Aquaculture is a growing industry worldwide and Canadian finfish culture is dominated by marine salmonid farming. In part due to increasing public and stakeholder concerns around fish welfare protection, the first-ever Canadian Code of Practice for the Care and Handling of Farmed Salmonids was recently completed, following the National Farm Animal Care Council’s (NFACC) rigorous Code development process. During this process, both the Scientific (responsible for reviewing existing literature and producing a peer-reviewed report that informs the Code) and Code Development (a diverse group of stakeholders including aquaculture producers, fish transporters, aquaculture veterinarians, animal welfare advocates, food retailers, government, and researchers) Committees identified research gaps in tandem, as they worked through the literature on salmonid physiology, health, husbandry, and welfare. When those lists are combined with the results of a public “top-of-mind” survey conducted by NFACC, they reveal several overlapping areas of scientific, stakeholder, and public concern where scientific evidence is currently lacking: (1) biodensity; (2) health monitoring and management, with a focus on sea lice infection prevention and management; (3) feed quality and management, particularly whether feed restriction or deprivation has consequences for welfare; (4) enclosure design, especially focused on environmental enrichment provision and lighting design; and (5) slaughter and euthanasia. For each of these five research areas, we provide a brief overview of current research on the topic and outline the specific research gaps present. The final section of this review identifies future research avenues that will help address these research gaps, including using existing paradigms developed by terrestrial animal welfare researchers, developing novel methods for assessing fish welfare, and the validation of new salmonid welfare indices. We conclude that there is no dearth of relevant research to be done in the realm of farmed salmonid welfare that can support crucial evidence-based fish welfare policy development.
INTRODUCTION

The number of fish bred, raised, and slaughtered each year for food is on the rise as the human population continues to rapidly increase (1). Due to a decline in capture fisheries worldwide (2, 3), there has been a subsequent expansion of the aquaculture industry to match fish production with increasing consumer demand (4). This trend has led to public interest and concern around aquaculture practices worldwide (5–9) and particularly their impact on fish welfare, which is now a high priority concern for consumers (10, 11) and a policy agenda item (12, 13). However, compared with farmed terrestrial species, fish have not been a priority for welfare researchers for nearly as long (9, 14–16), and thus there exists an urgent need to further our understanding to protect and improve their welfare in aquaculture.

Though elsewhere much of the recent industry expansion has centered around freshwater species, in Canada, the aquaculture industry is dominated by marine salmonid farming, which is valued at $1.1 billion per year (17). Accordingly, the first-ever Canadian Code of Practice for the Care and Handling of Farmed Salmonids was recently completed [available at (18)], following the National Farm Animal Care Council’s (NFACC) rigorous Code development process [see (19) for details on the development process]. Briefly, the process began with an online survey (reply window: February 26th–March 18th, 2019) asking stakeholders (including those in the farmed finfish industry), key partners, and concerned citizens for their “top of mind” welfare concerns for farmed fish in Canada [see (20) for survey results]. Two committees were then formed: (1) the Scientific Committee, comprised of experts in fish physiology, behavior, health, and welfare, who were tasked with reviewing scientific evidence on priority welfare issues and writing a peer-reviewed report [see (21) for Scientific Committee report]; and (2) the Code Development Committee, who used the Scientific Committee’s report to develop the Code’s specific requirements and recommendations. Members of the Code Development Committee were a diverse group of stakeholders including aquaculture producers, fish transporters, aquaculture veterinarians, animal welfare advocates, food retailers, government officials, and researchers. Dr. Victoria Braithwaite served as the National Animal Welfare Representative on the Code Development Committee and was an integral contributor to preliminary drafts of the Farmed Salmonids Code of Practice.

OBJECTIVE AND IDENTIFICATION OF RESEARCH GAPS

During the NFACC Code development process, both the Scientific and Code Development Committees identified research gaps in tandem, as they worked through the literature on salmonid physiology, health, husbandry, and welfare. When those lists are combined with the results of the public “top-of-mind” survey, they reveal several overlapping areas of concern where scientific evidence is currently lacking (Table 1), to the point where making specific and measurable Code requirements and recommendations was difficult for the Code Development Committee. Thus, herein, our objective is to highlight five of these overlapping welfare-relevant research areas that contain significant knowledge gaps (Table 1): (1) biodiversity; (2) health monitoring and management, with a focus on sea lice infection prevention and management; (3) feed quality and management, particularly whether feed restriction or deprivation has consequences for welfare; (4) enclosure design, especially focused on environmental enrichment provision and lighting design; and (5) slaughter and euthanasia.

For each of these five research areas, we provide a brief overview of current research on the topic and outline the specific gaps present in the current literature, with the final section of this paper identifying future research avenues that will help address these gaps, ideally in advance of future Code revisions. Specific research gaps we report on within each research area were identified by the Scientific and Code Development Committees during numerous meetings over the course of the 3-year Code development process, using both their own extensive reviews of the literature and their collective expertise spanning long research careers in fish physiology and aquaculture [see the Scientific Committee’s membership, detailed in (21)] and as aquatic veterinarians and aquaculture professionals (see the Code Development Committee’s membership in the Code available at: https://www.nfacc.ca/codes-of-practice/farmed-salmonids). Similar approaches that incorporate multiple perspectives from a variety of stakeholders have been encouraged in the field of animal welfare [e.g., (18, 23, 24)]. Importantly, we do not attempt to provide a comprehensive review of current salmonid welfare research nor a value judgment on what the most pressing future welfare research priorities are. Rather, we are reporting on and extending the work of a unique grouping of aquaculture experts, to highlight future research that is necessary for the continued development of evidence-based salmonid welfare policy in Canada, and thus likely elsewhere as well.

DEFINITION OF WELFARE AND HOW IT IS ASSESSED

There exist numerous definitions of “animal welfare” [c.f. (25–27)]. NFACC’s current definition includes consideration of affective states, as well as health and biological functioning, and exhibition of both normal and important behaviors. This definition mirrors the “three circles of welfare” approach outlined by Fraser (26), which posits that welfare is comprised of three overlapping concepts (in no particular order): (1) health and biological functioning, (2) affective states, and (3) natural living. Similarly, the Five Freedoms concept, as employed by the OIE (28), includes reference to affective states with words like “comfortable,” “suffering,” “fear and distress,” and “pain.” Though these different concepts have each received criticism [c.f. e.g., (29–32)], a unifying characteristic among them is that the ability to experience pain, suffering, or any other objectionable, negative affective state (i.e., to be capable of sentience) is relevant to welfare. So, following Duncan (25), we take an affective states
approach to welfare herein. There still exists some debate around whether fish are capable of sentience [cf. e.g., (33–35)]; however, similar to the Code Development Committee, in this paper we will be taking a precautionary approach that assumes fish are sentient and capable of suffering and experiencing other negative affective states.

The scientific assessment of animal welfare is dependent on validated and standardized measurable parameters known as “welfare indicators.” Welfare indicators can be used to gain insight into an animal’s welfare state and can either be direct, animal-based indicators (e.g., weight loss, fin damage, increased gasping at the surface) or indirect, environment-based indicators, centered on the resources and environment the animals are subjected to (e.g., water temperature, oxygen levels) (36–38). Most animal welfare assessment protocols use a combination of both animal and environmental indicators [e.g., (22, 39, 40)] and “operational” welfare indicators are those which are relevant, easy to use, reliable, comparable, suitable for aquaculture and appropriate for specific systems or routines (38). Although a number of validated operational welfare indicators have been developed for salmonids [e.g., (38, 41)], currently there is an ongoing debate and no consensus on the best set of indicators to use [e.g., Salmon Welfare Index Model (SWIM I.0); the FISHWELL handbook] for assessment of salmonid welfare in aquaculture. The literature reviewed herein uses a variety of operational welfare indicators that we have reported where possible.

**RESEARCH GAPS**

**Biodensity**

Salmonids have a wide range of social behaviors, depending on life-stage [c.f. e.g., for Atlantic salmon: (42, 43)] and species [c.f. e.g., juvenile Arctic charr vs. Atlantic salmon: (42, 44)], so inappropriate biodensities can impact their welfare in captivity. “Biodensity” (often used interchangeably with “stocking density”) is defined as the fish biomass per unit volume of water (usually in units of kg/m³). Though biodensity can facilitate useful comparisons, it is important to recognize that fish are rarely distributed consistently throughout a tank or net pen (21) and can instead cluster together or break into smaller groups depending on the species and enclosure conditions. As well, stocking density is constantly changing over time and will increase as fish grow or may decrease following grading or other farming procedures. Considering that fish density can influence water quality depending on flow of water per unit time through the system and that living in water enables fish to move freely in three dimensions (45), the concept of minimum space for fish is thus more complex than for terrestrial animals.

In the context of welfare, biodensity has important implications for managing water quality in net pens, tanks, and recirculating aquaculture systems. But changing the spatial relationship between conspecifics (i.e., altering biodensity independent of water quality considerations) in and of itself can have important implications that change depending on the species and life-stage in question, which makes it challenging to provide blanket guidelines, much less legislation on maximum densities (46). For example, stress response activation increases with increasing biodensity for Atlantic salmon [e.g., highest at 70 kg/m³; (47), 125 kg/m³; (48)], but increases with decreasing biodensity for Arctic char [highest at 30 kg/m³; (49)]. Aggression follows a similar pattern, with young rainbow trout being most aggressive at high biodensities [e.g., 316 fingerlings/m³; (50); > 1000 fingerlings/m³; (51)] and young-of-the-year Arctic char showing the most aggression at low biodensities [44 kg/m³; (44)], with adult Atlantic salmon exhibiting increased aggression during feeding (43). Moccia et al. (21) review further examples of how biodensity can impact the health and social behavior of several different salmonid species.

**TABLE 1 | Illustration of Research Gaps arising from the “top-of-mind survey” conducted by NFACC, the list of “outstanding issues not addressed in current literature” created by the Scientific Committee and circulated internally, and the list of “research needs” published online by the Code Development Committee (22).**

| “Top of mind” survey | Scientific Committee | Code Development Committee | Research gaps |
|----------------------|----------------------|-----------------------------|---------------|
| Top five concerns raised: | Report chapters with the most "outstanding issues not addressed in current literature" identified by chapter authors: | Preliminary “research needs” list identified by the entire Code committee: | Top five overlapping research areas containing significant knowledge-gaps: |
| - Stocking density¹ | - Biodensity¹ (8 issues) | - Rearing Units (5 issues; including topics on biodensity, environmental enrichment, and lighting)³⁴ | 1. Biodensity |
| - Health monitoring and management² | - Sea Lice: Infestation and Treatment² (8 issues) | - Feeding Management (2 issues)⁵ | 2. Health monitoring and management (with focus on sea lice) |
| - Humane euthanasia and slaughter⁶ | - Feed Deprivation² (5 issues) | - Sea Lice (5 issues)⁵ | 3. Feed quality and management |
| - Water quality | - Lighting³ (4 issues) | - Other (6 issues; including topics on euthanasia and stress)³⁵ | 4. Enclosure design (with focus on environmental enrichment and lighting) |
| - Humane handling | - Stress Indicators (4 issues) | | 5. Slaughter and euthanasia |
| Additional concerns raised: | - Water Quality Issues in Recirculating Aquaculture Systems (4 issues) | | |
| - Feed quality³ | - Ice Slurry Slaughter⁵ (2 issues) | | |
| - Enclosure design and maintenance⁶ | | | |
| - Behavioral monitoring and management | | | |
| - Emergency preparedness | | | |
| - Transportation | | | |

Superscript numbers indicate which issues identified by each group were combined to become the research gaps discussed herein.
Concerningly, most of the data on optimal biodensities come from experiments conducted in small rearing tanks with relatively small fish (typically parr), due to financial and spatial constraints on research. Thus, findings from experimental manipulations may not be scalable to large production systems, which may use different tank materials or have different tank wall surface to water volume ratios. For example, a typical rearing tank with 1 m diameter and 1 m depth has a ratio of tank wall surface area to water volume of 5:1, while a tank with 5 m diameter and 2 m depth has a ratio of 0.9:1 (21). This might be pertinent when assessing welfare indicators such as fin erosion, a condition in which fins are injured that is hypothesized to be due to abrasion against tank walls and/or conspecific aggression that persists likely due to secondary infection (52). Furthermore, net pens are flexible structures that can change shape in response to tidal and other hydraulic conditions and/or biofouling, which may affect how much living space is available at any given time (53). Finally, a number of biodiversity studies are confounded with water quality, such that the results cannot be strictly attributed to the changing number of conspecifics but might be instead a response to deteriorating water quality with increasing density. It is logistically challenging to control water quality in these types of studies, but this can limit how well we can draw clear conclusions on the impact of biodiversity independent of other factors.

Beyond the applicability limits of the current research, there exist several crucial gaps in our understanding of how biodiversity might impact salmonid welfare. First, we were unable to find studies where salmonid behavioral preferences for different biodensities were tested. Determining what densities different species and life-stages might choose for themselves would be challenging but may provide additional information about which biodensities could optimize salmonid welfare. Second, comparative studies, where species-specific responses to identical experimental parameters are compared, would be of considerable value, especially when trying to extend existing results from one species to many. Third, furthering our understanding of natural salmonid social behavior and how social interactions change with life-stage is important for making biodiversity adjustments throughout rearing. As mentioned previously, species-level differences in responses to biodiversity can be pronounced, but the salmonid life cycle is also complex, with variation in responses even between life-stages. For example, we know that Atlantic salmon conspecific interactions change a great deal from the parr to adult stages [e.g., (54–58)]. But how much variation is there between life-stages for other salmonids? And what is the relationship between fish size and optimal biodiversity? For details of the salmonid life cycle and the dynamic ecology of different life-stages, see Aas et al. (59). Fourth, biodensities are often higher during situations involving acute stress, such as handling and transport. We do not have a strong grasp of what species-specific biodensities could protect welfare in those situations while remaining logistically feasible, nor do we know what biodensities optimize recovery from those acute stressors. Finally, there is evidence that non-optimal biodensities may impact immune parameters and subsequent vulnerability to pathogens [(60–62): reviewed in (53)], but we need further research to elucidate how different biodensities might contribute to pathogen transmission within a given enclosure or system; something that is likely pathogen- and host species-specific as well as multi-factorial.

**Health Monitoring and Management**

Disease is a major cause of diminished health and increased mortality in salmon aquaculture (63, 64). Regular monitoring of fish appearance and behavior can help to facilitate early identification of health problems that affect welfare and may be associated with bacterial and viral pathogens, parasites, and/or pollutants [e.g., skin lesions, loss of equilibrium, decreased activity, change in feed intake; (7)]. However, even with regular health monitoring in place, sea lice infestations remain one of the most persistent and highly publicized challenges in salmonid aquaculture.

Sea lice are parasitic copepods (within the family Caligidae) of both wild and farmed marine fish, but the rearing densities and conditions present in salmon aquaculture can exacerbate infection intensities when compared with natural conditions (65, 66). Multiple species of sea lice have been found to infect farmed salmon and sea lice biology, infection, and development are highly dependent on water temperature and salinity [reviewed in (21)]. For example, *Lepeophtheirus salmonis salmonis*, *Caligus elongatus*, and *C. curtis* represents the greatest concern in the North Atlantic (67, 68), and *L. salmonis oncorhynchii*, *C. clemensis*, and *L. cuneifer* represent the greatest concern in the Northern Pacific (69, 70). Sea lice feed on the skin, mucus, and blood of their hosts and cause tissue damage (71, 72). In cases of severe infestation, sea lice may also cause significant lesions that lead to increased stress, reduced swimming performance, anemia, reduced growth, and they may even act as a vector for other diseases and pathogens [reviewed in (71); reviewed in (72, 73)]. It is thus essential for aquaculture managers to implement appropriate management and intervention strategies that maintain the welfare of farmed fish and attempt to reduce the impacts of severe sea lice infestations on wild salmonid populations in the area (74, 75).

The primary management approach in all major salmon-producing countries is to regularly monitor and report sea lice densities on salmon in sea pens, with mandatory delousing or other sanctions implemented before levels reach pre-determined limits (21). Sea lice thresholds at which intervention is required (i.e., numbers of sea lice of a particular sex or life stage per fish) are different between and even within countries (21). Currently, however, sea lice thresholds are set for conservation purposes rather than out of concern for captive fish welfare, due to the alleged role of sea lice in the decline of wild salmonid populations as a result of louse spillover infections [e.g., (66, 76–78)]. Although prior work has suggested that sea lice infestations become lethal around 0.12–0.15 lice per cm² of fish (37, 79), the impacts of sea lice are largely dependent on host species and size [e.g., salmon lice are rejected more rapidly by Coho, *Oncorhynchus kisutch*, and pink, *O. gorbuscha*, salmon than by Chinook, *O. tshawytscha*, and chum, *O. keta*, salmon; (69, 71, 72)]. Although, lethal limits are a late-stage indicator of welfare impacts; fish may be negatively affected long before their infection burden induces mortality [e.g., (80)]. There is
currently very little research on the sub-lethal effects of sea lice infestations on fish welfare across different salmonid species and life-stages. Research that addresses this gap would help policy makers establish firmer, welfare-based sea lice thresholds for when intervention is required [e.g., (81)].

There also exist a couple of important gaps in our understanding of how to control sea lice infestations. First, lice-infected fish are typically treated by applying chemical treatments in tarpaulin-enclosed net pens (to contain the chemicals), as a bath in well-boats, or by including them in feed (82). Currently, in feed treatments are considered advantageous due to their passive implementation (82), in comparison to bathing treatments which may cause stress and mechanical harm to fish through withholding feed and transfer prior to, and crowding and oxygen deprivation during, bathing (45, 83, 84). However, incorrect dosages of chemical sea lice treatments have been shown to cause mortality post-treatment in salmonids, which typically increases with increasing water temperature [e.g., hydrogen peroxide; (84, 85)]. As well, because some treatments are not completely effective and sea lice are becoming resistant to them (86–89), fish are often treated repeatedly over a 2–3 week period. We do not have a complete understanding of how repeated exposure to chemical therapeutants may impact fish welfare. Second, treatment-resistance has prompted a rapid and recent shift to non-chemical approaches to control infections including the use of altered temperature, salinity, and lighting, physical removal, mechanical barriers, and cleaner fish (21). However, preliminary studies suggest that some of these methods may compromise host salmonid welfare. For example, recent work suggests that temperatures used during thermal delousing treatments (28–34°C) may be noxious to fish (90), can initiate panic reactions [exposure <5 min; (90)], and may cause thermal injury [exposure to 34–38°C for 72–140 s; (91)] and even death [exposure to 34–38°C for >2 min; (91)]. Physical de-lousing systems such as the “Hydrolicer” also require fish to be crowded prior to treatment (85), which may induce an acute stress response. In severe cases, some of these methods can lead to elevated post-treatment mortality in comparison to the use of chemical methods (85). Thus, extensive research is needed to determine the potential impacts of these non-chemical sea lice treatments on fish welfare.

Furthermore, the use of a number of cleaner fish species (e.g., lumpfish and wrasse) that eat sea lice directly off host salmonids are gaining popularity as a biological alternative for infestation control. In the context of salmonid welfare, one of the most important considerations is the role that cleaner fish may play in pathogen transfer to salmonids [e.g., Tenacibaculum maritimum; (92); and others reviewed in (93)]. The close mixing of cleaner fish with salmon in net pens creates favorable conditions for the emergence and transfer of diseases, especially considering cleaner fish broodstock are often wild-caught and may pose a biosecurity risk (94, 95). However, the welfare of the cleaner fish themselves is of considerable concern because the biology, ecology, and population dynamics of these species are poorly understood. For example, individuals of some species are territorial (96) and territorial behavior may expose cleaner fish to attacks from the larger captive salmon and thus, exposure to injury and unavoidable chronic stress [e.g., (97–99)]. Reports of poor cleaner fish survival in commercial salmon sea nets [e.g., (99, 100)], with some individual farms observing up to 100% mortality or loss [e.g., (101)], add to this concern. There are also important ethical questions to consider when using cleaner fish. For example, cleaner fish are commonly euthanised after each production cycle when salmonids are slaughtered for harvest (95, 102). This leads to demand for additional, replacement cleaner fish at the beginning of the next salmon production cycle [e.g., (94, 95)] and raises the question: do the ethical implications of this practice outweigh the efficacy of cleaner fish as a sea lice control method? So before introducing these species as a legitimate alternative for sea lice control, we need considerable research at both the basic (e.g., describing cleaner fish ecology, behavior, etc.), applied (e.g., investigating welfare of cleaner fish in sea pens, comparing efficacy of cleaner fish to thermal de-lousing), and philosophical (e.g., is this practice ethical?) levels.

Feed Quality and Management

The quality of the diet, including feed formulation, affect salmonid health and welfare. For example, feeds with insufficient phosphorus cause potentially painful skeletal deformities [reviewed in (103)]. Popular salmonid feeds usually use fish meal and oil as their primary protein sources, which are limited resources whose harvest can have considerable environmental impact (104). In an effort to improve the sustainability of feeding farmed salmonids, alternative protein sources such as insect meals, poultry by-products, plant-based meals (e.g., soybean, canola, etc.) are being investigated and used (105, 106). However, emerging research suggests that some of these products may have welfare-relevant health impacts. For example, feeding unfermented soybean meal to Atlantic and chinook salmon may cause an intestinal inflammatory response (enteritis) that renders fish more susceptible to diseases like furunculosis (107, 108) but supplementing soybean meal with bacterial meal containing Methylococcus capsulatus appears to mitigate enteritis in Atlantic salmon (109). This enteritis also appears to differ in severity between species; unfermented soybean meal does not induce enteritis in pink salmon, and is less severe in Atlantic than in chinook salmon (108). Further research is needed to address species- and life-stage-level differences in how these alternative feed formulations may impact salmonid health and welfare.

Similarly, feed restriction (i.e., feeding a reduced ration) or withdrawal (i.e., not providing any feed) can have welfare consequences that are not well-understood. Feed is withheld in a variety of situations during salmon farming; before acutely stressful procedures like grading, vaccination, etc., it is often considered prudent to empty the gut through short-term feed restriction to maintain water quality during holding, lower hypoxia risk through lowered metabolic rates, and reduce the risk of needle damage during peritoneal injections (6). Prior to slaughter, feed may also be withheld for human food safety and product quality reasons [e.g., (110, 111)]. Further, during rarer events like superchill (112, 113), harmful algae blooms (114), and high temperature events (115), feed withdrawal is often required as it prevents death due to freezing, exposure to algal toxins at
the water’s surface, or elevated activity in temperatures outside a species’ optimal range [reviewed in (21)].

Under the assumption that fish have conscious affective states [as (34, 116), and others claim], the most obvious potential welfare consequence of feed restriction or withdrawal would be hunger, an aversive interoceptive state that can include aspects of pain and frustration and may involve considerable individual variation [e.g., (117)]. However, it is still unknown whether fish experience hunger, both because of doubts surrounding whether they are sentient [cf. e.g., (33, 118, 119)] and because most species (and all salmonids) are ectotherms. Warm-blooded farm animals have consistently high energy demands and therefore require regular meals to avoid hunger and maintain metabolism; however, the feed requirements of fish are dependent on temperature, the principal controlling factor of their metabolic rate (120). Recent research indicates that, when held at optimal temperatures, Atlantic salmon post-smolts can tolerate up to 4 weeks without food with negligible impacts on welfare (121). Some species of fish (including salmonids) also exhibit a natural decrease in appetite to the point of fasting during certain periods of their life cycle [e.g., (122)], so it is possible that hunger is either not as strong a motivator for these fish as it is for mammals, or fish have a physiological mechanism that decreases the aversiveness of hunger during these periods. Work done on transgenic salmon has contributed to our understanding of fish appetite [e.g., (123–125)], but much remains unknown about the endocrinological and neurological mechanisms controlling it and the affective component remains elusive.

Furthermore, welfare consequences may vary depending on the severity and duration of feed restriction or withdrawal, with very long-term situations potentially forcing fish into a stage of starvation requiring protein catabolism to mobilize stored nutrients, wherein vital organ function can be compromised (126). But even less severe feed restriction can have behavioral consequences; the sudden onset of restriction can increase aggression rates and subsequent fin damage (127), with these behavioral changes potentially becoming permanent, possibly depending on the life-stage at which feed is restricted [e.g., (128)]. There have been multiple calls for further research on the effect of feed withdrawal of varying lengths on stress physiology, behavior, and welfare (6, 110, 129). Currently, feeding regimes are often based on water temperature and calculations made using known relationships between body size and metabolic rate [for fish: on a log-log scale, body mass and standard metabolic rate are linearly related, with a slope of 0.8: (130), explained in (21)], with the aim of maintaining or increasing body mass. However, this method does not incorporate the numerous other factors that may play a role in how severe the welfare consequences of varying periods of feed restriction or withdrawal are such as water quality, species, life-stage, biodiversity, and disease status, among likely many others. In contrast, over-feeding (as a possible result of strong dominance hierarchies, incomplete training of personnel, etc.), though less studied, may have welfare consequences such as fouling of the holding tank or net-pen and/or obesity resulting in possible immunological disorders (131).

**Enclosure Design**

A variety of rearing unit types and conditions are used in the farmed salmonid industry, ranging from ponds, sea and lake net pens, and land-based flow-through and recirculating systems. Despite this diversity, aquaculture rearing conditions typically lack complexity, most often being plain, impoverished enclosures containing only water. Deliberately adding resources to the environment with the aim of improving fish welfare by meeting their needs and preferences is often termed “environmental enrichment” (132, 133). Environmental enrichment can take many forms, from physical objects added to the rearing unit that increase structural complexity to sensory, social, nutritional, or even occupational enrichment (133). Providing fish with environmental enrichment that increases the complexity of their rearing units while mimicking their natural environments may be an effective way to offer choice (134) and decrease stress responses. Although enrichment strategies are highly dependent on the natural history of the fish species and their preferences, there are some principles that have been found to hold true for several salmonid species used in research and aquaculture. For example, the use of dark tank backgrounds, tank floor substrate, and shelters, has the potential to reduce aggression and consequent fin damage [Rainbow trout: (135–137); Arctic char: (138); Coho salmon: (139)] and increase survival [Atlantic salmon: (140, 141)].

For a comprehensive overview of environmental enrichment research for cultured salmonid fishes, see Näslund and Johnsson (133); however to date, environmental enrichment research has been conducted mainly under laboratory conditions in small rearing tanks at relatively low biodensities. While several types of environmental enrichment have been adapted to aquaculture out of necessity (mainly in terms of reproduction success), almost nothing is known about the effects of environmental enrichment on fish welfare at the scale of intensive aquaculture. Furthermore, we do not know what, if any, forms of environmental enrichment are preferred by salmonids at different life-stages, nor what types of enrichment might be important for positive salmonid welfare. There are also some concerns about the application of environmental enrichment that require empirical study: some suggest that enrichment may exacerbate accumulation of food particles and feces [e.g., (142)] or act as a vector for pathogens [e.g., (143)] such that the drawbacks may outweigh the benefits. Accordingly, aquaculture managers are often concerned about effective and safe application of environmental enrichment, especially in a large-scale production context. Much more research is needed to investigate what types of environmental enrichment might be effective and feasible to deploy on-farm.

Lighting is another important aspect of housing design in the farmed salmonid industry. Light has three components: color, intensity, and duration (daylength or photoperiod); all of which can potentially influence animal welfare and can be manipulated by increasing or decreasing the number of lights on the farm, or by changing their strength or type (21). Currently, the manipulation of both photoperiod and light intensity represents key management tools used in salmonid aquaculture. For example, various artificial lighting regimes (e.g., extended or
reduced day length or continuous, 24-h lighting) are used to induce smoltification, advance or delay the timing of spawning, manipulate sexual maturation, promote fish growth, and prevent suffocation in the early swim-up stages of the salmonid life cycle (21). Concerningly, there are a number of welfare-relevant health and production issues associated with continuous lighting, including disrupted neurodevelopmental, reduced bone strength, poor smolt quality, failed smolting, and failed spawning (144–147). Similarly, sudden changes in light intensity or regime cause fear responses, increased oxygen consumption, injuries, or even suffocation in fish (148–150). So although artificial lighting is readily used and manipulated across the salmonid aquaculture industry, research is needed to investigate these welfare concerns. Furthermore, considering that light intensity influences the spatial distribution of fish within a tank, light intensity may be too low at depth in larger, deeper tanks, which could potentially inhibit feeding, growth, and smoltification (151). We need more information about how light distribution differs with depth in a variety of salmonid housing enclosures and how this impacts fish welfare.

**Slaughter and Euthanasia**

Generally, when farmed salmonids reach a certain size, they are slaughtered for human consumption, but it is sometimes also necessary to euthanize fish to prevent them from experiencing excessive pain or suffering (e.g., ill, injured, or diseased fish that do not have a reasonable prospect of improvement or do not respond to treatment). A “humane death” is one that is quick, causes minimal stress and pain, and results in a rapid loss of consciousness followed by death without the ability to regain consciousness (152–154). Under the assumption that fish have conscious affective states, humane approaches to the slaughter and euthanasia of farmed salmonids are expected by both society and the aquaculture industry. Importantly, humane slaughter and euthanasia of fish can only be fully achieved by minimizing stress and injury during, as well as, before the killing procedure itself. Considering procedures such as crowding, loading, and transporting fish from their pens to the place where they will be slaughtered or euthanised (e.g., by use of braille nets, pipes, and/or well boats) has the potential to induce stress and injury in fish [e.g., (155–158)], they must be minimized as much as possible in terms of intensity and duration [e.g., (22, 39, 40, 153)].

Aquaculture slaughter and euthanasia techniques are diverse, and fish species vary in their response to different methods [e.g., sensitivity to oxygen deprivation; (159)]. Unfortunately, some of the current methods are unacceptable under the definition of a “humane death” and have instead been developed with a focus on product quality and ensuring personnel safety (45). For example, immersion in CO₂ saturated water is sometimes used to kill farmed salmonids; however, it is losing popularity because it has been shown to cause narcosis and loss of brain function [e.g., (160)] over several minutes, during which time the fish exhibit pronounced distress and escape behaviors (161, 162).

Thus, considering the negative welfare consequences of these methods, they are being phased out and are only permitted for emergency situations [e.g., CO₂ may still be used for emergency depopulation events; (22)].

Of the methods presently available, when applied correctly, percussive and electrical stunning appear to be among the more humane methods for salmonid slaughter (163, 164), with electric stunning becoming the preferred method in Canada (21). Considering fish can only be stunned by the use of electricity [i.e., not killed; (162, 165)], electrical stunning must be followed by a kill method that prevents recovery of consciousness in order for it to meet requirements for humane slaughter [e.g., (22, 39, 153, 154)]. However, selection of the most appropriate (i.e., humane) method of slaughter in any situation will depend on the fish species, size, life-stage, number of individuals involved, available means of restraint, and personnel skill level [e.g., (22, 39, 153, 154)]. To date, electrical and percussive stunning methods have been tested on a limited number of fish species at harvestable size, mainly in laboratory conditions [e.g., Atlantic salmon, Common carp, Rainbow trout, Gilthead sea bream, European sea bass; reviewed in (166)], leaving gaps in our understanding of the potential of welfare impacts of these methods in additional fish species, at different life-stages, and in commercial settings. This is concerning because, for example, when the electrical current or voltage is too low, or the application duration too short, electrical stunning can be ineffective at stunning fish and thus, has the potential to cause pain [(154, 166); for a review in fish pain see (167)]. As well, additional considerations need to be taken into account for in-water vs. dry/semi-dry electrical stunning procedures such as the conductivity of the water [e.g., stunning a fish in sea water requires more power than fresh water; (154, 168)] and the orientation of the fish [e.g., incorrect orientation of the fish increases the risk of ineffective stunning; (154, 166)], respectively.

Despite existing research on humane salmonid slaughter and euthanasia, a number of research gaps remain that are hindering our understanding of how these different methods might impact salmonid welfare. First, comparisons between fish and mammalian brains are difficult [due to eversion of the telencephalon during embryonic development; see (169)]. Thus, what we know about relationships between mammalian brain regions and their functions cannot be directly applied to fish. It is therefore imperative that we continue to research teleost brain region function in commercially relevant lineages. Second, electroencephalography (EEG) has been used to assess brain electrical activity in fish in a number of laboratory experiments and has been shown to be one of the most reliable methods of assessing consciousness [e.g., (162, 165, 170–173)]. However, in a commercial fish farm setting, registration of EEGs is impossible to perform, instead forcing farmers to rely exclusively on behavioral indicators to evaluate the degree of consciousness in fish [e.g., coordinated swimming and escape behaviors, ability to maintain equilibrium, “eye roll” reflex, and ventilatory reflexes; (170)]. The use of behavioral indicators alone are problematic: for example, some commercially used slaughter methods may only induce sedation and/or paralysis in fish without loss of consciousness [e.g., ineffective electrical stunning, ice slurry slaughter; (163, 166, 170, 174, 175)]. Thus, in order to fully validate the use of behavioral indicators of unconsciousness in
the absence of EEGs on farms, more research is needed to investigate additional commercially-relevant fish species and a variety of types of slaughter. Third, we do not fully understand what the actual cause of death is during some of the currently used slaughter and euthanasia techniques. For example, the cause of death during ice slurry slaughter, a method of trout (O. mykiss) slaughtered used in Canada, is unknown but likely to be asphyxiation from either a lack of gill irrigation or hypoxia ([176]; reviewed in [21]). The chilled water reduces the fishes’ activity level but may not render the fish insensible to pain and may thus cause a prolonged period of distress before death (163, 176). Understanding the cause of death can thus be important for assessing welfare impacts, since it can play a role in how long a slaughter method takes to cause death and how potentially painful it may be, especially if another method that causes insensibility (e.g., anesthesia) is not used immediately prior. Thus, methodological studies of how to measure fish brain activity and investigation into the improvement or possible further development of humane slaughter and euthanasia methods would be of use for both fundamental and applied work. Finally and importantly, though fundamental and percussive stunning methods are the recommended methods of slaughter at present, this does not preclude the discovery of more humane methods in the future.

**FUTURE DIRECTIONS**

Herein, several gaps in the field of salmonid welfare have been identified, with pertinent questions to guide future research summarized in Table 2. However, further, more in-depth work is required to review the full extent of relevant salmonid welfare research and a complete suite of research gaps, beyond those most relevant to policy development in Canada that we have presented in this review. We strongly suggest that researchers consider performing a scoping review (177) of the literature to provide a complete picture of the state of research and identify a full suite of research deficits. Some valuable reports like this already exist, such as the gap analysis study conducted by the Standing Committee on Agricultural Research [SCAR: (178)], and narrative reviews on various relevant topics by Ashley (6), Overton et al. (85), Macaulay et al. (179), Hvas et al. (180), among others. However, since the aquaculture industry includes a variety of expert stakeholders hailing from different backgrounds, we also recommend borrowing methods from the social sciences [e.g., a systematic review of text and opinion (181), survey-based research (182): Chapter 9], and/or participatory methods [discussed in (24)] to help reveal important anecdotal or experiential understanding from working aquaculture professionals that could inform novel research questions or policy developments [as suggested in relation to the issue of surplus dairy calves, by (24)].

With regards to the research questions summarized in Table 2, there are many promising methods that may assist in addressing them, particularly non-lethal physiological indicators of salmonid health such as the quantification of water-borne cortisol [e.g., (183)], fin erosion scoring schemes [e.g., (184)], bioelectrical impedance analysis (185), and hematological indicators of health [reviewed in (186)] and stress [reviewed in (187)]. However, many of these research questions remain unanswered, possibly for several reasons: some of the aforementioned indicators and methods have yet to be fully validated [e.g., (188, 189)], some research questions are yet unanswerable because we lack the necessary tools, and/or we, as fish biologists, have not yet pursued interdisciplinary research to its fullest extent.

The field of animal welfare has been largely focused on terrestrial species but offers many experimental paradigms that can be used to investigate the welfare of aquatic species as well. For example, preference tests commonly used by poultry and cattle welfare researchers [e.g., (190)] have been used to investigate what types of environmental enrichment are most preferred by laboratory zebrafish [e.g., (191)]. These simple preference tests can be extended into investigations of motivation, in which a cost is titrated against access to a resource to determine how valuable it is to an animal [e.g., (192)]. For example, using motivation tests, welfare researchers discovered that farmed mink will pay a high “price” for access to pools for swimming and experience a stress response indistinguishable from that elicited by food deprivation when they are prevented from accessing their favorite resource (193). Further, validated tests of judgment bias, a concept borrowed from human psychology in which one’s underlying mood state affects whether neutral stimuli are perceived as potentially rewarding (optimistic) or threatening [pessimistic; e.g., (194)], are gaining popularity for assessing non-human animal mood states [e.g., (195)]. For example, a judgment bias task was recently validated for laboratory mice, wherein mice housed with preferred and welfare-improving environmental enrichment and tumor-bearing nude mice showed optimistic and pessimistic responses, respectively (196). Judgment bias tasks have been attempted for zebrafish [e.g., (197)], but a validated method for salmonids has yet to emerge.

Going forward, a focus on methods development (both building on existing tools and experimental paradigms and creating new ones) would help facilitate the necessary research on salmonid welfare. Of particular interest might be the development of validated judgment bias tasks, ways to assess fish motivation for resources, and other behavioral measures of fish distress, fearfulness, etc. for use on-farm, as well as other non-invasive techniques for investigating fish physiological responses. Considerable work describing salmonid natural ecology exists [e.g., (59, 198, 199), among many others]; however, deepening our understanding of their natural behavior across life-stages (especially during enigmatic at-sea life-stages), would help us further develop and validate behavioral indices of welfare. We may also need to explore how other sensory modalities are affected in production, both as potential welfare implications but also to discover new indices—for example, what sounds can salmon in net pens and land-based enclosures detect and/or produce, and are they relevant to welfare state? How do different enclosure designs affect how salmon use their lateral line, and are there properties of the lateral line that are affected by overall
Health monitoring and management

- What are the sub-lethal effects of sea lice infestations on salmonid welfare, and at what threshold number of lice per fish do they occur at welfare-compromising levels?
- What are the welfare impacts of repeated exposure to chemical therapeutics for managing sea lice infections?
- How do alternative sea lice treatment methods (e.g., thermal and physical de-lousing, etc.) impact salmonid welfare?
- How does the introduction of cleaner fish species to a given enclosure impact the welfare of captive salmonids?
- What are the potential areas of concern for cleaner fish welfare?

Feed quality and management

- Do fish experience hunger as an aversive affective state?
- If hunger is aversive to fish, how motivating is it?
- How might the aversiveness of hunger interact with different social dynamics (e.g., dominance hierarchies) to impact welfare?
- What protein alternative is best for the welfare of different salmonid species?
- What period of feed restriction or withdrawal is appropriate (i.e., does not compromise welfare), and how does it change with different environmental conditions?

Enclosure design

- What types of environmental enrichments do farmed salmonids prefer at different life-stages?
- What types of environmental enrichment positively impact fish welfare at different life-stages?
- What types of environmental enrichment are feasible to deploy on-farm?
- What effect does the spectral composition of light have on fish welfare at different life-stages?
- What effect do differing photoperiods have on fish welfare?
- How is light intensity distributed in differing tank depths and how might this affect fish welfare?

Slaughter and euthanasia

- What brain region(s) is/are responsible for consciousness in fish?
- How do we measure brain function in fish?
- At what point does unconsciousness occur during differing slaughter and euthanasia methods?
- What is the cause of death in slaughter and euthanasia methods (e.g., ice slurry slaughter and electrical or percussive stunning)?
- Are there more humane methods of slaughter and euthanasia than presently available?

TABLE 2 | Examples of outstanding research questions that exist in each Research Gap identified herein, as informed by the Scientific Committee, Code Development Committee, and the authors’ perspective as fish welfare researchers.

| Research Gap | Examples of Research Questions |
|--------------|--------------------------------|
| Biodensity   | What biodensities are preferred by different salmonid species and life-stages? |
|              | How does social behavior change throughout the entire salmonid life cycle? Are these patterns species-specific? |
|              | What is the relationship between fish body size and optimal biodensity? |
|              | Do patterns and relationships identified in the current biodiversity literature scale up to large production systems? |
|              | How does biodensity affect salmonid recovery from acute stress? |
|              | For different welfare-relevant pathogens, how does biodensity contribute to pathogen transmission? |
| Health monitoring and management | What are the sub-lethal effects of sea lice infestations on salmonid welfare, and at what threshold number of lice per fish do they occur at welfare-compromising levels? |
|              | What are the welfare impacts of repeated exposure to chemical therapeutics for managing sea lice infections? |
|              | How do alternative sea lice treatment methods (e.g., thermal and physical de-lousing, etc.) impact salmonid welfare? |
|              | How does the introduction of cleaner fish species to a given enclosure impact the welfare of captive salmonids? |
|              | What are the potential areas of concern for cleaner fish welfare? |
| Feed quality and management | Do fish experience hunger as an aversive affective state? |
|              | If hunger is aversive to fish, how motivating is it? |
|              | How might the aversiveness of hunger interact with different social dynamics (e.g., dominance hierarchies) to impact welfare? |
|              | What protein alternative is best for the welfare of different salmonid species? |
|              | What period of feed restriction or withdrawal is appropriate (i.e., does not compromise welfare), and how does it change with different environmental conditions? |
| Enclosure design | What types of environmental enrichments do farmed salmonids prefer at different life-stages? |
|              | What types of environmental enrichment positively impact fish welfare at different life-stages? |
|              | What types of environmental enrichment are feasible to deploy on-farm? |
|              | What effect does the spectral composition of light have on fish welfare at different life-stages? |
|              | What effect do differing photoperiods have on fish welfare? |
|              | How is light intensity distributed in differing tank depths and how might this affect fish welfare? |
| Slaughter and euthanasia | What brain region(s) is/are responsible for consciousness in fish? |
|              | How do we measure brain function in fish? |
|              | At what point does unconsciousness occur during differing slaughter and euthanasia methods? |
|              | What is the cause of death in slaughter and euthanasia methods (e.g., ice slurry slaughter and electrical or percussive stunning)? |
|              | Are there more humane methods of slaughter and euthanasia than presently available? |

welfare? Longer-term, a non-invasive way to measure brain activity in tanks, and further work on fish brain neuroanatomy and function [e.g., (200, 201)], would help us understand and potentially validate new welfare indicators. Overall, developing a suite of validated, non-lethal welfare indicators that facilitate rapid and reliable assessment of welfare on-farm would be of considerable value. Such a panel of indicators could help us understand welfare at the fish level on-farm, since there is likely to be high individual variation in welfare and stress coping ability within a given group of farmed salmonids [e.g., (202)].

There is obviously no dearth of relevant research to be done in the realm of farmed salmonid welfare. In particular, it is essential to address these and other research gaps to ensure that policy guidelines do not rest solely on assumptions about whether these gaps represent welfare issues or not. Evidence-based policies safeguard welfare in meaningful ways while preventing pointless and potentially damaging impacts on valuable industries. Together with the work done by both the NFACC Scientific and Code Development Committees, we hope that this review serves to guide future studies toward the most pressing and policy-relevant research questions, ideally in advance of future NFACC Code of Practice revisions. But regardless of timelines, it is important that we support and conduct basic and applied research that can address some of the gaps in our understanding of how to safeguard farmed fish welfare, especially considering increasing expressions of concern for fish well-being from farmers and the general public and the continuing expansion of the salmonid aquaculture industry.

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