© 2018 Universities Federation for Animal Welfare The Old School, Brewhouse Hill, Wheathampstead, Hertfordshire AL4 8AN, UK www.ufaw.org.uk 193

A review of factors affecting the welfare of Atlantic salmon (Salmo salar)

E Santurtun^{†§}, DM Broom[‡] and CJC Phillips^{*†}

[†] Centre for Animal Welfare and Ethics, School of Veterinary Science, University of Queensland, Gatton 4343, Queensland, Australia

[‡] Centre for Animal Welfare and Anthrozoology, Department of Veterinary Medicine, University of Cambridge, Madingley Road, Cambridge CB3 0ES, UK

[§] The Donkey Sanctuary-UNAM Programme, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Mexico

* Contact for correspondence and requests for reprints: c.phillips@uq.edu.au

Abstract

In the expanding salmon industry, many farmers use production methods that could result in poor welfare of the fish at various points of their lifecycle. We have reviewed methods used for producing salmon for food with the aim of identifying and drawing attention to factors likely to affect farmed Atlantic salmon (Salmo salar) welfare. In addition to water conditions and high stocking density at sea, other issues are important for fish welfare. Handling and transport of salmon between fresh- and seawater phases and before slaughter can have severe negative effects and research should continue to seek improved methods. Stocking densities in fresh- or seawater have substantial effects on the welfare of salmon and a reduction in densities should be considered in order to reduce fin damage in particular. Currently used feeding systems result in starvation for some fish and fin damage for others, hence new systems should be developed. Some on-demand feeding systems improve welfare. All farmed fish should be stunned prior to slaughter, not left to die of asphyxia. Carbon dioxide and electrical stunning methods do not always stun salmon humanely. The widely used methods of percussive stunning, manual or automatic, must be precise to effectively stun large numbers of fish. Welfare outcome indicators, such as fin damage, morbidity and mortality rate, should be used in standards and laws relating to salmon welfare.

Keywords: animal welfare, aquaculture, Atlantic salmon, fish farming, stocking density, welfare outcome indicators

Introduction

Aquaculture is the world's fastest growing meat production industry globally, averaging approximately 6% annual growth from 2002 to 2012, after 10% growth for the 20 years prior to this (Food and Agriculture Organisation [FAO] 2014). The major producers of Atlantic salmon (*Salmo salar*) are Norway, Chile, Scotland and Canada, with the first two providing over 80% of global output (Burridge *et al* 2010). Most feed provided for salmon is derived from other fish, some of which could be used directly as human food and some could constitute a disease risk for the salmon, so efforts are being made to find alternative sources (Stones 2003). At present, up to 14% of salmon food can be of plant origin.

The production of salmon starts with the extraction of eggs and sperm from anaesthetised fish, followed by incubation in oxygenated freshwater, hatching, and then rearing in flowing water. Fingerlings (known as parr) are transferred to larger freshwater tanks, where they are in either flowthrough tanks or a re-circulating system. Here, they remain until smoltification, a physiological adaptation from freshto seawater. The smolts are then either transported into large, floating cages in sheltered bays or sea lochs, where they grow for 1-2 years before slaughter or grown in enclosed large-tank systems throughout their life.

There is evidence to show that fish can show the physiological and behavioural responses that indicate fear and pain (Sneddon et al 2003; Chandroo et al 2004; Portavella et al 2004; Nordgreen et al 2007; Braithwaite 2010; Broom 2016). The cognitive ability of certain fish in some circumstances can be better than mammals, for example, as a result of their extensive experience in nature, cleaner fish can learn complex foraging tasks that some great ape species cannot (Salwiczek et al 2012). It should be noted that areas exist within the brains of fish that closely parallel those of the amygdala and hippocampus, that deal with emotion, learning and memory in mammals (Agetsuma et al 2010; Broom 2014). Scientific evidence indicates that salmon and other fish are sentient beings and surveys such as the Special Eurobarometer 442 (http://docplayer.net/24590693-Special-eurobarometer-442-summary-attitudes-ofeuropeans-towards-animal-welfare.html) indicate high levels of public concern about sentient animals. There is considerable consumer concern about salmon welfare, with



them being increasingly covered by animal welfare law in many jurisdictions. Moreover, scientific information about their welfare is increasing (Broom 1999, 2007; Turnbull 2006; Grimsrud *et al* 2013; Broom & Fraser 2015).

Researchers constructing a welfare model for farmed Atlantic salmon have emphasised that consideration of multiple welfare components is essential in such a highly complex and multifaceted production process (Turnbull et al 2005). Following publications by the Farm Animal Welfare Council (FAWC) (1996) and European Food Safety Authority (EFSA) (2007, 2008, 2009), Stien et al (2013a) recently reviewed the needs of Atlantic salmon in the seacage phase and developed a model, using selected welfare indicators, to enable fish farmers to make an objective assessment of welfare. The same team has developed a salmon welfare model for use by fish health professionals, using the following indicators: eyes, cardiac condition, abdominal organs, gills, opercula, skeletal muscles, vaccinerelated pathology, aberrant fish, necropsy of the dead fish and euthanasia (Pettersen et al 2014). In this paper, we primarily examine the impact of factors affecting Atlantic salmon welfare that were not covered adequately in the Stien et al model: handling and transport, high stocking densities during the freshwater phase, feeding systems and slaughter. We also comment on research developments since the publication of the Stien et al model. The initial review was undertaken in 2014, as a commissioned review for the Royal Society for the Prevention of Cruelty to Animals (RSPCA) Australia, but was extended with subsequent drafts of the report to the RSPCA and subsequently as a manuscript submitted to this journal. The main search engine utilised was Web of Science, augmented by Google Scholar and UQ internet searches, as well as accessing EFSA reviews as necessary. Our initial search term was just 'salmon' because not all relevant papers would include 'welfare' in the title or abstract. It was time-limited up to 2014. This produced 43,696 published papers in journals, including 19,804 with salmon in the title. Most were connected with ecology and pollution, some of which had relevance to the review. Of the published papers, 175 had farm in the title and were directly relevant to the review and 332 had salmon and welfare in the topic. These two sets formed the basis of the initial draft of the review. Subsequent searches conducted over the next three years of this study updated the review and introduced specific new terms, eg on fin innervation, and the final search was conducted in early 2018. References of included articles were also searched to identify studies not found in the initial database search.

Handling and transport

The transport of salmon smolts from freshwater conditions to sea cages is unavoidable and, unless stunning and killing equipment is brought to sea cages, there will also be transport at that time. This transport and any transport that occurs at other times, eg during changes of net and some sea lice treatments, is likely to have serious welfare implications.

Handling smolts

The initial procedures of gathering together, counting, capturing and loading smolts are the most stressful stages of salmon transport (King 2009; Nomura et al 2009). Crowding, pumping, vaccination and sorting during the freshwater phase also expose the smolts to welfare challenges. Handling for a duration of 30 s, using a net, produces an elevation of plasma cortisol in juvenile (10-14 months) salmonid species (Barton 2000) as does loading salmon smolts onto a well-boat (Gatica et al 2010). Cortisol elevation is known to occur in salmon kept out of water in a net for a short period and can be associated with immunosuppression (Maule & Schreck 1991). It can also injure the epithelial layer covering the surface of the body, increasing the risk of pathogen infection which, together, may impair the behaviour and survival of the fish after release (Oldenburg et al 2011). The use of rubber or sanctuary nets is advocated (Oldenburg et al 2011). The capture of the smolts leads to increases of plasma cortisol, which remain high even after 48 h, glucose and lactate (Iversen et al 1998). Smolts would also have increased plasma cortisol concentration in preparation for migration to the sea (Shrimpton et al 2000; Nomura et al 2009) but the effects of capture are additional to these. Recognising these concerns, some sectors of the industry have attempted to minimise air exposure by pumping smolts into water-filled tubes after grading into different size categories. Allowing the smolts to passively pass through a grid, rather than being pumped through, potentially reduces the amount of scale damage, which is greatest at fast turbine speeds (Brackley et al 2016).

The stress of transfer from fresh- to seawater can be ameliorated by a sedative, such as isoeugenol (Iversen & Eliassen 2009) but the full impact of this on welfare remains to be determined. The smolts may be transferred to their respective sea sites by road and then by sea transport, usually in a well-boat or by helicopter.

Road transport

Several potential stressors are involved during road transport, including handling and loading, alterations in water quality, osmoregularity disruption and novel transport containers (King 2009). Road transport of 30–60 min in a closed tank, increased plasma cortisol concentrations in Atlantic salmon smolts (Nomura *et al* 2009). Similarly, in juvenile salmonids, cortisol concentrations remained high for 1–2 days after 2 h of experimental transport (Barton 2000).

Sea transport

In 2001, there was a 13% loss rate in 135 million smolts transferred by well-boat in Norway, mostly during and shortly after sea transport. The high mortality rate was a result of disease, wounds, smoltification failure, or the transport itself (Iversen *et al* 2005). The loading of smolts before sea transport produces an initial increase in plasma cortisol (Iversen *et al* 2005), and the accumulation of smolts at the bottom of well-boat tanks may be due to their desire

^{© 2018} Universities Federation for Animal Welfare

to aggregate there in response to the stress of the loading procedure (Nomura et al 2009). Unloading led to small cortisol increases (Iversen et al 2005), perhaps because concentrations of cortisol were already elevated. Generally, though, unloading appears less stressful than loading, with only minor cortisol increases (Iversen et al 2005). If conditions are good in the well-boat, in that oxygen concentration is high enough and stocking density low enough, the welfare during boat movement has much less negative effect on welfare than the loading. However, the impact of sea conditions on fish welfare is an aspect of sea transport that has not been adequately investigated. During a commercial transport between Norway and Scotland with rough sea conditions (wave height of 3-5.5 m), plasma cortisol of Atlantic salmon smolts remained high up to and including unloading and there was higher than usual mortality (Iversen et al 2005).

Water quality during transport

Sea transport may use flow-through of ambient water or water re-circulated within the ship. Flow-through systems can expose the fish to dangerous ambient water conditions, such as algal blooms or oil spills (Tang et al 2009). Oxygen concentrations have large effects on welfare and should be meticulously monitored (King 2009). Both CO₂ and NH₃ concentrations can also affect fish; nonetheless, it is CO₂ that most often reaches dangerous levels and results in poor welfare in the salmon (Wedemeyer 1996). Salmonids are sensitive to accumulation of expired CO₂ during transport (King 2009). The main concern regarding water re-circulation systems used on live-haul vessels, which have a closed hold, is the accumulation of CO₂, the complex and expensive measurement of which represents a challenge during commercial transport (Tang et al 2009). Tang et al (2009) recommended that movement by ship should last no more than 2.5 h at low density (70 kg m⁻³) and movement at high density (170 kg m⁻³), normally by helicopter, should be for no more than 19 min. This should be restricted in order to avoid reaching a partial pressure of CO₂ of 10 mm Hg, as this concentration of CO₂ could adversely affect salmon welfare but not kill them. The Norwegian industry has developed a CO₂-stripping technique to overcome this problem (Cañon Jones et al 2012), the use of which is predicted to improve the profitability of the industry (Noble et al 2012).

Recovery period after transport

A period described as 'recovery' between road and sea transport, or occurring after transport has been completed, has been reported to reduce stress of salmon (Iversen *et al* 1998; Gatica *et al* 2010). It would be scientifically surprising if recovery always occurred because, for transport of land animals, 'recovery' in sub-optimal lairage conditions usually results in worse welfare, more disease and poorer meat quality in slaughter animals than immediate slaughter or movement directly to the final, good conditions (Broom & Fraser 2015). The multiple stressors that salmon are exposed to during transport can adversely affect immunocompetence, seawater tolerance, growth and survival (Iversen *et al* 2005). Recovery from handling procedures and road transport can occur in the well-boat, which has been reported to be beneficial for fish welfare (Iversen *et al* 2005; Nomura *et al* 2009). Recovery using net pens after 2 h of transport in a tank was reported to reduce plasma cortisol and improve survival in sea cages (Finstad *et al* 2003). A recovery period of one day at the extremely high density of 108 kg m⁻³ after a well-boat transportation of 8 h in Chile was reported to reduce blood stress measures (Gatica *et al* 2010). These results emphasise that the whole procedure of moving smolts to sea-cages is stressful and methods of reducing these adverse effects are clearly necessary.

Removal from cages and transport to slaughter is also stressful. Reported beneficial effects of 'rest' after transport from sea cages to a fish processing plant (Erikson *et al* 1997) seem unlikely to be optimal practice. It has been reported that 'rest' after transport from sea cages to a fish processing plant is beneficial but experience with other animals suggests that good conditions for rest are not likely to be possible and if appropriate measures of welfare were used, benefits might not be found to occur (Erikson *et al* 1997).

Stocking density, related factors and welfare outcome indicator use

Although it is helpful to individually consider the various factors that affect salmon welfare, these factors interact. When high stocking density in salmonids was combined with insufficient water flow (Ellis et al 2002) or with too much disturbance (Turnbull et al 2005), welfare was worse than when only one adverse factor was present. In the salmon industry, perhaps because of a long-standing preoccupation with oxygen availability as a key factor affecting production, specific water flow, which takes into account flow rate per kg of biomass, is considered an important measure. However, any such measure should be combined with measures of the animals themselves that indicate the outcome of the situation (EFSA 2008). Examples of welfare outcome measures are growth rate, feed conversion efficiency, mortality rate, percentage morbidity and proportion of fish with fin damage. High stocking density can reduce growth rate and feed conversion efficiency without necessarily affecting mortality or fish body condition (Liu et al 2015). Serum indicators of poor welfare induced by high stocking density have also been studied, with reduced immunoglobulin M and increased cortisol being observed (Liu et al 2015).

When high stocking density is combined with insufficient water flow (Ellis *et al* 2002), farmed salmon kept at high stocking densities usually have damaged fins. This is often called 'fin erosion' (Ellis *et al* 2008), but this term implies that the tissue loss is a consequence of rubbing the fins against something, whereas the loss may be multi-causal, hence we use the term 'fin damage' (Broom & Fraser 2015). It does not occur in wild salmon but is generally initiated in farmed salmon by bite wounds (Turnbull *et al* 1996). Densely stocked farmed salmon (30 kg m⁻³) show high levels of fin-biting and damage (0.35 fin bites per hour and 15% of fish with damage; Cañon Jones *et al* 2011). Damage includes total loss of the dorsal fin, necrosis and sloughing

Table I Freshwater production tank densities from fry, parr up to smolt stages recommended by RSPCA (2015).

Mean liveweight	Stocking density (kg m ⁻³)
Up to I g	10
> I-5 g	20
> 5-30 g	30
> 30 g	50

of the superficial epithelium, haemorrhagic lesions, peripheral erosion, with clefts in the surface epithelium, exposed rays with bacteria adhering to them, and epithelial hyperplasia creating visible nodules which, in most severe cases, reduces the fins' capacity for movement (Turnbull et al 1996). Typically, fins show evidence of secondary infection, inflammation and healing. Since the fins of salmonids appear to be highly innervated and may even function, in part, as mechanosensory organs (Buckland-Nicks et al 2012), any biting of fins is likely to be painful. Fin damage in trout was higher when there was food deprivation (Winfree et al 1998). Cañon Jones et al (2010), using social network analysis, showed that dorsal fin damage in salmon was positively correlated with aggression and fin-biting. It was seen only in groups subjected to feed restriction. Fish initiating aggression were less likely to have fin damage. As a result of the way in which farmed salmon are usually fed, the number of individuals that are feed-restricted increases with stocking density. Fin-biting behaviour and dorsal fin damage in salmon are higher at high than at low stocking density (Cañon Jones et al 2011; Hammenstig et al 2014). Fin damage may also occur as a result of contact with other fish or with the cage or tank. It is clear that high stocking density is a major cause of poor welfare in salmon, as measured by the number of animals with damaged fins and a range of other welfare indicators. It may be possible to mitigate adverse effects of high stocking density by providing shelter, but further research is needed to find the optimum design (Persson & Alanara 2014). Reduction in the extent of damaged fins has been observed in a re-circulation aquaculture system compared to a flow-through water circulation system, possibly because of lower water alkalinity in the latter system (Kolarevic et al 2014).

Stocking density during the freshwater phase

High stocking densities have the potential to adversely affect growth, feed conversion ratio and fin condition, as there is increased competition between the salmon and decreased visibility in the water (Hosfeld *et al* 2009; Riley *et al* 2009). Stocking density is usually expressed as weight of fish per unit volume of water in which they are kept, and maximum densities have been proposed to prevent poor welfare (North *et al* 2006; FW1.5 in RSPCA 2015) (Table 1), although no evidence of the sources for these recommendations is provided. Overt aggression can also be increased at low stocking densities, probably because there is more space in which to fight (Adams *et al* 2007). Great

increases in aggression are observed in freshwater if water quality, including dissolved oxygen, declines, with an associated accumulation of fish metabolites, NH_3 and CO_2 . The dissolved gases accumulate because of the high stocking densities and minimal water flow, especially in re-circulating water systems. Fish exposed to even low levels of ammonia experience stress and immunosuppression (Ackerman *et al* 2006), but this can be ameliorated in high pH water (Wicks *et al* 2002).

Land-based re-circulating aquaculture systems are intensive methods of rearing salmon, at various stages of development, that incorporate re-use of water after treatment. These are gaining popularity in smolt farms as they minimise water flushing and facilitate water filtration and radiation treatment when necessary. High stocking densities are an inherent feature of these systems, in part to recover the high cost of investment (Martins et al 2010) but, as discussed above, welfare will often be worse at higher stocking densities. Maximisation of nutrient retention by the fish and effective treatment and recovery of waste matter is critical to the success of these systems. Carbon dioxide may also accumulate in such systems to the detriment of the welfare of the fish (FAWC 2014b). Total ammonia nitrogen is particularly likely to accumulate in re-circulating water systems, but a partial water reuse system has been developed which controls accumulation of total ammonia nitrogen by make-up water and avoids the use of a biofilter (Summerfelt et al 2009). In Chile, potentially toxic levels of heavy metals have also been recorded, but water treatment with crushed marble or sodium silicate is possible (Pessot et al 2014).

Norwegian regulations for stocking density of Atlantic salmon brood stock set an upper limit of 25 kg m⁻³ (Hosfeld *et al* 2009) but, because of the multifactorial nature of welfare responses to different stocking densities (EFSA 2008), this density might be too high if, for example, oxygen concentration was low. Adult Atlantic salmon in freshwater circular tanks have been kept at up to 125 kg m⁻³ without elevation of cortisol (Kjartansson *et al* 1988), but adaptation of cortisol response does not mean lack of problems for the fish (Broom & Fraser 2015). The main requirements are for physiological demand for oxygen and the need for space to allow for movements required for locomotion, feeding, and avoidance of contact with other fish.

The impact of stocking density on Atlantic salmon welfare has been reviewed mainly in seawater conditions (eg Stien *et al* 2013a). In terms of freshwater stocking densities, there is limited research on the different stages from egg to smolt before transfer to seawater cages. Hosfeld *et al* (2009) reviewed the impact of four different stocking densities (21, 43, 65, 86 kg m⁻³) on pre-smolt salmon (mean weight 71 g) during fresh- and seawater stages. They found no general effects of different densities, including the maximum density (86 kg m⁻³), on fin condition, growth, plasma glucose and chloride, and gill activity. However, they emphasised that no negative effects were found because they used high quality water conditions and sufficient food

^{© 2018} Universities Federation for Animal Welfare

rations during experimental procedures. Cañon Jones et al (2011) observed smolts (mean weight 113 g) under two different densities, high (30 kg m⁻³) and low (8 kg m⁻³) and found that some fish in the high-density groups initiated aggression whilst others only received aggression. The more intense aggressive behaviours included fin-biting. The fish in the low-density groups were more frequently aggressive but those in the high-density groups showed more finbiting and this resulted in more fin damage. The fish in the low-density groups had lower bodyweights and body lengths and poorer body condition, perhaps because of their greater activity. In a study that investigated effects of different densities (from 80 to 310 kg m⁻³) on Atlantic salmon parr (mean weight 5.8 g), a density of 146 kg m⁻³ was suggested to be an appropriate maximum stocking density, provided water quality could be maintained, to avoid negative impacts on growth, food conversion or mortality, with a preferred density of less than 80 kg m⁻³ (Soderberg et al 1993). Soderberg et al (1993) and Hosfeld et al (2009) came to similar conclusions for the numbers of fish reared in land-based systems, but emphasised the greater importance of the quality and characteristics of water than stocking density. This conclusion was supported by Turnbull et al (2008). A note of caution must be sounded regarding research methodology since, in many experiments, stocking density has been varied by altering fish number, without taking into account the fact that changes in group size also affect behaviour and production.

Feeding systems

Efficient feeding systems have not only to meet the salmons' nutrient requirements and minimise water pollution (Alver et al 2004) but also result in good salmon welfare. Factors such as appetite, number and size distribution of fish and feed distribution influence pellet concentration in a sea cage and hence discarded pellets (Alver et al 2004; Alfredsen et al 2007). Agonistic behaviour at feeding times not only adversely affects the fish welfare, it also increases feed intake by dominant individuals and hence causes size divergence within the group, making a uniform product at a single point in time unattainable (Kadri et al 1996). Such an effect could lead to a positive feedback situation in which agonistic behaviour causes size disparity and this further increases agonistic behaviour. This is complicated by the fact that at least at low stocking densities Atlantic salmon show territorial behaviour and are able to defend an area within their tank or enclosure, preventing others from accessing pellets that arrive there (Kadri et al 1996).

Atlantic salmon are often fed with a pelleted diet through automatic feeding services which can deposit pellets at either a pre-determined rate or at a rate that increases or decreases according to fish activity ('on demand'). They are normally fed in sea cages using a pneumatic conveying system with a rotor spreader (Aarseth *et al* 2006; Oehme *et al* 2012). Ondemand feeding systems have been developed to replace imposed regime systems in order that agonistic behaviour and competition are reduced and growth is more uniform within the group of salmon (Noble *et al* 2007b; Lopez-Olmeda *et al* 2012). In a study with salmon parr, the ondemand system reduced dorsal fin injuries, competition and overfed fish, leading to more efficient food conversion (Noble *et al* 2007b). Offering a single daily meal increases conspecific aggression, even though the fish are fed to satiation (Lopez-Olmeda *et al* 2012).

Pneumatic conveying systems have raised a number of concerns as pellets colliding with the pipe wall may break and not be uniformly distributed or go outside the cage and cause water pollution. Therefore, aspects such as the revolutions per minute of the air blower, particle size and spreader arrangements should be considered in the development of an efficient feeding system (Aarseth et al 2006; Aas et al 2011; Oehme et al 2012). Spatial distribution of pellets within an enclosure can influence food intake and water pollution with ammonia, with the type and intensity of the water current playing important roles (Jørgensen et al 1996). Circular water tanks with current at the edge produce a more uniform feed distribution over the entire water body compared with water tanks without such currents. Hence, the latter are not used in salmon production, as they lead to aggression, lower growth rates and more individual and group food intake variability (Jørgensen et al 1996).

Modifying fish feeding behaviour represents a useful tool for determining feeding regime efficiency (Alver *et al* 2004; Alfredsen *et al* 2007), with information on swimming patterns and spatial distribution of the fish contributing to improved feeding systems, providing that they can be accurately measured (Føre *et al* 2011). Salmon show fast swimming in a vertical orientation towards pellets during high intensity feeds, disrupting their natural schooling behaviour. Depth transmitters have revealed that fish approach the surface zone during feeding (1–2 m) and later swim to deeper areas (8–9 m) (Føre *et al* 2011).

Salmon feed in a synchronised fashion and feeding rhythms need to be considered when implementing feeding systems, as they can influence appetite, consumption, uniformity of growth, feed wastage and water pollution. Natural feeding rhythms are primarily circadian and seasonal, but tidal and lunar rhythms are also reported (Lopez-Olmeda et al 2012). Salmon are preferentially diurnal feeders but, at certain stages in their lifecycle, can seasonally change to nocturnal feeding under natural feeding conditions (Lopez-Olmeda et al 2012). Thus, season has to be considered when attempting to feed the fish at their most active time of day. Salmon parr also have natural feeding rhythms that vary with season, including a morning peak in late summer, and a midday feeding during spring (Noble et al 2007a). Attempts to maintain their natural behaviour, and hence welfare, should take this into account. The daily ration is also affected by seasonal and environmental factors, correlated with temperature variations and day length in ondemand feeding systems. Highest intake has been observed at 14°C and lowest at both 18 and 6°C in Atlantic salmon smolts (Handeland et al 2008).

The predictability of the feeding time can influence feed intake and stress levels in the fish. There is increased frequency and severity of dorsal fin damage when there is unpredictable feeding of 1+ salmon parr. However, aggression and attacks can also occur with predictable feeding, probably because of food anticipatory activity (Cañon Jones et al 2012). When food was distributed consistently at the same time and place, dominant fish ate first at the surface and the subordinate ones later, with the latter using different strategies, such as eating in the middle or bottom of the sea cage (Kadri et al 1996). Some fish may receive no food at all. In other farmed animals, feeding systems that seriously disadvantage subordinate animals are either not recommended or not permitted. Feeding systems that result in starvation (a severe deficiency in the intake of nutrients necessary for the maintenance of life; Anon 2018) and severely damaged fins for a significant number of salmon would clearly be unacceptable to most consumers. As the fish that consumed most had less variation in day-to-day intake, Kadri et al (1996) recommended unpredictable feeding times to make intake more even across fish. However, this might lead to more fin damage. Cañon Jones et al (2012) found that with an unpredictable feeding time, initiators of aggressive interactions were heavier and longer and had less fin damage in comparison with receivers. The solution would seem to be to find better feeding systems. The range of size in fish groups is normally recommended to be kept to a minimum (eg Cañon Jones et al 2012) but some authors suggest the use of older fish (1+ parr) within a younger group (0+ parr) to reduce agonistic behaviours (Adams et al 2000). The older fish should not be of a size where they might eat the younger fish so this might be difficult to manage.

Slaughter procedures

Pre-slaughter fasting

Fasting is routinely used just prior to slaughter primarily so that the fish have minimal gastrointestinal contents postslaughter (Einen et al 1998). Other aims are to reduce metabolic rate and physical activity and hence oxygen consumption prior to transport to slaughter (EFSA 2009; RSPCA 2012; FAWC 2014a). The removal of food from animals that have been fed on a regular basis results in stress, as evidenced by a cortisol response (Waagbø et al 2017) and possibly poor welfare, and should never be carried out unless essential. Even then, food reduction should be carried out progressively, never abruptly, to a maximum of three days at normal temperatures, which is sufficient to empty the gut (Einen et al 1998), or up to seven days at low temperatures (Waagbø et al 2017). Two days of fasting will reduce tissue mass and metabolic enzyme activity (Krogdahl & Bakke-McKellep 2005). Some salmon producers use longer periods of food deprivation during periods of overproduction and oversupply but this constitutes deliberate starvation. Although salmon slow their metabolism when deprived of food in this way, including reduced activity in organs related to swimming and

nutrition, there is no evidence that this reduces stress responses prior to slaughter because they are conserving energy for digestion and metabolic processes (Waagbø *et al* 2017). The argument that wild fish experience periodic food deprivation, and survive it, does not necessarily mean that it is not a welfare problem for the fish. Wild mammals also survive starvation but it is not permitted for captive mammals. However, the adaptive growth changes of fish may mean that the longer-term effects of food deprivation are less in fish than in mammals or birds. A long period of starvation (eg five weeks) may improve fillet quality (Morkore *et al* 2008) but probably harms the fish if it suppresses emergency responses.

Pre-slaughter handling

Crowding, capture and pumping are all potentially stressful to salmon (EFSA 2009) but there is a lack of quantitative scientific data on welfare at these times. Indicators of poor welfare during the crowding procedure are: escape behaviour, air gasping, colour change, lateral rotation, increased number of tail beats and turns and presence of fish scales in the water (EFSA 2009; FAWC 2014a). It is recommended that the maximum total duration of periods of such treatment should be 2 h (RSPCA 2012; FAWC 2014a) and that high stocking densities should be avoided at these times (FAWC 2014a). Inadequate pumping systems may produce physical damage and stress, and therefore observations must take place after this to guarantee that the fish can swim and maintain equilibrium, without inversion, signs of asphyxiation or leaping out of the water (HSA 2005; EFSA 2009; Lines & Spence 2012).

Pre-slaughter chilling

Chilling of salmon is commonly used to cool their muscles, reduce activity before slaughter, avoid panic responses to crowding and delay the onset of rigor (Foss *et al* 2012). Scientific studies since the Stien *et al* model have shown that salmon cope with a reduction of water temperature from 16 to 4° C in 1 h and or 16 to 0° C in 5 h without an increase of cortisol (Foss *et al* 2012). More extreme chilling, from 16 to 0° C in 1 h, resulted in severe stress and death. Live-chilling procedures can attenuate pre-slaughter stressors, such as crowding (Skjervold *et al* 2001; Foss *et al* 2012), but a review of studies of the effects of chilling on various species of fish has concluded that cold shock may paralyse the fish so that they lose sensibility slowly and are unable to display signs of suffering (Lines & Spence 2014).

Methods of stunning pre-slaughter

The aim of any method used to slaughter fish is to produce instantaneous unconsciousness without stress and pain (EFSA 2009). Although early research indicated that electrical stunning had reduced effectiveness compared with percussive stunning, with injuries to the spinal cord, aorta and veins (Roth *et al* 2003) and death as a frequent outcome (Roth *et al* 2007), more recent research has indicated that electrical stunning of small fish is humane (Roth *et al* 2012; Kleingeld 2013). If used for salmon, either in water (wet stunning) or out of water (dry stunning), they are likely to

^{© 2018} Universities Federation for Animal Welfare

die from hypoxia before they are able to recover consciousness (Lines & Spence 2014). The placement of fish to avoid pre-stun shocks is important. Percussive stunning using a club, or 'priest', is the traditional method, but automated percussive stunning is the method recommended in Europe (EFSA 2009; FAWC 2014a). The method must be prepared according to fish size (Lines & Spence 2012), and the type of hammer and force used are two key aspects that must be considered to minimise the number of fish that fail to be effectively stunned and avoid injuries (Roth et al 2007). According to Roth et al (2007), the cylindrical hammer is the best shape that produces a general shaking of the entire brain, rather than other shapes that damage the skull but may not stun the fish. Other shapes are problematic because of the small size of the brain. The scientific evidence about the force applied to the head of the salmon is that forces below 72 N do not reliably produce unconsciousness in some fish. Forces incorrectly applied, which may be higher forces than this, affect welfare if the fish is not stunned but has painful damage, such as eye haemorrhage or eye burst. Manual percussive stunning should be avoided as this is a less-efficient method, except in those cases where the automated method fails (FAWC 2014a). In both cases, consciousness could be checked by seeing if a fish shows eye roll and breathing reflexes (EFSA 2009).

EFSA (2009), Kleingeld (2013) and FAWC (2014a) do not recommend the use of carbon dioxide (CO₂) (with or without chilling water) and asphyxia as these methods have resulted in evidence of very poor welfare and slow onset of insensibility in different farmed fish species, including Atlantic salmon. Norway recently banned the use of CO₂ as a stunning method (Bjørlykke et al 2013). Erikson et al (2006) suggest that mild carbon dioxide CO₂ combined with live chilling is a less stressful procedure than traditional CO2, but physiological and behavioural indicators of poor welfare were not included in their study, so their conclusion is not justified. If fish are not stunned but left to die of asphyxia in air, the welfare will be very poor for the period prior to unconsciousness. This period is much longer if the fish are on ice. In trout, the period before unconsciousness during asphyxia in air is 10 min at 2°C as compared with 3 min at 14°C (Robb & Kestin 2002).

Despite the fact that carbon monoxide (CO) is largely insoluble in water, it has been investigated as an alternative stunning method (Bjørlykke *et al* 2011, 2013). Bjørlykke *et al* (2013) investigated CO at two concentrations for 60 and 120 min. Cortisol elevation and behavioural observations indicated an aversive response to CO, but this could have been due to other elements of the experiment, such as turbulence and handling. However, it took 30 min for respiration to cease after a transition period with significant gasping. The very low solubility makes it unlikely to be usable for killing fish.

Research developments since the publication of the Stien et al model

Publications on fish welfare continue to increase in number and impact (Huntingford & Kadri 2014). As well as providing a means of reducing sea lice infestation, Stien *et al* (2013b) recognised the importance of using submersible lighting in sea cages to avoid salmon schooling at high densities near the surface at night to obtain light and potentially leading to frustration. A study by Handeland *et al* (2013) has identified that provision of adequate light is also important during the smolt stage in Atlantic salmon. Light intensities between 10 and 650 lux were tested. Although a minimum of 43 lux was required to avoid suppressing growth and quality of the smolts, the major welfare concern of inadequate light, that of spinal abnormalities, was kept within 1-3% of the fish at all intensities except 10 lux, when it increased significantly to 6.9% of the fish.

Several advances in identifying nutritional requirements of Atlantic salmon have been made, which could be used to elaborate on the definition of adequate nutrition in the Stien et al (2013a) model. The model used two output (animalrelated) rather than input (feed-related) measures: emaciation and fish condition. Adequate histidine supply is vital in avoidance of cataracts, with a critical level of 14.4 g histidine per kg feed determined (Remo et al 2014). Stien et al (2013a) had identified that high stocking density at sea was a factor influencing the development of cataracts, particularly when density exceeded 26.5 kg m⁻³. Similarly, a high energy diet has been linked to fatty deposits in the cardiac ventricles of farmed, but not wild, Atlantic salmon, potentially predisposing them to cardiac disease (Kristensen et al 2012). Whilst it is recognised that it is not possible to incorporate these dietary requirements into the Stien et al (2013a) model, further developments along these lines would enable more accurate dietary standards for fish welfare (rather than growth and development) to be developed.

Animal welfare implications and conclusion

As with other farm animal species, the transport of salmon can cause poor welfare and increased mortality. To minimise poor welfare, it is important to reduce the time spent handling and capturing juvenile fish, build land facilities close to seawater facilities, and improve loading procedures and water quality. Adaptation to the sea-cage condition requires further research.

Stocking density should be considered as one of the most important of the interacting factors that affect Atlantic salmon welfare (Turnbull *et al* 2008). In order to propose an appropriate maximum density for Atlantic salmon during the freshwater stage, the specific conditions used to maintain juvenile salmon should be investigated, taking into account water characteristics, the design of tank and feeding systems in particular. When deciding on new laws and standards, or revising old ones, both maximum stocking density and other welfare indicators should be specified to ensure fish welfare. Stocking densities of salmon in fresh- or seawater should be lower than those that result in fin damage.

In order to guarantee an adequate feed intake by all salmon, several factors should be considered and reviewed, such as feeding rhythms, optimal temperature for feeding and water current, among others. Many currently used feeding systems result in starvation for some fish and fin damage for others, so hence they are unacceptable. On-demand systems seem to be a better solution as they have improved welfare, nonetheless further research should take place integrating additional welfare measurements.

All farmed fish should be stunned, not left to die of asphyxia. Electrical stunning is widely used for smaller fish species but some currently available equipment may not be suitably set for salmon (EFSA 2009; Line & Spence 2014). Carbon dioxide does not stun salmon humanely. The widely used methods of percussive stunning, manual or automatic, have to be precise to effectively stun large numbers of fish. Alternative methods have been investigated but, so far, they do not produce better welfare or carcase quality.

Our ability to assess pain and other welfare problems in salmon is improving rapidly. Welfare outcome indicators, such as fin damage, morbidity and mortality rate, should be used in standards and laws relating to salmon welfare. Standards are already used in accreditation schemes as many consumers prefer ethically produced Atlantic salmon (Martinez-Espirana *et al* 2015). All of the concerns listed above, some of which are not included in the Stien *et al* (2013a) model of animal welfare, should be taken into account when monitoring the welfare of fish in the Atlantic salmon industry. Those in the industry who change methodologies to improve salmon welfare before more consumers start avoiding purchasing the product will benefit from doing so.

Acknowledgements

RSPCA Australia kindly provided financial support for ES. The authors are grateful to two anonymous reviewers for helpful comments.

References

Aarseth KAV, Perez J, Boe K and Jeksrud WK 2006 Reliable pneumatic conveying of fish feed. *Aquacultural Engineering* 35: 14-25. https://doi.org/10.1016/j.aquaeng.2005.06.006

Aas TS, Oehme M, Sørensen M, He G, Lygren I and Åsgård T 2011 Analysis of pellet degradation of extruded high energy fish feeds with different physical qualities in a pneumatic feeding system. *Aquacultural Engineering* 44: 25-34. https://doi.org/10.1016/j.aquaeng.2010.11.002

Ackerman PA, Wicks BJ, Iwama GK and Randall DJ 2006 Low levels of environmental ammonia increase susceptibility to disease in Chinook salmon smolts. *Physiological and Biochemical Zoology* 79: 695-707. https://doi.org/10.1086/504615 Adams C, Huntingford F, Turnbull J, Arnott S and Bell A 2000 Size heterogeneity can reduce aggression and promote growth in Atlantic salmon parr. *Aquaculture International 8*: 543-549. https://doi.org/10.1023/A:1009255612529

Adams CE, Turnbull JF, Bell A, Bron JE and Huntingford FA 2007 Multiple determinants of welfare in farmed fish: Stocking density, disturbance, and aggression in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 64: 336-344. https://doi.org/10.1139/f07-018

Agetsuma M, Aizawa H, Aoki T, Nakayama R, Takahoko M, Goto M, Sassa T, Amo R, Shiraki T, Kawakami K, Hosoya T, Higashijima S-I and Okamoto H 2010 The habenula is crucial for experience-dependent modification of fear responses in zebrafish. *Nature Neuroscience 13*: 1354-1356. https://doi.org/10.1038/nn.2654

Alfredsen JA, Holand B, Solvang-Garten T and Uglem I 2007 Feeding activity and opercular pressure transients in Atlantic salmon (*Salmo salar* L): application to feeding management in fish farming. *Hydrobiologia* 195: 199-207. https://doi.org/10.1007 /s10750-006-0554-9

Alver MO, Alfredsen JA and Sigholt T 2004 Dynamic modelling of pellet distribution in Atlantic salmon (*Salmo salar* L) cages. *Aquacultural Engineering* 31: 51-72. https://doi.org/10.1016 /j.aquaeng.2004.01.002

Anon 2018 *Starvation definition*. https://medical-dictionary.the-freedictionary.com/starvation

Barton BA 2000 Salmonid fishes differ in their cortisol and glucose responses to handling and transport stress. *North American Journal of Aquaculture* 62: 12-18. https://doi.org/10.1577/1548-8454(2000)062<0012:SFDITC>2.0.CO;2

Bjørlykke GA, Kvamme BO, Raae AJ, Roth B and Slinde E 2013 Slaughter of Atlantic salmon (*Salmo salar* L) in the presence of carbon monoxide. *Fish Physiology and Biochemistry* 39: 871-879. https://doi.org/10.1007/s10695-012-9747-5

Bjørlykke GA, Roth B, Sørheim O, Kvamme BO and Slinde E 2011 The effects of carbon monoxide on Atlantic salmon (Salmo salar L). Food Chemistry 127: 1706-1711. https:/ /doi.org/10.1016/j.foodchem.2011.02.045

Brackley R, Bean C, Lucas M, Thomas R and Adams C 2016 Assessment of scale-loss to Atlantic salmon (*Salmo salar* L) smolts from passage through an Archimedean screw turbine. In: Webb JA, Costelloe JF, Casas Mulet R and Lyon JP (eds) *11th International Symposium on Ecohydraulics*. 7-12 February 2016, Melbourne School of Engineering, University of Melbourne, Australia

Braithwaite V 2010 *Do Fish Feel Pain*? Oxford University Press: Oxford, UK

Broom DM 1999 Fish welfare and the public perception of farmed fish. *Proceedings of Aquavision 98, Second Nutreco Aquaculture Business Conference* pp 1-6. May 1998, Stavanger, Norway

Broom DM 2007 Cognitive ability and sentience: which aquatic animals should be protected? *Diseases of Aquatic Organisms* 75: 99-108. https://doi.org/10.3354/dao075099

Broom DM 2014 Sentience and Animal Welfare. CABI: Wallingford, UK. https://doi.org/10.1079/9781780644035.0000

Broom DM 2016 Fish brains and behaviour indicate capacity for feeling pain. *Animal Sentience* 2016.010 (5 pages). https://www.neuroscience.cam.ac.uk/publications/download.php?id=39835

^{© 2018} Universities Federation for Animal Welfare

Broom DM and Fraser AF 2015 Domestic Animal Behaviour and Welfare, Fifth Edition. CABI: Wallingford, UK. https://doi.org /10.1079/9781780645391.0000

Buckland-Nicks JA, Gillis M and Reimchen TE 2012 Neural network detected in a presumed vestigial trait: ultrastructure of the salmonid adipose fin. *Proceedings of the Royal Society B-Biological Sciences* 279: 553-563. https://doi.org/ 10.1098/rspb.2011.1009

Burridge LJ, Weis S, Cabello F, Pizarro J and Bostick K 2010 Chemical use in salmon aquaculture: A review of current practices and possible environmental effects. *Aquaculture 306*: 7-23. https://doi.org/10.1016/j.aquaculture.2010.05.020

Cañon Jones HA, Hansen LA, Noble C, Damsgård B, Broom DM and Pearce GP 2010 Social network analysis of behavioural interactions influencing fin damage development in Atlantic salmon (*Salmo salar*) during feed-restriction. *Applied Animal Behaviour Science* 127: 139-151

Cañon Jones HA, Noble C, Damsgård B and Pearce GP 2011 Social network analysis of the behavioural interactions that influence the development of fin damage in Atlantic salmon parr (*Salmo salar*) held at different stocking densities. *Applied Animal Behaviour Science 133*: 117-126

Cañon Jones HA, Noble C, Damsgård B and Pearce GP 2012 Investigating the influence of predictable and unpredictable feed delivery schedules upon the behaviour and welfare of Atlantic salmon parr (*Salmo salar*) using social network analysis and fin damage. *Applied Animal Behaviour Science 138*: 132-140

Chandroo KP, Duncan IJH and Moccia RD 2004 Can fish suffer? Perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science* 86: 225-250. https://doi.org/10.1016 /j.applanim.2004.02.004

Einen O, Waagan B and Thomassen MS 1998 Starvation prior to slaughter in Atlantic salmon (*Salmo salar*): 1. Effects on weight loss body shape slaughter- and fillet-yield proximate and fatty acid composition. *Aquaculture* 166: 85-104. https://doi.org/10.1016/S0044-8486(98)00279-8

Ellis T, North B, Scott AP, Bromage NR, Porter M and Gadd D 2002 The relationships between stocking density and welfare in farmed rainbow trout. *Journal of Fish Biology 61*: 493-531. https://doi.org/10.1111/j.1095-8649.2002.tb00893.x

Ellis T, Oidtmann B, St-Hilaire S, Turnbull J, North B, MacIntyre C, Nikolaidis J, Hoyle I, Kestin S and Knowles T 2008 Fin erosion in farmed fish. In: Branson E (ed) *Fish Welfare* pp 121-149. John Wiley and Sons: Chichester, UK. https://doi.org/10.1002/9780470697610.ch9

Erikson U, Hultmann L and Erik Steen J 2006 Live chilling of Atlantic salmon (*Salmo salar*) combined with mild carbon dioxide anaesthesia: I Establishing a method for large-scale processing of farmed fish. *Aquaculture* 252: 183-198. https://doi.org/10.1016 /j.aquaculture.2005.05.013

Erikson U, Sigholt T and Seland A 1997 Handling stress and water quality during live transportation and slaughter of Atlantic salmon (*Salmo salar*). Aquaculture 149: 243-252. https://doi.org/10.1016/S0044-8486(96)01453-6

European Food Safety Authority (EFSA) 2007 Animal welfare aspects of husbandry systems for farmed fish in relation to Atlantic salmon. *EFSA Journal*: 1-24 **European Food Safety Authority (EFSA)** 2008 Animal welfare aspects of husbandry systems for farmed Atlantic salmon. *Scientific Opinion of the Panel on Animal Health and Welfare.* (*Question No EFSA-Q-2006-033*). http://www.efsa.europe.eu/en/ efsajournal/pub/736

European Food Safety Authority (EFSA) 2009 Species-specific welfare aspects of the main systems of stunning and killing of farmed Atlantic salmon. http://efsa.onlinelibrary.wiley.com /hub/issue/10.1002/efs2.2009.7.issue-4/

Farm Animal Welfare Council (FAWC) 1996 Report on the Welfare of Farmed Fish. https://www.gov.uk/ government/uploads/system/uploads/attachment_data/file/325555 /FAWC_report_on_the_welfare_of_farmed_fish.pdf

Farm Animal Welfare Council (FAWC) 2014a Opinion on the Welfare of Farmed Fish at the Time of Killing. http://www.defra gov_uk/fawc/files/Opinion-on-the-welfare-of-farmed-fish-at-thetime-of-killing pdf

Farm Animal Welfare Council (FAWC) 2014b Opinion on the Welfare of Farmed Fish. https://www.gov.uk/ government/uploads/system/uploads/attachment_data/file/319323 /Opinion on the welfare of farmed fish.pdf

Finstad B, Iversen M and Sandodden R 2003 Stress-reducing methods for releases of Atlantic salmon (*Salmo salar*) smolts in Norway. *Aquaculture* 222: 203-214. https://doi.org/10.1016/S0044-8486(03)00112-1

Food and Agriculture Organisation (FAO) 2014 Food and Agriculture Organization of the United Nations Fisheries and Aquaculture Department Statistics. http://www fao org/fishery/statistics/en

Føre MJ, Alfredsen A and Gronningsater A 2011 Development of two telemetry-based systems for monitoring the feeding behaviour of Atlantic salmon (*Salmo salar* L) in aquaculture sea-cages. *Computers and Electronics in Agriculture* 76: 240-251. https://doi.org/10.1016/j.compag.2011.02.003

Foss A, Grimsbo E, Vikingstad R and Nortvedt R 2012 Live chilling of Atlantic salmon: physiological response to handling and temperature decrease on welfare. *Fish Physiology and Biochemistry* 38: 565-571. https://doi.org/10.1007/s10695-011-9536-6

Gatica MC, Monti GE, Knowles TG, Warriss PD and Gallo CB 2010 Effects of commercial live transportation and preslaughter handling of Atlantic salmon on blood constituents. *Archivos De Medicina Veterinaria* 42: 73-78. https://doi.org /10.4067/S0301-732X2010000100010

Grimsrud KM, Nielsen HM, Navrud S and Olesen I 2013 Households' willingness-to-pay for improved fish welfare in breeding programs for farmed Atlantic salmon. *Aquaculture* 372: 19-27. https://doi.org/10.1016/j.aquaculture.2012.10.009

Hammenstig D, Sandblom E, Axelsson M and Johnsson JL 2014 Effects of rearing density and dietary fat content on burstswim performance and oxygen transport capacity in juvenile Atlantic salmon Salmo salar. *Journal of Fish Biology 85*: 1177-1191. https://doi.org/10.1111/jfb.12511

Handeland SO, Imsland AK, Ebbesson LOE, Nilsen TO, Hosfeld CD, Baeverfjord G, Espmark A, Rosten T, Skilbrei OT, Hansen T, Gunnarsson GS, Breck O and Stefansson SO 2013 Low light intensity can reduce Atlantic salmon smolt quality. *Aquaculture* 384: 19-24. https://doi.org/10.1016/j.aquaculture.2012.12.016 Handeland SO, Imsland AK and Stefansson SO 2008 The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. *Aquaculture* 283: 36-42. https://doi.org /10.1016/j.aquaculture.2008.06.042

Hosfeld CD, Hammer J, Handeland SO, Fivelstad S and Stefansson SO 2009 Effects of fish density on growth and smoltification in intensive production of Atlantic salmon (*Salmo salar* L). Aquaculture 294: 236-241. https://doi.org/10.1016/j.aqua-culture.2009.06.003

Humane Slaughter Association (HSA) 2005 Humane harvesting of salmon and trout. Guidance notes No 5. HSA: Wheathampstead, Herts, UK

Huntingford FA and Kadri S 2014 Defining, assessing and promoting the welfare of farmed fish. *Revue Scientifique et Technique -Office International des Epizooties 33*: 233-244. https://doi.org /10.20506/rst.33.1.2286

Iversen M, Finstad B, McKinley RS, Eliassen RA, Carlsen KT and Evjen T 2005 Stress responses in Atlantic salmon (*Salmo salar* L) smolts during commercial well boat transports, and effects on survival after transfer to sea. *Aquaculture* 243: 373-382. https://doi.org/10.1016/j.aquaculture.2004.10.019

Iversen M, Finstad B and Nilssen KJ 1998 Recovery from loading and transport stress in Atlantic salmon (Salmo salar L) smolts. Aquaculture 168: 387-394. https://doi.org/10.1016/S0044-8486(98)00364-0

Iversen MH and Eliassen RA 2009 The effect of AQUI-S-[®] on primary, secondary and tertiary stress responses during salmon smolt, *Salmo salar* L, transport and transfer to sea. *Journal of the World Aquaculture Society* 40: 216-225. https://doi.org /10.1111/j.1749-7345.2009.00244.x

Jørgensen EH, Baardvik BM, Eliassen R and Jobling M 1996 Food acquisition and growth of juvenile Atlantic salmon (*Salmo salar*) in relation to spatial distribution of food. *Aquaculture* 143: 277-289. https://doi.org/10.1016/0044-8486(96)01287-2

Kadri S, Huntingford FA, Metcalfe NB and Thorpe JE 1996 Social interactions and the distribution of food among onesea-winter Atlantic salmon (Salmo salar) in a sea-cage. Aquaculture 139: 1-10. https://doi.org/10.1016/0044-8486(95)01163-3

King HR 2009 Fish transport in the aquaculture sector: An overview of the road transport of Atlantic salmon in Tasmania. *Journal of Veterinary Behavior: Clinical Applications and Research 4*: 163-168. https://doi.org/10.1016/j.jveb.2008.09.034

Kjartansson H, Fivelstad S, Thomassen JM and Smith MJ 1988 Effects of different stocking densities on physiologicalparameters and growth of adult Atlantic salmon (*Salmo salar*) reared in circular tanks. *Aquaculture* 73: 261-274. https://doi.org/10.1016/0044-8486(88)90060-9

Kleingeld DW 2013 Aspects of animal welfare protection at stunning and slaughter procedures of fish. *Fleischwirtschaft 93*: 188-192 Kolarevic J, Baeverfjord G, Takle H, Ytteborg E, Reiten BKM, Nergard S and Terjesen BF 2014 Performance and welfare of Atlantic salmon smolt reared in recirculating or flow through aquaculture systems. *Aquaculture 432*: 15-25. https://doi.org/10.1016/j.aquaculture.2014.03.033 **Kristensen T, Urke HA, Poppe TT and Takle H** 2012 Atrial natriuretic peptide levels and heart morphology in migrating Atlantic salmon (*Salmo salar*) smolts from 4 rivers with different environmental conditions. *Aquaculture* 362: 172-176. https://doi.org/10.1016/j.aquaculture.2011.08.003

Krogdahl Å and Bakke-McKellep MA 2005 Fasting and refeeding cause rapid changes in intestinal tissue mass and digestive enzyme capacities of Atlantic salmon (*Salmo salar* L). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 141*: 450-460. https://doi.org/ 10.1016/j.cbpb.2005.06.002

Lines JA and Spence J 2012 Safeguarding the welfare of farmed fish at harvest. Fish Physiology and Biochemistry 38: 153-162. https://doi.org/10.1007/s10695-011-9561-5

Lines JA and Spence J 2014 Humane harvesting and slaughter of farmed fish. Revue Scientifique et Technique de Office Internationale Epizootie 33: 255-264. https://doi.org/ 10.20506/rst.33.1.2284

Liu B, Liu Y and Wang X 2015 The effect of stocking density on growth and seven physiological parameters with assessment of their potential as stress response indicators for the Atlantic salmon (Salmo salar). Marine and Freshwater Behaviour and Physiology 48: 177-192. https://doi.org/10.1080/ 10236244.2015.1034956

Lopez-Olmeda JF, Noble C and Sanchez-Vazquez FJ 2012 Does feeding time affect fish welfare? *Fish Physiology and Biochemistry* 38: 143-152. https://doi.org/10.1007/s10695-011-9523-y

Martinez-Espineira R, Chopin T, Robinson S, Noce A, Knowler D and Yip W 2015 Estimating the biomitigation benefits of Integrated Multi-Trophic Aquaculture: A contingent behavior analysis. *Aquaculture* 437: 182-194. https://doi.org/ 10.1016/j.aquaculture.2014.11.034

Martins CIM, Eding EH, Verdegem MCJ, Heinsbroek LTN, Schneider O, Blancheton JP, Roque d'Orbcastel E and Verreth JAJ 2010 New developments in recirculating aquaculture systems in Europe: A perspective on environmental sustainability. Aquacultural Engineering 43: 83-93. https://doi.org/ 10.1016/j.aquaeng.2010.09.002

Maule AG and Schreck CB 1991 Stress and cortisol treatment changed affinity and number of glucocorticoid receptors in leukocytes and gill of coho salmon. *General and Comparative Endocrinology 84*: 83-93. https://doi.org/10.1016/0016-6480(91)90067-G

Morkore T, Mazo PI, Tahirovic V and Einen O 2008 Impact of starvation and handling stress on rigor development and quality of Atlantic salmon (*Salmon salar* L). *Aquaculture* 277: 231-238. https://doi.org/10.1016/j.aquaculture.2008.02.036

Noble C, Kadri S, Mitchell DF and Huntingford FA 2007a The impact of environmental variables on the feeding rhythms and daily feed intake of cage-held 1+ Atlantic salmon parr (*Salmo salar* L). Aquaculture 269: 290-298. https://doi.org/10.1016/j.aquaculture.2007.04.079

Noble C, Kadri S, Mitchell DF and Huntingford FA 2007b Influence of feeding regime on intraspecific competition, fin damage and growth in 1+ Atlantic salmon parr (*Salmo salar* L) held in freshwater production cages. *Aquaculture Research* 38: 1137-1143. https://doi.org/10.1111/j.1365-2109.2007.01777.x

© 2018 Universities Federation for Animal Welfare

Noble C, Kankainen M, Setala J, Berrill IK, Ruohonen K, Damsgaard B and Toften H 2012 The bio-economic costs and benefits of improving productivity and fish welfare in aquaculture: utilizing CO_2 stripping technology in Norwegian Atlantic salmon smolt production. Aquaculture Economics and Management 16: 297-314. https://doi.org/10.1080/13657305.2012.729251

Nomura M, Sloman KA, von Keyserlingk MAG and Farrell AP 2009 Physiology and behaviour of Atlantic salmon (Salmo salar) smolts during commercial land and sea transport. *Physiology and Behavior* 96: 233-243. https://doi.org/10.1016/j.physbeh.2008.10.006

Nordgreen J, Horsberg TE, Ranheim B and Chen ACN 2007 Somatosensory evoked potentials in the telencephalon of Atlantic salmon (*Salmo salar*) following galvanic stimulation of the tail. *Journal of Comparative Physiology. A Neuroethology Sensory Neural and Behavioral Physiology 193*: 1235-1242. https://doi.org /10.1007/s00359-007-0283-1

North BP, Turnbull JF, Ellis T, Porter MJ, Migaud H, Bron J and Bromage NR 2006 The impact of stocking density on the welfare of rainbow trout (*Oncorhynchus mykiss*). Aquaculture 255: 466-479. https://doi.org/10.1016/j.aquaculture.2006.01.004

Oehme M, Aas TS, Sørensen M, Lygren I and Åsgård T 2012 Feed pellet distribution in a sea cage using pneumatic feeding system with rotor spreader. *Aquacultural Engineering 51*: 44-52. https://doi.org/10.1016/j.aquaeng.2012.07.001

Oldenburg EW, Colotelo AH, Brown RS and Eppard MB 2011 Holding of juvenile salmonids for surgical implantation of electronic tags: a review and recommendations. *Reviews in Fish Biology and Fisheries* 36: 776-784. https://doi.org/10.1007/s11160-010-9186-2

Persson L and Alanara A 2014 The effect of shelter on welfare of juvenile Atlantic salmon (*Salmo salar*) reared under a feed restriction regimen. *Journal of Fish Biology 85*: 845-656. https://doi.org/10.1111/jfb.12443

Pessot CA, Atland A, Liltved H, Lobos MG and Kristensen T 2014 Water treatment with crushed marble or sodium silicate mitigates combined copper and aluminium toxicity for the early life stages of Atlantic salmon (*Salmo salar L*). Aquacultural Engineering 60: 77-83. https://doi.org/10.1016 /j.aquaeng.2014.04.001

Pettersen JM, Bracke MBM and Midtlying PJ 2014 Salmon welfare index model 2.0: an extended model for overall welfare assessment of caged Atlantic salmon, based on a review of selected welfare indicators and intended for fish health professionals. *Reviews in Aquaculture* 6: 162-169. https://doi.org/ 10.1111/raq.12039

Portavella M, Torres B and Salas C 2004 Avoidance response in goldfish: Emotional and temporal involvement of medial and lateral telencephalic pallium. *Journal of Neuroscience* 24: 2342-2335. https://doi.org/10.1523/JNEUROSCI.4930-03.2004

Remo SC, Hevroy EM, Olsvik PA, Fontanillas R, Breck O and Waagbo R 2014 Dietary histidine requirement to reduce the risk and severity of cataracts is higher than the requirement for growth in Atlantic salmon smolts, independently of the dietary lipid source. *British Journal of Nutrition 111*: 1759-1772. https://doi.org/10.1017/S0007114513004418 **Riley SC, Tatara CP, Berejikian BA and Flagg TA** 2009 Behavior of steelhead fry in a laboratory stream is affected by fish density but not rearing environment, *North American Journal* of *Fisheries Management* 29: 1806-1818. https://doi.org/10.1577/M09-035.1

Robb DHF and Kestin SC 2002 Methods used to kill fish: Field observations and literature reviewed. *Animal Welfare* 11: 269-292

Roth B, Grimsbo E, Slinde E, Foss A, Stien LH and Nortvedt R 2012 Crowding, pumping and stunning of Atlantic salmon, the subsequent effect on pH and rigor mortis. *Aquaculture 326*: 178-180. https://doi.org/10.1016/j.aquaculture.2011.11.005

Roth B, Imsland A, Moeller D and Slinde E 2003 Effect of electric field strength and current duration on stunning and injuries in market-sized Atlantic salmon held in seawater. North American Journal of Aquaculture 65: 8-13. https://doi.org/10.1577/1548-8454(2003)065<0008:EOEF-SA>2.0.CO;2

Roth B, Slinde E and Robb DHF 2007 Percussive stunning of Atlantic salmon (*Salmo salar*) and the relation between force and stunning. *Aquacultural Engineering* 36: 192-197. https://doi.org /10.1016/j.aquaeng.2006.11.001

Royal Society for the Prevention of Cruelty to Animals (**RSPCA**) 2012 Welfare standards for farmed Atlantic salmon, October 2012. RSPCA: Horsham, West Sussex, UK

RSPCA 2015 RSPCA welfare standards for farmed Atlantic salmon. https://view.pagetiger.com/RSPCAWelfareStandardsforFarmedAtl anticSalmon

Salwiczek LH, Prétôt L, Demarta L, Proctor D, Essler J, Pinto Al, Wismer S, Stoinski T, Brosnan SF and Bshary R 2012 Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orang-utans in a complex foraging task derived from cleaner – client reef fish cooperation. *PLoS ONE 7*: e49068. https://doi.org/10.1371/journal.pone.0049068

Shrimpton JM, Björnsson BT and McCormick SD 2000 Can Atlantic salmon smolt twice? Endocrine and biochemical changes during smolting. *Canadian Journal of Fisheries and Aquatic Sciences 57*: 1969-1976. https://doi.org/10.1139/f00-143

Skjervold PO, Fjæra SO, Østby PB and Einen O 2001 Livechilling and crowding stress before slaughter of Atlantic salmon (*Salmo salar*). Aquaculture 192: 265-280. https://doi.org /10.1016/S0044-8486(00)00447-6

Sneddon LU, Braithwaite VA and Gentle MJ 2003 Novel object test: examining nociception and fear in the rainbow trout. *Journal of Pain 4*: 431-440. https://doi.org/10.1067/S1526-5900(03)00717-X

Soderberg RW, Meade JW and Redell LA 1993 Growth, survival, and food conversion of Atlantic salmon reared at four different densities with common water quality. *The Progressive Fish-Culturist* 55: 29-31. https://doi.org/10.1577/1548-8640(1993)055<0029:GSAFCO>2.3.CO;2 Stien LH, Bracke MBM, Folkedal O, Nilsson J, Oppedal F, Torgersen T, Kittilsen S, Midtlyng PJ, Vindas MA, Overli O and Kristiansen TS 2013a Salmon Welfare Index Model (SWIM 1.0): a semantic model for overall welfare assessment of caged Atlantic salmon: review of the selected welfare indicators and model presentation. *Reviews in Aquaculture 5*: 33-57. https://doi.org/10.1111/j.1753-5131.2012.01083.x

Stien LH, Fosseidengen JE, Malm ME, Sveier H, Torgensen T, Wright DW and Oppedal F 2013b Low intensity light of different colours modifies Atlantic salmon depth use. *Aquacultural Engineering* 62: 42-48. https://doi.org/10.1016 /j.aquaeng.2014.05.001

Stones DAJ 2003 Dietary carbohydrate utilization by fish. Reviews in Fisheries Science 11: 337-369. https://doi.org/10.1080/ 10641260390260884

Summerfelt ST, Sharrer M, Gearheart M, Gillette K and Vinci BJ 2009 Evaluation of partial water reuse systems used for Atlantic salmon smolt production at the White River National Fish Hatchery. Aquacultural Engineering 41: 78-84. https://doi.org/10.1016/j.aquaeng.2009.06.003

Tang S, Thorarensen H, Brauner CJ, Wood CM and Farrell AP 2009 Modeling the accumulation of CO₂ during high density, recirculating transport of adult Atlantic salmon, (*Salmo salar*) from observations aboard a sea-going commercial live-haul vessel. *Aquaculture* 296: 102-109. https://doi.org/10.1016/j.aquaculture.2009.07.020

Turnbull J, Bell A, Adams C, Bron J and Huntingford F 2005 Stocking density and welfare of cage farmed Atlantic salmon: application of a multivariate analysis. *Aquaculture 243*: 121-132. https://doi.org/10.1016/j.aquaculture.2004.09.022

Turnbull JF 2006 Current issues in fish welfare. Journal of FishBiology68:332-372.https://doi.org/10.1111/j.0022-1112.2006.001046.x

Turnbull JF, North BP, Ellis T, Adams CE, Bron J, MacIntyre CM and Huntingford FA 2008 Stocking density and the welfare of farmed salmonids. In: Branson EJ (ed) Fish Welfare pp 111-120. Blackwell Publishing Ltd: Oxford, UK. https://doi.org/10.1002/9780470697610.ch8

Turnbull JF, Richards RH and Robertson DA 1996 Gross, histological and scanning electron microscopic appearance of dorsal fin rot in farmed Atlantic salmon, *Salmo salar L*, parr. *Journal of Fish Diseases* 19: 415-427. https://doi.org/10.1111/j.1365-2761.1996.tb00381.x

Waagbø R, Jørgensen SM, Timmerhaus G, Breck O and Olsvik PA 2017 Short-term starvation at low temperature prior to harvest does not impact the health and acute stress response of adult Atlantic salmon. *PeerJ* 5: e3273. https://doi.org/ 10.7717/peerj.3273

Wedemeyer GA 1996 Transportation and handling, In: Pennell W and Barton BA (eds) Developments in Aquaculture and Fisheries Science, Volume 29 pp 727-758. Elsevier: Amsterdam, The Netherlands. https://doi.org/10.1016/S0167-9309(96)80015-9

Wicks BJ, Joensen R, Tang Q and Randall DJ 2002 Swimming and ammonia toxicity in salmonids: the effect of sub lethal ammonia exposure on the swimming performance of coho salmon and the acute toxicity of ammonia in swimming and resting rainbow trout. Aquatic Toxicology 59: 55-69. https://doi.org/10.1016/S0166-445X(01)00236-3

Winfree RA, Kindschi GA and Shaw HT 1998 Elevated water temperature, crowding and food deprivation accelerate fin erosion in juvenile steelhead. *Progressive Fish-Culturist 60*: 192-199. https://doi.org/10.1577/1548-8640(1998)060<0192:EWT-CAF>2.0.CO;2