the behaviour and injury status of juvenile Atlantic salmon during fasting since this can lead to increased fin damage, most likely arising from increases in the frequency of aggressive interactions between conspecifics.[159] Injuries such as fin damage can also make the fish more susceptible to bacterial infections which can become a serious welfare problem.[160,161] Therefore, feed withdrawal is likely to specifically exacerbate aggressive interactions of Atlantic salmon parr (Figure 3).

Interestingly, in recently smoltified salmon that were conditioned to a flashing light signalling forthcoming feed delivery, flashing this light without providing feed led to aggressive behaviour.[162] It can therefore be hypothesized that fasted post-smolt salmon will exhibit fin biting if they believe that food is coming, for example as a reaction to hearing the noise from fish being fed in a neighbouring sea cage, but otherwise stay calm limiting their energy usage. Moreover, it is well known that individual salmon do not eat at every feeding.[163] The amount and speed of feeding is therefore calibrated to not all fish wanting to eat. Scarcity of food pellets can therefore be a possible source of aggression when fish are re-fed after a period of feed withdrawal.

In the seawater phase, feed withdrawal may motivate Atlantic salmon to eat co-habitant cleaner fish species that commonly are deployed in the cage environment to mitigate lice infestations. Cleaner fish are much smaller in size and could easily be swallowed by an Atlantic salmon during the latter phases of production cycles. To our knowledge, this potential interaction has not yet been investigated but has been considered elsewhere.[164] However, if it did occur, it would add to the long list of welfare problems when cleaner fish are used as pest controls.[165–167]

4.8 | Welfare scoring of fasted Atlantic salmon

Finally, the welfare of farmed fish can routinely and more practically be assessed from physical appearance where visible traits are scored

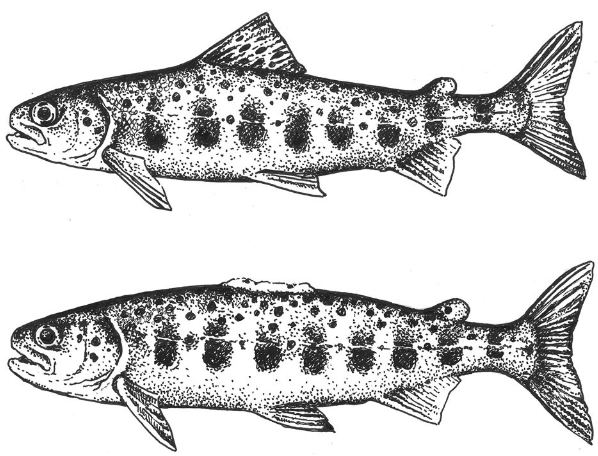

FIGURE 3 Illustrations of Atlantic salmon parr without (top) and with (bottom) fin damage (specifically fin erosion). In the freshwater phase of fish production, Atlantic salmon elicit a more aggressive and territorial personality compared to the following seawater phase. This reflects resource and spatial limitations in river environments versus the open ocean with abundant feeding opportunities. As such, high stocking densities together with insufficient feeding regimes during the parr stage of production can result in excessive fin biting that causes fin damage (splitting, erosion and haemorrhaging).

based on damage to fins, skin, eyes or obvious deformities and health abnormalities.[168,169] After an 8-week fasting period in Atlantic salmon post-smolts, welfare was scored based on appearance traits, where only minor deviations were found and at similar regularities as in the fed control group, thus providing no evidence for reduced welfare.[156] However, had a similar study been performed on pre-smolts in freshwater it would presumably have found negative welfare scores in fasted fish owing to the proclivity for aggression at this life-stage.[159,170]

4.9 | Summary of responses and tolerance to fasting in farmed Atlantic salmon

In farmed Atlantic salmon, seawater acclimated post-smolts appear well adapted to long periods of feed withdrawal. As an ectothermic species they can rely on stored energy reserves for very long periods while still preserving key performance traits. As such, we are not aware of any studies that have documented apparent impairment in physiological performance, immunological function, behaviour or appearance as a result of various fasting periods in post-smolt Atlantic salmon. However, in the preceding freshwater phase of production, salmon parr may suffer reduced welfare following enforced fasting periods or restricted feeding owing to increased proclivity for competing over resources at this life-stage.

5 | FEED WITHDRAWAL PRIOR TO OPERATIONS: TRANSPORT, DELOUSING AND PRESLAUGHTER

It is standard practice in Atlantic salmon aquaculture to cease feeding before operations that involve crowding, pumping, handling, and movement of the fish. Common operations include vaccination, splitting of fish groups, grading and fish movements between tanks or cages, transportation of smolts to sea cages, delousing several times in a production cycle, and finally prior to slaughter.[46,171] Other large-scale health related treatments may also involve feed withdrawal, for instance freshwater baths to treat amoebic gill disease.[172]

The purpose of feed withdrawal is to empty the gastrointestinal tract of the fish. The fish will then have a lower oxygen demand and excrete less carbon dioxide, as specific dynamic action effects are avoided which lowers the risks of hypoxia and hypercapnia. Additionally, this is assumed to improve acute stress tolerance since a higher aerobic scope is available when the fish are not digesting food,[44] and may then mitigate risks of delayed mortality from unrecoverable accumulated stress afterwards.[173] Finally, feed withdrawal provides a practical advantage for hygiene reasons prior to slaughter, and anecdotally, fasted Atlantic salmon are believed to be calmer.

The duration of feed withdrawal protocols prior to operations are based on estimations of gut evacuation rates. Gut evacuation rates of Atlantic salmon are well described and dependent upon fish size, temperature, and feed compositions. For instance, in Atlantic salmon of 150–200 g held at 9°C, gastrointestinal evacuation was near complete after 27 h when fed a standard fish meal diet and extended to 33 h when diets also included either soybean or bacterial protein.[174] Similarly, full clearance was observed after 48 h in Atlantic salmon of 700 g at 7°C when fed meals of different protein concentrations and particle sizes.[175] When assessing gut evacuation across differing temperatures in Atlantic salmon of 70–300 g, rates were highest at 18°C with near completeness after 24 h, intermediate at 10 and 14°C at 48 h, and slowest at 6°C where 72 h was required to obtain near complete evacuation.[8] In larger Atlantic salmon of 5300 g at 4°C, 7 days were required for complete gut evacuations.[44] As such, gut evacuation becomes substantially slower at low temperatures and more so in larger fish.

Based on the above, typical feed withdrawal recommendations are 2–3 days prior to transport, delousing operations, or other health related procedures such as freshwater baths to treat for amoebic gill disease. This may be insufficient for complete gut evacuation at low temperatures. However, when it gets colder, oxygen demands will be depressed by default in ectothermic fish while oxygen solubility in the water is improved. As such, 2–3 days of feed withdrawal prior to transport and delousing will presumably still be adequate at low temperatures.

Feed withdrawal periods prior to slaughter have been reported to be longer, where an older report stated an average fasting time of 9 days before transport followed by 2–3 days in harvest cages.[176] Furthermore, in the 1990's it was common practice to fast for substantially longer to manipulate flesh quality and biomass.[132] However, as stated earlier, fasting farm animals for such purposes is now considered unethical from an animal welfare perspective.[86] We are unaware of recent reports of average preslaughter fasting periods in modern Atlantic salmon aquaculture.

Knowledge of gut evacuation rates allows for optimal feed withdrawal practices so that feeding downtimes are kept at a minimum and thus reducing assumed forgone growth potential.[39] Fasting periods used prior to major farm operations are also relatively short when considering that post-smolt Atlantic salmon are well-adapted to endure weeks and even months without feeding. The welfare of Atlantic salmon post-smolts around marine handling operations should therefore not be compromised due to feed withdrawal on its own. However, major welfare problems are associated with some of the rather stressful operations associated with feed withdrawal practices, where mechanical and thermal delousing operations presently are the most worrying as these are a significant cause of mortality.[42,177] Considering the various benefits of performing operations on fasted fish with empty guts, feed withdrawal periods beforehand will likely be a net positive for the fish. This is supported by a recent report on commercial production of triploid and diploid Atlantic salmon that found a negative correlation between fish mortality after delousing and number of fasting degree days before delousing for both ploidies.[178]

Finally, as there is limited information on the welfare effects of feed withdrawal upon fry and parr in the hatchery phase around handling operations, until this information becomes available a cautionary approach could be considered regarding the potential risks posted by feed withdrawal[160] during this life stage. For example, if an increase in aggressive behaviour is observed, or a farmer sees an increase in the prevalence of dorsal fin damage among their stock during feed withdrawal, due considerations should be made regarding the timing and management of re-feeding.

6 | FASTING IN RAS AND OFFSHORE AQUACULTURE

Since its inception in the 1970's, the Atlantic salmon aquaculture industry has continued to evolve and innovate at an accelerating pace to accommodate further growth. However, it soon became clear that future increases in smolt production would be limited by available freshwater resources unless new technologies permit the production of smolts with reduced water usage.[179] In addition, persisting concerns regarding negative environmental impacts has enforced a limit on allowable sea cage production sites in Norway, the world's largest producer of Atlantic salmon. The primary obstacle is the spread of the ectoparasitic copepod *Lepeophtheirus salmonis* into the adjacent marine environment where it poses a significant threat to wild salmonid species.[180] This has motivated the development of various alternative production systems that do not rely on extensive freshwater resources or traditional fjord and coastal sites. We will outline two case studies on these non-traditional production systems and the challenges they potentially pose in relation to fasting and feed restriction.

First, there can be a switch from using flow through systems in hatcheries, to RAS. This also allows the opportunity for farming Atlantic salmon longer or entirely on land. Second, there is a possibility to move production further offshore where environmental impacts will be different and presumably diminished. Either approach offers a potential solution for further growth of the industry in a more sustainable way. Additionally, both methods require novel considerations and approaches regarding feed withdrawal practices.

6.1 | Feed withdrawal in RAS

In RAS, rearing water is treated to remove fish metabolites such as ammonia, carbon dioxide and organic matter. A key component in the water treatment process is biological filtration in biofilters where nitrification occurs, which is a two-step process where toxic ammonia is oxidized to nitrite and nitrate by nitrifying microorganisms.[181] Similar to other farming systems, feed withdrawal and restricted feeding is necessary in RAS at various points in production cycles prior to major operations such as vaccination, grading and transfer (see Section 5). However, feed withdrawal in RAS can drive oscillations in ammonia availability, either daily or over extended periods, which can have negative effects on biofilters as a continuous supply of ammonia is needed for optimal operations of nitrifiers.[182] Feed withdrawal or restricted feeding can therefore facilitate water quality issues in RAS, potentially causing fish welfare issues.

For instance, in a study where the production of Atlantic salmon smolts in RAS was compared to production in flow-through systems, mortality increased 1-week post-vaccination in RAS.[183] It was suggested that handling stress and a compromised immune system in combination with the possible higher bacterial load in the RAS water could have been the cause of mortalities. At the same time an increase in total ammonia nitrogen (TAN) concentration was observed indicating disturbance in the biofilter operation. However, more knowledge is needed to fully understand the correlation between feed withdrawal, vaccination and fish health and welfare.

Another example is RAS facilities with higher salinities, where more sulphate is introduced, increasing the risk for increased microbial production of hydrogen sulfide (H_2S) which is highly toxic.[184,185] Several incidents of mass mortality in RAS have occurred prior to post-smolt transfer to sea cages when the feeding of fish was intentionally stopped and consequently the production of nitrate, as the final product of nitrification, ceased. Depletion of nitrate and other favourable electron acceptors from water and aerobic layers can create a favourable habitat for sulphate-reducing bacteria (SRB) producing H_2S in thick biofilms with deep anoxic layers in the biofilters. Under these suboptimal operational conditions biofilters can become potential hotspots for the production of H_2S.[186] During feed withdrawal in saltwater RAS, for instance in preparation for transfer to sea cages, it is therefore suggested that one should maintain the nitrate concentration in water at a high enough concentration to prevent the production of H_2S.[186]

In RAS and other freshwater farm systems, a general challenge is that harvest sized fish may accumulate geosmin and 2-methylisoborneol in the flesh that gives an undesirable earthy or musty flavour. These compounds are produced by certain cyanobacteria and actinomycetes.[187,188] However, it is possible to cleanse the fish to remediate off-flavour prior to slaughter by fasting them in odour-free holding tanks.[189] Appropriate feed withdrawal protocols for harvest sized Atlantic salmon produced in RAS have been investigated in a series of studies. For instance, one study subjected Atlantic salmon for up to 20 days of fasting and concluded that 10 to 15 days were required to obtain sufficient reduction in geosmin and 2-methylisoborneol in either a flow-through system or a recently cleaned RAS.[50] In another study that tested fasting periods of up to 10 days, it was found that using hydrogen peroxide to disinfect depuration systems beforehand as well as avoiding high-surface water aeration media could reduce off-flavour compounds and thus reduce required fasting periods.[51] On the other hand, the depuration process could not be accelerated via the manipulation of current speeds and dissolved oxygen levels in RAS over a 10-day fasting period.[52] Most recently, RAS reared Atlantic salmon of 5–6 kg were fasted for 1 day and then transferred to depuration tanks where they were fasted for another 7 days.[190] Here, geosmin and 2-methylisoboreal levels in water and fish were generally low, and it was concluded that a 7-day depuration period was excessive and that the fish could have been harvested after just 2–3 days, as long as gut evacuation was complete.[189] These examples suggest it is possible to manage and mitigate off-flavour compounds in RAS by manipulating environmental, microbial, and technological conditions. Ongoing refinement of novel RAS practices may therefore eventually prevent the necessity for prolonged feed withdrawal periods prior to slaughter. Regardless, the fasting periods used previously for depuration purposes are still well-within the tolerance limits of harvest sized Atlantic salmon and should therefore not constitute serious fish welfare concerns.

6.2 | Feed withdrawal in offshore aquaculture

Offshore aquaculture is defined by FAO, 2022 as farm sites that are located more than 2 km from the coast, at depths above 50 m, with occasional waves above 5 m in height, and with strong currents and winds.[191] As such, offshore sites provide more extreme environmental conditions when compared to more traditional sheltered sites.[192,193] Strong persisting water currents and powerful waves can here become a fish welfare concern if they exceed the physiological limits of the fish.[47] Offshore aquaculture initiatives started more recently and are presently not as widespread as RAS. The risks of enforced fasting periods discussed next are therefore based on precautionary considerations owing to a lack of available reports on offshore production management.

At farm sites exposed to stronger water currents than which is common in more traditional farming locations, feeding of the fish becomes more difficult as pellets may quickly disperse more rapidly out of the sea cage and the fish may struggle to catch the pellets. Moreover, in rough weather conditions with powerful waves and strong water currents, the fish will have to divert substantial energy towards maintaining swimming position within the sea cage, meaning that they may not have sufficient aerobic capacity at their disposal to simultaneously feed and digest food.[194] As such, it is likely not feasible to feed the fish during stormy conditions. Potential feed withdrawal periods will therefore depend on the duration of extreme weather events. As discussed previously, post-smolt Atlantic salmon are well-adapted to endure extended fasting periods and they preserve both their critical and sustained swimming capacities following up to 4 weeks of feed withdrawal at different temperatures.[126,137] They are therefore likely able to cope during prolonged stormy weather events in offshore sea cages. However, occurrences of bad weather that reduce conditions for optimal feeding will be a concern from a production perspective, especially if they reoccur and lead to a substantial number of accumulated days without proper feeding. Stormy weather could also cause logistical issues with transport where feed supplies cannot be delivered on time to offshore farm sites, which could result in additional unwarranted fasting periods. As such, when choosing new offshore sites for Atlantic salmon aquaculture, thorough considerations of weather patterns and risks of extreme weather events are therefore necessary.[195] Future observations in emerging offshore farm concepts will reveal whether reoccurring unplanned fasting periods become problematic with regards to both fish welfare and growth performance.

7 | ENVIRONMENTAL EXTREMES CAN INDUCE VOLUNTARY FASTING

There are various published data on optimal as well as suboptimal environmental conditions for the growth performance of Atlantic salmon.[6,8,10,11] However, this information does not cover the full range of water quality parameters the fish can be subjected to, nor all life stages and rearing systems. Whilst the flow through hatchery environment often subjects fish to suboptimal water temperatures and metal concentrations as well as increased CO_2 and TAN concentrations at maximal production intensities,[196] RAS offers the potential for maintaining more stable water quality parameters compared to traditional flow through systems.[183] In addition, the sea cage environment changes with season, with depth, and varies between geographically distinct sites. Farmed Atlantic salmon can therefore be exposed to substantial variations in temperature, oxygen levels, salinity, photoperiods and current speeds.[155] This means that sea cages will not always provide ideal conditions for growth, and occasionally environmental extremes can become a serious welfare concern. Suboptimal environments reduce appetite and growth, and if specific gradients exceed the biological limits of the fish, they will start fasting voluntarily as a temporary coping mechanism. The most relevant parameters to consider are elevated temperatures, insufficient oxygen levels, as well as their interactive effects.

7.1 | Suboptimal temperatures

Atlantic salmon have a wide thermal niche, but above 18–19°C appetite and growth start to decline,[197,198] and at chronic temperatures of 22–23°C they will stop feeding completely and eventually die.[199,200] These thermal limits naturally restrict the geographical latitudes where Atlantic salmon aquaculture is possible. With the increasing threat from anthropogenic climate change where more severe and frequent heatwaves are predicted, suitable farm sites may become further geographically restricted in the future. For instance, Tasmania can be considered the climate change frontier of Atlantic salmon aquaculture, as fish here are cultured at substantially higher temperatures than typically found in Northern Europe and Canada. Reports from Tasmania have documented that Atlantic salmon are cultured in sea cages subjected to prolonged periods of temperatures above 19°C in the summer.[31–33] Furthermore, it has been predicted that some Tasmanian sites will be unsuitable for Atlantic salmon aquaculture in future climates.[201]

One study was performed during an unprecedented Tasmanian heatwave and presently provides the most detailed report on Atlantic salmon production performances in an extreme climate scenario.[33] The farm site that was monitored experienced 117 days above 18°C and 83 days above 20°C at 5 m depth, which induced long periods of voluntary fasting. Both fish weight and condition factor declined during the Tasmanian summer between December and April, coinciding with a lack of appetite, and a threshold for the complete cessation of feeding for all fish was estimated to be 21.5°C.[33] In total, individual fish may have been voluntarily fasting for more than 3 months owing to extreme environmental conditions. The average oxygen levels were 90% saturation and did not fall below 70% saturation. Whilst these oxygen concentrations can be considered close to optimal at these temperatures (see section below), these levels were measured outside the cages, and the oxygen levels experienced by the fish would likely have been lower owing to the biomass of the fish and obstructed water flow from the cage structure.[33] Whilst mortality rates were not reported during these extreme environmental conditions at the Tasmanian farm site, other studies on Atlantic salmon have documented mortality rates of 15%–30% following 1–4 weeks of acclimation to 22 or 23°C.[199,200]

At low temperatures appetite is reduced accordingly. Anecdotally, salmon farmers report lack of appetite and some stop feeding for months when temperature drop below 3°C. Similarly, a recent study found that appetite started declining at 6°C and at 1°C appetite was completely lost, and moreover, very low seawater temperatures caused osmoregulatory disturbances, elevated cortisol levels, symptoms of liver dysfunction, and increased mortality rates.[34]

7.2 | Environmental hypoxia

Together with temperature, oxygen levels are the primary environmental parameters monitored in Atlantic salmon flow through and sea cage production systems, while in RAS more parameters are regularly monitored such as pH, nitrogen compounds, alkalinity and CO_2. Oxygen in RAS is monitored in real time in individual tanks, and it is automatically added when saturation drops below a desired concentration to prevent exposing the fish to suboptimal oxygen levels during production. However, environmental hypoxia (low oxygen levels) is a prevailing concern in sea cages and is caused by high stocking densities and inadequate water exchange rates.[155] Since oxygen solubility in water decreases with increasing temperature and the oxygen demand of the fish simultaneously increases owing to accelerated metabolic rates, the risk of hypoxia in the sea cage becomes higher as it gets warmer, while the tolerance of the fish to hypoxia worsens. Hence, elevated temperatures and hypoxia work synergistically to the detriment of the fish.

The appetite of Atlantic salmon starts to decline when oxygen levels fall below a threshold that is highly temperature dependent. Specifically, in post-smolts at 19°C oxygen levels above 75% saturation are required to maintain maximum feed intake, while this decreases approximately linearly with temperature down to 42% saturation at 7°C.[11] If oxygen levels fall further, appetite will decrease and in severe hypoxia feed intake becomes zero. One study estimated via regression analyses that the threshold for zero feed intake would be 24%, 33%, 34%, and 40% at 7, 11, 15, and 19°C, respectively.[11] These theoretical thresholds approach measurements of the critical oxygen tension in Atlantic salmon.[202,203] The critical oxygen tension marks the point where the fish no longer can supply its basal metabolic requirements via aerobic respiration, and the aerobic scope by definition is therefore zero. In such conditions the fish can no longer engage in any sustained activities, and prolonged exposure will cause suffocation.

Feeding and digestion may elevate aerobic metabolic rates by a factor of 2–3 relative to resting levels,[140] and in warmer and more hypoxic conditions the factorial aerobic scope of Atlantic salmon decreases.[128,199] The onset of reduced appetite and eventual voluntary fasting has therefore been hypothesized as a behavioural response to avoid being forced into anaerobiosis and thereby preserve the aerobic scope in warmer and more hypoxic environments.[204,205] For instance, if the energetic costs of feeding and digesting exhausts most of the aerobic scope the fish is left in a highly vulnerable state as they will struggle to perform other activities such as swimming away from a predator.

Even in colder production regions Atlantic salmon are occasionally subjected to appetite limiting conditions in sea cages owing to insufficient oxygen levels.[206] Although, more extreme reports of poor oxygen conditions exist in warmer regions such as Tasmania.[31,32] Temperature and oxygen levels typically change with depth inside the sea cage meaning that Atlantic salmon behaviourally have some choice in environmental exposure. Interestingly, Atlantic salmon appear to first and foremost choose its depth distribution based on its thermal preference while disregarding unfavourable oxygen levels. For instance, two studies observed that the fish avoided the warmer upper layers where the temperature exceeded 20°C, but this forced them into the hypoxic zone of the cage where oxygen levels were less than 60% saturation, although the temperature was more favourable here at 16.5–17.5°C.[31,32]

7.3 | Voluntary fasting caused by environmental extremes is a serious welfare concern

Earlier in this review, we have shown that Atlantic salmon are well adapted to extended fasting periods. However, declining appetite or forcing the fish into voluntary fasting owing to either suboptimal or extreme environments is a cause for serious concern. Fasting will here be a symptom rather than a cause for poor welfare. As such, failing appetite and low growth are generally some of the strongest indicators for poor welfare.[46] If the sea cage environment does not allow the fish to feed normally, it cannot be considered suitable for responsible aquaculture production. Owing to climate change, heat waves and hypoxia will be an ongoing welfare challenge in Atlantic salmon aquaculture.

8 | POOR HEALTH AND VOLUNTARY FASTING

Like suboptimal environmental conditions, biological factors such as parasites, diseases, chronic stress, and other health related issues can affect appetite and, in more severe cases, induce voluntary fasting. However, the literature on non-lethal effects of prevailing pathogens and parasites in aquaculture is scarce and little detailed. Aquaculture studies will instead typically report reduced growth and link this with observations of specific pathogens, parasites, or injuries.[37,207,208] Thorough observations of changes in appetite, the onset and extent of voluntary fasting periods, and the subsequent capacity for recovery of appetite in farmed Atlantic salmon following a disease outbreak are practically non-existent. This is due to it being difficult to study the nuances of non-lethal pathophysiological effects at the level of the individual. Typically, in aquaculture research large numbers of fish in holding tanks or in sea cages are monitored at group level, and if reduced feed intake is observed it can generally not be established whether all the fish on average are feeding less or if a subgroup stopped feeding completely. Occurrences of voluntary fasting in health compromised individuals may instead be inferred from a lower condition factor and heterogenous size distributions within the group, or by assessing stomach fullness in any fish that need to be euthanized for sampling or health auditing purposes.

The fact that disease impacts in aquaculture are primarily assessed from diagnosing the presence of pathogens or parasites, combined with reports of mortality rates is worrisome from a fish welfare perspective. Some diseases, for example, cardiomyopathy syndrome (CMS) can be relatively acute in nature, and dead fish diagnosed with the condition often exhibit no external signs of poor health or welfare and often exhibit no signs of emaciation.[209] In other cases, health compromised Atlantic salmon may have been exhibiting increasingly poorer health for longer time periods, and likely been fasting voluntarily in the final phases of the disease, before potentially dying. The accumulating severity of experienced distress would therefore have been substantial.

8.1 | Pancreas disease

The most well-known anorexigenic pathogen in Atlantic salmon aquaculture is the salmonid alphavirus that causes pancreas disease (PD), where symptoms are necrosis of exocrine pancreas, cardiomyocytic necrosis, muscle inflammation, loss of appetite and emaciation.[36,210] Mortality rates are highly variable and associated with added stress from handling procedures such as delousing operations.[211] Since the exocrine pancreas is responsible for secreting digestive enzymes into the gastrointestinal tract and thereby is essential for the processing of ingested feed, it is not surprising that necrosis of this organ is associated with loss of appetite. Pancreas disease can allegedly cause voluntary fasting for several months in affected Atlantic salmon. Interestingly, recovery from pancreas disease with part or full regeneration of damaged pancreas tissue has been reported in the period 4 weeks to 3 months after infection.[35,212,213] Clinically affected fish would therefore presumably undergo an extended fasting period followed by a recovery period where appetite eventually returns, if they survive.

8.2 | Infectious pancreatic necrosis virus

Another pathogen that affects the pancreas and thereby appetite is the infectious pancreatic necrosis virus (IPN). In a 44-day experimental laboratory trial, Atlantic salmon had a lower feed intake and lower specific growth rate starting approximately 20 days after infection, and some of the fish were observed to completely lose their appetite, while no fish died over the study period.[214] Although IPN is much less of a problem since the introduction of IPN resistant broodstock, there are still relatively many reports each year.[38] IPN outbreaks can happen both in freshwater and in sea water and can vary from being subclinical with little or no mortality, to acute outbreaks with more than 50% mortality.[215] Typical clinical findings include an empty gut.

8.3 | Gill diseases

Farmed salmon are at a risk of a variety of gill problems and gill diseases. This includes the amoebic gill disease (AGD) caused by the marine amphizoic *Neoparamoeba perurans*,[216] but gill diseases can also be caused by bacteria, harmful algae, and often have several causes at once, so called 'complex gill disease (CGD).[217] The first observed clinical sign of AGD is often a reduction in appetite.[217] This is probably due to the damaged gill tissue giving lowered gas exchange across the gills, thereby affecting the appetite of the fish.[218] As discussed above, having sufficient oxygen is a key part of digestion.

8.4 | Pathophysiological effects predict appetite impairment

Whether, and to what extent, a pathogenic agent will impair appetite depends on its pathophysiological effects on the fish. As such, based on known clinical effects, one can speculate how other pathogens and parasites in Atlantic salmon aquaculture may affect appetite and potentially induce voluntary fasting. For instance, the ectoparasitic copepod *L. salmonis* is the biggest health concern in sea cage production of Atlantic salmon, and major non-lethal pathophysiological effects include osmotic stress and increased metabolic maintenance costs once parasites have progressed to the mobile stages.[150,219] Moreover, infestations have been associated with reduced growth over a 30-day experimental laboratory trial coinciding with osmotic stress.[218] Severely infested individuals are therefore likely to become temporarily anorexic. As such, other diseases or parasites that causes osmoregulatory challenges, interferes with metabolism, or compromises the gastrointestinal system can be expected to also affect appetite and eventually induce voluntary fasting once a certain pathogenic threshold has been exceeded.

8.5 | Growth-stunted fish

A common occurrence in Atlantic salmon aquaculture are growth-stunted fish also known as 'loser fish' or 'runt fish' (Figure 4). These are characterized by abnormally small sizes and poor condition factors relative to healthy conspecifics, which indicate long-term anorexia.

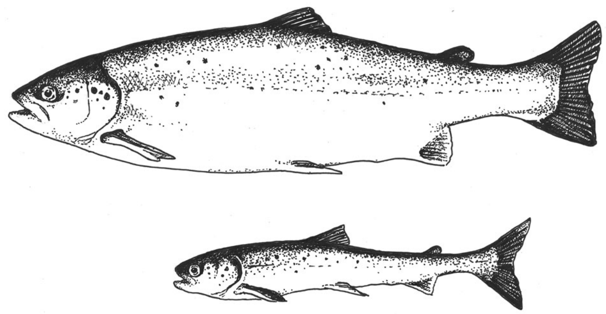

FIGURE 4 Illustrations of a normal farmed Atlantic salmon post-smolt (top) together with an emaciated 'loser' fish (bottom) from the same cohort. Owing to poorly understood reasons, some fish in a production cycle fail to cope in the aquaculture environment where they cease to eat and grow for long periods of time.

Growth-stunted fish tend to be easily catchable as they position themselves towards the edge of the sea cage close to the surface and show little behavioural response to environmental stimuli.[168,220] The stress physiology of growth-stunted Atlantic salmon has been studied, and here it was found that these fish had elevated baseline serotonergic activity in the brain as well as elevated baseline plasma cortisol levels.[221] Moreover, growth-stunted individuals responded poorly to additional acute stress compared to healthy conspecifics. This suggested allostatic overload as well as chronic activation of the hypothalamic–pituitary–adrenal axis system, and interestingly, the behavioural and serotonergic profile described for growth-stunted Atlantic salmon were reminiscent of depression-like states in mammals.[221] It is presently unknown why a potential substantial proportion of a fish stock subjected to conventional aquaculture conditions can become so 'depressed' that they stop eating for long periods. This is a serious fish welfare issue that deserves more attention so that potential mitigation strategies can be developed.

8.6 | Impaired appetite is a strong welfare indicator

Reduced appetite and the complete cessation of feeding are some of the strongest welfare indicators in aquaculture.[46,168] Provided that the farm environment otherwise is within normal ranges, such observations strongly suggest that the health of the fish is compromised, likely owing to prevailing diseases, parasites or states of chronic stress that can unfortunately be common in Atlantic salmon aquaculture. Similar to voluntary fasting induced by environmental extremes, the proximal welfare concern is here not the fasting per se, but the underlying cause for a lack of appetite. More knowledge is generally needed on the occurrences of health-related fasting periods as induced by any prevailing pathological state found in Atlantic salmon aquaculture, including whether the fish are able to eventually recover and regain their appetite.

A final note here is that some readers may object to calling fasting induced by poor health as 'voluntary', as it can be said to be forced by the attacking pathogen, but we have still chosen to call it 'voluntary' as it is part of the coping mechanism of the fish to deal with the disease. There are, however, some diseases that can lead to the mouth of the salmon becoming so damaged and deformed that it becomes difficult, and sometime eventually impossible for the inflicted individual to eat. Examples of this are bone deformations such as pug-headedness[222] and screamer disease,[223] and bacterial infections such as tenacibaculosis that can attack the snout leading to mouthrot.[224] In such cases, it is possible that the salmon still want to feed, but is not able to, and that the fasting, strictly speaking, cannot be said to be voluntary.

9 | DO ATLANTIC SALMON FEEL HUNGRY WHEN FASTING?

Earlier in this review we described various responses and tolerances to fasting in Atlantic salmon. Here we concluded that this species, with the exception of the earliest freshwater life-stages, is well-adapted to endure extended periods of fasting while still preserving key physiological functions. One may therefore generally assume that welfare is not compromised during periods of feed withdrawal, as the fish appear to maintain good health. However, farmed Atlantic salmon have been conditioned to being fed every day, and a sudden unexpected divergence from such daily routines may be experienced as distressing. An important question to consider is therefore whether the salmon actually *feels* hungry when subjected to feed withdrawal, and if so, how uncomfortable are the hunger feelings the salmon perceives? Moreover, how can the severity of negative or painful experiences be quantified from the point of view of the fish when assessing welfare implications?

9.1 | Endocrine control of appetite in animals

The physiological basis for the control of appetite is generally well conserved among vertebrates, including fish, and is regulated by the central nervous system where specific neuropeptides released from the gastrointestinal tract communicate with the hypothalamus to either induce or inhibit appetite.[225,226] For instance, during fasting the hormone ghrelin is released in the stomach and stimulates hunger via neurological signalling to the hypothalamus, and conversely, the hormone leptin acts as an anorexigenic factor during periods where feeding is not a priority by facilitating an opposite neurological signal.[225,227] As such, assessments of neuroendocrine appetite signals, whether orexigenic or anorexigenic, in response to various stages or contexts of fasting, are likely the only feasible way to infer whether Atlantic salmon actually feels hungry.

9.2 | Hunger stimulating signals in fasting Atlantic salmon

In one study of Atlantic salmon it was found that plasma levels of ghrelin increased after 2 days of fasting relative to fed controls, suggesting that the fish indeed were feeling increased hunger at this time.[228] However, after 2 weeks of fasting in the same study there was no difference in ghrelin when compared to fed controls.[228] In Atlantic salmon fasted for 4 days, it was found that changes in ghrelin and associated orexigenic signalling genes and neuropeptides were minimal when compared to fed controls.[229] Additionally, after a substantially longer enforced fasting period of 4–6 weeks, orexigenic signals were shut down or neutralized as assessed from changes in relevant appetite regulating genes and neuropeptides.[230] Combined, these studies suggest that hunger stimulating signals are most active on the short term within the first few days of fasting, meaning that Atlantic salmon presumably do not feel excessive hunger when subjected to fasting for four days or longer. Furthermore, this could be an adaptation to save energy from foraging activities during catabolic conditions when feeding opportunities are limited, and also to reduce any fasting-induced stress effects.[230]

9.3 | Appetite suppressing signals in sub-optimal environments

When exposed to elevated suboptimal temperatures, similar appetite controlling signalling has been observed. For instance, at 18°C plasma levels of the anorexigenic hormone leptin were elevated while appetite was reduced in Atlantic salmon.[197] Furthermore, at 19°C ghrelin levels were reduced in Atlantic salmon,[231] leading these authors to suggest that its regulation plays a role in voluntary anorexia. Hence, appropriate neuroendocrine responses are presumably telling the fish not to be hungry in suboptimal environments. It is therefore reasonable to assume that under such conditions of voluntary fasting, the fish are not experiencing increased hunger.

9.4 | Atlantic salmon likely do not experience a chronic sensation of hunger

In truth, we can never know exactly how other animals are feeling or how they perceive various experiences. Nevertheless, owing to shared evolutionary histories and intricate knowledge of comparative physiology, we may infer certain things about the perceptive world of fish such as their ability to feel pain[53] and even hunger.[225] Regarding feelings of hunger in Atlantic salmon, it seems appropriate to conclude that prolonged fasting, whether forced or voluntary, does not involve a chronic sensation of hunger owing to upregulated anorexigenic signalling.[197,230] From an evolutionary perspective this would also make sense, as this species naturally encounters fasting periods of various lengths, as discussed previously. It would seem maladaptive if such naturally occurring fasting periods were associated with immense distress owing to a chronic feeling of severe hunger.

10 | COMPENSATORY GROWTH AND POSSIBLE BENEFITS FROM FASTING AND FEED RESTRICTION

So far this review has focused on whether various occurrences of fasting in Atlantic salmon aquaculture could have a negative impact on fish welfare. It has been assumed implicitly that fasting is something that should be avoided or at least minimized, if not owing to welfare concerns, then because of the projected economic loss due to unrealized growth potential. In the following section we consider if such worries of production losses are warranted owing to the capacity for compensatory growth in Atlantic salmon. Furthermore, we propose that strategic fasting and feed restriction regimes potentially could be beneficial by mitigating sexual maturation and improving the health of the fish.

10.1 | Compensatory growth

After a period of restricted feeding or fasting many fish species are able to compensate weight loss by increasing feed intake and growth rates to higher levels than in continuously feeding counterparts, provided that favourable feeding opportunities are presented.[232,233] As such, growth patterns in fish can be highly flexible depending on food availability and other environmental factors.

In Atlantic salmon, compensatory growth has been reported on several occasions following periods of reduced feeding or fasting.[156,234–236] Sometimes only partial growth compensation was reported, but this can be ascribed to time restricted experimental trials while growth curves were being monitored on intermediate sized fish.[235,236]

From an aquaculture production perspective, the main interest would be whether compensatory growth was partial or full at the time of harvest. To investigate this, a recent study subjected Atlantic salmon of 1.1 kg to 8 weeks of fasting whereafter compensatory growth performance was monitored relative to a continuously fed control group all the way to harvest 7 months later.[156] After the fasting period the fish had lost 7.4% of their body mass and the fed control group were on average 50% bigger. During subsequent refeeding the fasted group achieved higher feed intake than the control group and 3 months after the fasting period the size differences were small, albeit still significant. At harvest the sizes had become similar with an average weight of 6.1 kg, thus demonstrating full compensatory growth.[156]

While complete growth compensation took several months to achieve, one should consider that an 8-week fasting period is quite extreme in the context of Atlantic salmon aquaculture. More realistically encountered feed withdrawal events, such as those associated with delousing or transportation, will only last a few days and will therefore be much easier to compensate for afterwards, unless the procedure itself impose lasting negative impacts. As such, the capacity for growth compensation along with flexible growth trajectories in Atlantic salmon puts into perspective whether daily ad libitum feeding regimes really are necessary for achieving the maximum growth potential, both at the individual and the group level. Moreover, it questions whether less feeding days during a production cycle readily can be converted into economic loss based on projected growth deficiencies that actually reflect the biological reality. Chances are that farmed Atlantic salmon will inevitably reach the same size within the same amount of time regardless of being fed every single day as long as they still are allowed to periodically feed until satiation, provided they remain clinically healthy. Here it is worth reiterating that farmed Atlantic salmon tends to be overfed owing to the fear of growth loss,[22] despite feed being the highest production expense.[26]

10.2 | Delayed maturation in feed-restricted Atlantic salmon

A reoccurring observation in studies that have subjected farmed Atlantic salmon to fasting or restricted feeding regimes is that fewer fish would become mature. For instance, by fasting Atlantic salmon every second week over a two-month period maturation rates were reduced by 35%.[237] Another bi-weekly fasting study reported similar reductions in maturation rates.[238] Moreover, a two-month fasting period during winter caused a 48% and 32% reduction in mature females and males, respectively,[234] and following 8 weeks of fasting, 25% less mature fish were observed 7 months later at harvest than in the control group.[156] The exact mechanism by which maturation rates are reduced in Atlantic salmon with a feed restricted history is presently unclear, but presumably involves both nutrient and environmental signalling at critical timepoints that either triggers or delays maturation processes.

Reduced maturation is a positive effect from a production perspective owing to immature fish being substantially larger than maturing fish that are diverting their resources on gonad development instead of somatic growth.[156] As such, maturing fish are considered undesirable and selection for delayed maturity along with growth performance has therefore been the primary focus during the domestication of Atlantic salmon.[12] In one study, it was noted that owing to compensatory growth the losses in meat production may be so low that strategic food deprivation could be used as a tool to reduce the problem of early maturation.[238] This was corroborated by another study where harvest sizes were unaffected by a previous fasting period while maturation rates were reduced.[156]

10.3 | Health benefits from fasting and slower growth

A strict focus on maximizing growth throughout all stages of production may be associated with some unforeseen problems during the later stages in Atlantic salmon aquaculture. This also includes unwanted maturation as excellent growth during the early post-smolt phase has been linked to maturation after one sea winter.[239] A higher condition factor in July has similarly been associated with increased likelihood for maturation the following spring, indicating that time of maturity is influenced by growth patterns earlier in life.[238]

A more recent case study has linked accelerated growth in the freshwater phase with deviating heart morphology in larger sized fish and increased mortality risks following stressful operations during the final sea cage phase of Atlantic salmon production.[240] Accelerated early growth is also linked to the development of abnormal otoliths, which suggests that farmed Atlantic salmon have impaired hearing.[241,242] As such, a slower and less intense growth regime earlier in life that is more akin to the natural growth patterns of Atlantic salmon could prove to be a good investment in relation to improved survival rates and overall health later in the production cycle. Perhaps a less intense freshwater production regime could also mitigate the proportion of fish that become chronically stressed and end up as emaciated and growth-stunted.[221] Norwegian farmers are also considering reducing temperatures from 12–14 to 10–12°C and rearing densities from 75 to 60 kg m^{-3} during production of post-smolts on land to increase robustness and performance of Atlantic salmon in the sea.[243]

A concept that is being employed in agriculture is skip-a-day feeding which is used to manage the body condition and health status of terrestrial animals such as pigs and chickens that have been artificially selected for accelerated growth.[110] Reported benefits include lower mortalities, reduced developmental abnormalities, improved meat quality and improved feed conversion.[110] Skip-a-day feeding implies a mild form of fasting, and if applied in aquaculture a longer fasting period would likely be required to obtain similar benefits owing to the much lower metabolic rates in fish. In other species of farmed fish, it has been shown that feed conversion rates could be improved followed a fasting period.[244–246] To what extent production efficiency could be improved in Atlantic salmon aquaculture by introducing strategic fasting periods is certainly worthy of further investigation, and more so when considering other possible benefits such as reduced risks of maturation and higher stress resilience through improved cardiovascular health.

11 | CONCLUSION: WELFARE GUIDELINES FOR FASTING IN ATLANTIC SALMON

In this review we have described the diverse range of situations that involves fasting, whether voluntary or involuntary, in Atlantic salmon aquaculture. Furthermore, to interpret the impact on fish welfare during various periods and contexts of fasting, we have described the responses and tolerances to fasting in Atlantic salmon, based on the available literature (Table 1, Section 4).

11.1 | Atlantic salmon are resilient to prolonged fasting

It is clear that Atlantic salmon naturally are well-adapted to endure long periods of fasting owing to their migratory and anadromous lifestyle. As such, experimental studies have so far not been able to

TABLE 1 Summary of a selection of experimental studies using Atlantic salmon subjected to various periods of fasting presented in chronological order.

References	Fasting time	Temperature	Start size	Weight loss	Themes studied
106	6–11 months	NA	1–3 kg	NA	Cholesterol and high-density lipids in blood, Atherosclerotic lesions
101	78 days	NA (ambient, winter)	≈2400 g	11%	Body composition
234	9 weeks	5.5°C	≈5500 g	6%	Maturation, compensatory growth
247	5 weeks	8°C	≈2200 g	9%	Slaughter quality, body composition, fat deposition
102	12 weeks	8°C	≈2200 g	9%	Body composition, light manipulation
248	6 weeks	14°C	≈20 g	NA	Carbohydrates and ketone bodies in brain and liver
131	12 weeks	NA (ambient, winter)	≈2500 g	8%	Body condition, astaxanthin, vitamin and mineral status, innate immune activity
103,132	86 days	4.1°C	≈5 kg	11.3%	Body composition, fatty acids, fillet-yield, raw and cooked fillet properties
238	7–18 days	0.7–8.2°C (ambient, winter)	≈500 g	NA	Intermittent food deprivation, Rate of sexual maturation
249	8 weeks	13°C	≈10 g	NA	Growth-enhanced transgenic fish, metabolic rates, body composition
250	22 days	16°C	≈66 g	NA	Endocrinology (growth hormone, insulin like growth factors)
251	5 weeks	11°C	≈2900 g	3%	Pre-slaughter stress, rigour development, flesh quality
252	32 days	8°C	≈1300 g	6.9%	Muscle gene expression following refeeding, Compensatory growth
253,254	6 days	8°C	≈44 g	NA	Endocrinology, nutrient uptake, functional gene expression of ghrelin, cholecystokinin, and peptide YY
181	4 weeks	12°C	≈55 g	14.8%	Innate immune response in liver after acute bacterial infection
228	2 weeks	10°C	≈128 g	3.1%	Appetite, endocrinology (ghrelin, insulin-like growth factors and binding proteins)
50	20 days	9°C	≈2400 g	5.8%	RAS, mitigation of off-flavour compounds
51	10 days	13–14°C	≈4000 g	NA	RAS, mitigation of off-flavour compounds
44	2 weeks	4°C	≈5300 g	NA	Gut emptying, stress responses, nutritional related genes
45	4 weeks	12°C	≈600 g	NA	Metabolic rates, acute stress response
255	3 days	9°C	≈215 g	NA	Hypothalamic protein responses to gastrointestinal states
52	10 days	15°C	≈6800 g	NA	RAS, effects of swimming speed and oxygen levels on depuration
229	4 days	10°C	≈250 g	NA	mRNA expression of ghrelin and peptide transporters
137	4 weeks	12°C	≈250 g	6.3%	Swimming performance, Blood parameters, Stress recovery
190	8 days	12–15°C	≈5500 g	NA	RAS, water quality, off-flavour characterization
156	8 weeks	12°C	≈1200 g	7.3%	Behaviour, welfare scoring, skeletal deformities, compensatory growth
126	4 weeks	9 and 18°C	≈500 g	7.3% and 8.3%	Swimming energetics, blood parameters
230	6 weeks	12°C	≈1200 g	5.0%	Appetite regulating genes in the stomach-hypothalamus axis

Note: The purpose of each study is summarized in the final column. NA: Not applicable in cases where a category was not reported, or the data did not allow for an estimate (e.g., weight loss due to low replication levels).

define obvious limits in fasting periods based on impairments in physiological functions and health. To induce severe starvation where all lipid stores have been depleted and the fish clearly is in a compromised state will take substantially longer than any of the fasting regimes tested experimentally on farmed Atlantic salmon, and such durations should therefore not be relevant to consider in aquaculture contexts. While we cannot know exactly how a fish is feeling, it has been shown that appetite signalling becomes downregulated during prolonged fasting which suggests that Atlantic salmon are not experiencing chronic hunger. However, a strong sensation of hunger is present during the first few days of feed withdrawal. Following periods of fasting or restricted feeding Atlantic salmon display an impressive capacity for compensatory growth, which should alleviate some of the fish farmers concerns of economic loss owing to foregone growth potential.

TABLE 2 Overview of the fasting periods encountered in Atlantic salmon aquaculture and minimum recommended guidelines for context-dependent fasting periods with considerations of fish welfare.

	Reason	Approximate duration	Purpose or Cause	Welfare issues	Recommendations
Feed withdrawal	Grading	1–2 days	Gut emptying, hygiene, water quality, improve stress resilience, reduce oxygen demands	Yes – during fry and parr phase when fish can be aggressive	Depends on gut evacuation rates, which is influenced by temperature and fish sizes. Ranges from 2 to 7 days. RAS biofilter operation should be maintained and closely monitored to ensure stable system operation. In brackish/seawater RAS nitrate should be maintained in water to prevent sudden mortalities caused by H_2S toxicity.
	Vaccination	2–3 days			
	Splitting of fish groups	1–2 days			
	Transport	2–3 days		No	
	Delousing	2–3 days		Yes, by the procedure itself	
	Pre-slaughter	3–7 days		No	
	Off-flavours in RAS	3–15 days	Depuration process to purge off-flavours	No	Depends on the depuration process to purge off-flavours. Up to 15 days, but often less.
	Offshore farms	Days – Weeks	Extreme weather, supply issues	Maybe	Depends on the duration of stormy weather and fish condition. Principle concern is that waves and currents do not exceed the physiological limit of the fish.
Voluntary fasting	High temperatures	Days – Months	Summer heat waves, climate change	Yes	Ideally 0 days. Fish should not be in environments that induce anorexia.
	Hypoxia	Days – Weeks	Limited water exchange vs. biomass	Yes	
	Poor health	Weeks – Months	Diseases, parasites, chronic stress	Yes	Depends on severity. If the individual fish cannot regain appetite and compensate growth within a production cycle, they should be euthanized.

Note: Welfare issues are not always caused by fasting on its own, as they can be driven by other factors in the associated categories, such as the delousing procedure itself.

11.2 | Fish welfare guidelines for feed withdrawal should be more lenient

This review also described existing welfare legislations and guidelines with regards to feeding and fasting practices in Atlantic salmon aquaculture. While these, for the most part, are sparsely detailed, feed withdrawal practices prior to operations are generally recommended to be 48–72 h, and otherwise it is recommended that such practices should be as short as possible. However, the often-cited feed withdrawal periods of 48–72 h should not be considered a hard limit from a fish welfare point of view. There is no scientific evidence that suggests that a longer period, for instance 4–15 days, would reduce the fish welfare, with the notable exception of the early fry and parr phases of the life-cycle. Therefore, the recommended feed withdrawal practices prior to on-growing operations or slaughter should primarily be based on estimations of gut evacuation rates. In larger fish and at lower temperatures, gut evacuation is slower, and 48–72 h will sometimes be insufficient. In such conditions it is reasonable to extend feed withdrawal practices owing to the various benefits of performing operations on fish with empty guts. Similarly, when fasting Atlantic salmon for depuration purposes in RAS prior to slaughter, required feed withdrawal periods of up to 15 days are not associated with any specific fish welfare issues.

11.3 | Existing fish welfare guidelines do not consider voluntary fasting

When reviewing fish welfare legislations and guidelines we noted that none of them considers the welfare implications associated with voluntary fasting. This is notwithstanding that voluntary fasting can last for much longer than any feed withdrawal practice. As such, we find that the largest causes for welfare concerns reviewed here are the various factors that can induce voluntary fasting.

First, these include extreme farm environments with high temperatures and low oxygen levels. The associated thresholds for appetite reduction and complete cessation of appetite are well described in the literature. Moreover, since aquaculture environments are readily monitored and mostly predictable over time, there is no reason to ever expose farmed Atlantic salmon to thermal and hypoxia extremes that severely impair appetite. Keeping the fish in such conditions involves significant stress as well as elevated mortality risks and will be a cause for unacceptable welfare on any time scale.

Second, voluntary fasting can occur in health compromised fish owing to diseases, parasites and chronic stress. In these situations, fish could potentially have been fasting voluntarily for weeks or months, and their welfare will clearly have been markedly compromised. Generally, much more knowledge is needed on potential non-lethal pathological effects of various challenges upon farmed Atlantic salmon, including their impacts on appetite. For instance, are fish that suffer from prevailing diseases and parasites eventually able to recover their health and regain their appetite? If not, they should be euthanized to prevent prolonged suffering. However, if recovery is possible, it may be considered acceptable to let them endure an extended voluntary fasting period in some situations, although generally it should be considered unacceptable to maintain fish in such poor health that they become chronically anorexic. A prevailing problem here is the logistical challenge with monitoring the individual health status of fish in commercial aquaculture where a single sea cage normally contains up to 200,000 fish. The fish farmer is therefore unlikely to notice voluntary fasting in sick individuals before substantial reductions in condition factors are evident, which already implies several weeks of fasting.

11.4 | Final remarks

In Table 2, we have summarized our recommended guidelines for context-dependent fasting based on the welfare impact considerations that have been described throughout this review. Hopefully, this review will provide a more thorough and nuanced basis for assessing the welfare impacts for farmed Atlantic salmon undergoing voluntary or involuntary fasting. Whilst we have specifically focused on Atlantic salmon, the underlying biological considerations, assessments of gut evacuation rates, as well as pathological and environmental thresholds for appetite impairment may be used as a template for formulating similar guidelines in other farmed fish species, especially other salmonids.

AUTHOR CONTRIBUTIONS

Malthe Hvas: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; data curation; writing – review and editing; visualization; validation; formal analysis. **Jelena Kolarevic:** Investigation; conceptualization; methodology; validation; writing – review and editing; funding acquisition. **Chris Noble:** Funding acquisition; investigation; conceptualization; writing – review and editing; validation. **Frode Oppedal:** Conceptualization; investigation; funding acquisition; writing – review and editing; visualization; validation; supervision. **Lars Helge Stien:** Supervision; resources; project administration; conceptualization; investigation; funding acquisition; writing – review and editing; visualization; validation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

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

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