Hydrobiologia (2016) 783:347–359
DOI 10.1007/s10750-015-2572-y

Review Paper

Environmental conditions required for intensive farming of Arctic charr (*Salvelinus alpinus* (L.))

Bjørn-Steinar Sæther · Sten Ivar Siikavuopio · Malcolm Jobling

Received: 30 June 2015 / Revised: 28 October 2015 / Accepted: 31 October 2015 / Published online: 23 December 2015

Abstract The Arctic charr (*Salvelinus alpinus*) is a relativelystenothermal fish that displays a high degree of biological plasticity. Although primarily a freshwater fish, there are anadromous populations at the northernmost limits of the distributional range. Developmental plasticity has both advantages and disadvantages for establishment in culture, with variable growth rates and early onset of sexual maturation at small size being distinctly disadvantageous. In addition, a requirement for water of low temperature for egg production (4–7°C) and early development limits the possibilities of farming Arctic charr outside of its natural distributional range. On the other hand, a tolerance of high stocking density (60–150 kg m^{-3}) makes it a candidate for rearing in recirculation systems where effective use of both water and rearing unit volume are at a premium. It is possible to farm some strains of charr in either fresh water or brackish water (20 ‰) throughout the year, but year-round farming in full-strength seawater (33–35 ‰) does not seem to be feasible. Photo-thermal manipulation can be used to influence feeding, growth, salinity tolerance and the reproductive cycle. Water quality requirements seem to be similar to those of other salmonids.

Keywords Salmonid culture · Water quality · Temperature requirements · Dissolved gases · Metabolic wastes · Fish welfare · Recirculating aquaculture systems (RAS)

Guest editors: M. Power, R. Knudsen, C. Adams, M.J. Hansen, J.B. Dempson, M. Jobling & M. Ferguson/Advances in Charr Ecology and Evolution

B.-S. Sæther (✉) · S. I. Siikavuopio
Nofima AS, 9291 Tromsø, Norway
e-mail: bjorn-steinar.saether@nofima.no

M. Jobling
Department of Arctic and Marine Biology, BFE, University of Tromsø, 9037 Tromsø, Norway

Introduction

Arctic charr (*Salvelinus alpinus*) has the most northern distribution of all freshwater fishes and it is the most cold-adapted species within the salmonid family (Johnson, 1980). Due to its occurrence at high latitudes, the Arctic charr experiences large seasonal changes in environmental conditions and the species is well-adapted to exploit the associated changes in resource availability (Johnson, 1980; Jørgensen & Johnsen, 2014). Arctic charr has a high degree of biological plasticity, life-history patterns can vary within groups of siblings, and growth is highly variable (Johnson, 1980; Hammer, 1984, 2014; Damsgård et al., 1999; Klemetsen et al., 2003; Klemetsen, 2013; Jørgensen & Johnsen, 2014; Knudsen et al., 2015).

The Arctic charr is primarily a freshwater fish, and although many populations are landlocked, typically within deep lakes, others occur in watercourses with access to the sea. Here some of the fish may adopt an anadromous life-style. Anadromous Arctic charr typically occur towards the northern limit of the distribution range, and both anadromous and resident, non-migratory charr often occur in the same watercourses (Johnson, 1980; Jonsson & Jonsson, 2001; Klemetsen et al., 2003; Rikardsen et al., 2004; Klemetsen, 2013; Hammar, 2014). Lake-dwelling Arctic charr are often polymorphic, with habitat segregation and variations in body form between morphs. This is often related to the food upon which the fish feed, resulting in trophic polymorphism, but morphs usually differ in several biological characteristics (Jonsson & Jonsson, 2001; Klemetsen et al., 2003; Klemetsen, 2013; Hammar, 2014; Knudsen et al., 2015). Some lakes may contain four sympatric morphs—planktivorous, small and large benthivorous, and piscivorous—which have some degree of reproductive isolation from each other. The inherent developmental plasticity of the Arctic charr has both advantages and disadvantages for the establishment of the species in culture. For example, the ability to adapt to a range of feeding regimes may be advantageous, but variability in growth rates and size and age at sexual maturity may be disadvantageous for aquaculture production.

At present, charr from several sources, and from both anadromous and landlocked populations, are used for commercial farming. Small-scale producers may rely upon farming fish taken from local waters, but domestication and selective breeding programmes have been carried out in some countries, e.g. Sweden, Iceland and Canada, so commercial producers may have access to selected stocks for on-growing (Johnston, 2002; Didlecadet et al., 2006; Nilsson et al., 2010). Although farming of Arctic charr is commercially viable in several countries, production in areas outside its native range is often problematic (Jobling et al., 1993, 1998, 2010; Johnston, 2002). One major problem that hinders the establishment of Arctic charr farming in some regions relates to the requirement of the species for water of low temperature. Low water temperatures are required particularly during the final stages of the reproductive cycle, during egg incubation and for the early development of the hatchlings. This means that the successful holding of broodstock, and hatchery operations, are only possible in locations where river and lake temperatures are low at the appropriate times of the year, or where suitable well-bore water is available (Jobling et al., 2010; Gillet et al., 2011; Jeuthe et al., 2013, 2015).

Global aquaculture production of Arctic charr is 6000–10,000 metric tonnes, with all main producers located in northern Europe (Sæther et al., 2013). Farming of Arctic charr in the Nordic countries constitutes more than 90% of the European production, with 45–50 farms of different sizes using a range of production strategies (Sæther et al., 2013).The farms use floating net cages in fresh water or brackish water, flow-through tank systems and recirculation systems (RAS) (Johnston, 2002; Eriksson et al., 2010; Jobling et al., 2010; Sæther et al., 2013).

The purpose of this short review is to describe current knowledge of water quality requirements of Arctic charr and provide information about environmental factors that have major influences on production.

Farmed fish and their environment

Many abiotic and biotic factors combine to make the rearing environment to which farmed fish are exposed; all influence the physiology, behaviour, and performance of the fish to a greater or lesser extent. Fish within culture units can be exposed to various hazards that are capable of having adverse effects upon feeding, growth, health, and welfare (Colt, 2006; Lekang, 2007; Branson, 2008; Harmon, 2009; Jobling, 2010). These may be categorized as physical, chemical, and biological hazards. Physical hazards include those associated with handling and transport, unfavourable temperatures, and particulate matter and suspended solids present in the water. Chemical hazards include water with low concentrations of dissolved oxygen (hypoxic or anoxic water), accumulated metabolic wastes, organic and inorganic pollutants and contaminants, such as heavy metals, and residues of disinfectants and other chemicals used on the farm. Biological hazards may range from pathogens and parasites to competitors and predators.

Farmed fish face the challenge of temporally variable exposure to combinations of hazards, making the defining of characteristics that represent a good rearing environment a difficult undertaking. For example, factors that influence and define water quality include concentrations of dissolved oxygen, concentrations of metabolic waste products (ammonia and carbon dioxide), water pH, and the presence of toxicants, such as heavy metals or organic pollutants. In addition, requirements, such as those for water temperature, dissolved gas concentrations, and ionic concentrations, vary with the life-history stage of the fish, and environmental factors may interact to influence physiological and behavioural responses in a variety of ways (Jobling, 1994, 2010; Colt, 2006; Lekang, 2007; Branson, 2008; Harmon, 2009). In the final reckoning, the environment to which farmed fish are exposed will represent a compromise between what is desirable and what is feasible within the confines of the technology available and the economic constraints placed upon the producer.

Temperature

How temperature influences a fish depends on its thermal history, so short-term (acute) thermal tolerances and preferences depend on the recent thermal conditions experienced by the fish (Jobling, 1994, 2010). On the other hand, the ultimate upper and lower incipient lethal temperatures are independent of recent thermal history and acclimation, and reflect the limits for survival. For Arctic charr, which is a relatively stenothermal cold-water fish, the limits span 0–24°C (Table 1) (Lyttikäinen et al., 1997a; Thyrel et al., 1999; Johnston, 2002). Arctic charr prefer colder water, in the region of 10–12°C (Larsson, 2005; Siikavuopio et al., 2014), than trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*), and European whitefish (*Coregonus lavaretus*). They grow more efficiently than both brown trout and salmon at temperatures below 10°C (Larsson, 2005; Elliott & Elliott, 2010; Jobling et al., 2010; Siikavuopio et al., 2010), and charr can grow in water with a temperature

Table 1 Environmental and water quality thresholds and requirements for intensive rearing of Arctic charr (*Salvelinus alpinus*)

Environmental factor		Sources
Temperature		
Thermal range	0–24°C	Lyytikäinen et al. (1997a), Johnston (2002)
Broodstock	4–7°C	Gillet (1991), Jobling et al. (1995), Jeuthe et al. (2013)
Egg incubation (to eyed stage)	<6°C	Jeuthe et al. (2013), Janhunen et al. (2010)
Egg incubation (eyed stage to hatch)	<12°C	Johnston (2002)
Start-feeding	8–10°C	Johnston (2002)
Juveniles	14–16°C	Jobling et al. (1993), Lyytikäinenet al. (1997b)
On-growing	11–12°C	Larsson (2005), Siikavuopio et al. (2013)
Salinity (Anadromous charr)		
Summer	Up to 33–35 ‰	Jobling (1994), Duston et al. (2007)
Year-round	Up to 20 ‰	Jobling (1994), Árnason et al. (2014), Gunnarsson et al. (2014)
Water quality		
Dissolved gases		
Oxygen saturation	70%	Jobling (1994)
Carbon dioxide	10–15 mg l^{-1}	Johnston (2002), MacIntyre et al. (2008)
pH	6.5-8.5	Jobling (1994), MacIntyre et al. (2008)
Metabolic wastes		
Total ammonia (TAN)	<1 mg l^{-1}	Jobling (1994), MacIntyre et al. (2008)
Ammonia (NH_3)	<0.015 mg l^{-1}	Jobling (1994), MacIntyre et al. (2008)
Nitrite	<0.1 mg l^{-1}	Jobling (1994) , MacIntyre et al. (2008)
Nitrate (egg incubation)	1 mg l^{-1}	MacIntyre et al. (2008)
Suspended solids	<25 mg l^{-1}	MacIntyre et al. (2008)

General recommendations for farmed salmonids

Sources: [1] Lyytikäinen et al. (1997a); [2] Johnston (2002); [3] Gillet (1991); [4] Jobling et al. (1995); [5] Jeuthe et al. (2013); [6] Janhunen et al. (2010); [7] Jobling et al. (1993); [8] Lyytikäinenet al. (1997b); [9] Larsson (2005); [10] Siikavuopio et al. (2013); [11] Jobling (1994); [12] Duston et al. (2007); [13] Árnason et al. (2014); [14] Gunnarsson et al. (2014); [15] MacIntyre et al. (2008)

as low as 0.3°C (Brännäs & Wiklund, 1992; Siikavuopio et al., 2009a).

Optimal temperatures for raising Arctic charr change with life-history stage. Maturing females have narrow tolerance limits because low water temperatures (4–7°C) are required for oocyte development and the final stages of egg maturation (Jobling et al., 1995; Jeuthe et al., 2013, 2015). Ovulation of females held at 8°C is delayed compared to females kept at 5°C and is completely inhibited at 11°C (Gillet, 1991; Gillet et al., 2011). Exposure of the eggs to temperatures over 10°C is deleterious to development and survival (Jobling et al., 2010), and reduced hatching success of eggs has been reported for incubation temperatures as low as 6°C (Table 1) (Janhunen et al., 2010).

Growth rates for fingerlings and juveniles peak at 14–16°C (Table 1) (Jobling et al., 1993; Lyttikäinen et al., 1997b; Siikavuopio et al., 2013), although the fish may be able to sustain quite good growth within a range of 10–18°C. Larsson (2005) and Siikavuopio et al. (2013) reported that Arctic charr in the on-growing stage perform well at 11–12°C, with the fish combining high growth rates, good feed utilization, and low occurrence of diseases and fungal attack.

Both the short-term thermal history (acclimation temperature) and life stage need to be considered in temperature management under farming conditions, and it should be remembered that the optimal temperature for growth is not optimal for feed utilization (Jobling, 2010). If fish are to be subjected to changes in temperature during production, they should be allowed to gradually acclimate by stepwise change of 1–2°C per day.

Salinity

Growth of anadromous Arctic charr held in seawater is variable and is seasonally dependent (Duston et al., 2007), although it may be possible to raise charr in saline water year-round provided that an adequate salinity acclimation protocol is adopted (Arnesen et al., 1994; Árnason et al., 2014; Gunnarsson et al., 2014). In the wild, anadromous charr spend most of the year in fresh water. They migrate to the sea in late-spring, and return to fresh water after spending 6–8 weeks in coastal waters (Jobling et al., 2010; Jørgensen & Johnsen, 2014). Such waters often have salinities that are lower than full-strength seawater (33–35 ‰). When farmed charr are transferred to seawater in spring or early summer some fail to resume feeding and lose weight, despite appearing to maintain ion and water balance (Arnesen et al., 1993a, b). By contrast, others start to feed after a few days and grow well, particularly during the summer (Delabbio et al., 1990; Arnesen et al., 1993b). As summer turns to autumn, and then to winter the growth and survival of Arctic charr cultured in seawater can be compromised (Arnesen et al., 1994). Charr have reduced salinity tolerance at this time, and wild anadromous charr will have returned to fresh water to overwinter by late summer or early autumn (Jobling et al., 2010; Jørgensen & Johnsen, 2014). Factors implicated in the loss of salinity tolerance include the seasonal changes in temperature and photoperiod along with the onset of sexual maturation, but the relative importance of each factor remains uncertain (Delabbio et al., 1990; Eliassen et al., 1998; Duston et al., 2007; Jørgensen & Johnsen, 2014).

Anadromous charr seem to undergo a parr-smolt transformation that resembles that seen in other anadromous salmonids (Jørgensen & Johnsen, 2014) and they tolerate full-strength seawater (33–35 ‰) during an approximately 2-month long period during summer. Charr of some strains may be able to cope well with being reared in brackish water (20 ‰) for the remainder of the year (Árnason et al., 2014; Gunnarsson et al., 2014). The ability to tolerate exposure to saline water year-round is also dependent on fish size and temperature (Johnston, 2002; Duston et al., 2007). Salinity tolerance of small fish may be poor, particularly at low temperature.

Whether non-anadromous Arctic charr can develop seawater tolerance has been a matter of debate. Offspring of landlocked strains of Arctic charr reared in captivity have shown limited ability to hypo-osmoregulate when transferred to full-strength seawater in spring, and mortality has often been high (Staurnes et al., 1992; Eliassen et al., 1998; Ojima et al., 2009). Ojima et al. (2009) were able to improve the hypo-osmoregulatory capacity of landlocked charr by treating them with growth hormone and cortisol. These are hormones that are implicated in the promotion of increased hypo-osmoregulatory ability in anadromous salmonids during the parr-smolt transformation (McCormick, 2013), and anadromous charr have elevated plasma titres of growth hormone and cortisol during the spring (Jørgensen & Johnsen, 2014). This suggests that the lack of development of hypo-osmoregulatory ability often seen in landlocked populations of Arctic charr may depend, at least partly, on a lack of the hormonal activation seen in anadromous populations (Ojima et al., 2009).

Dissolved gases

The solubility of gases in water depends on temperature, salinity, and their individual partial pressure gradients across the surface (Lekang, 2007). The dissolved gases that are of primary interest for fish production and water management are oxygen and carbon dioxide.

Dissolved O_2 (DO)

Oxygen is required to sustain basic bodily functions, and is considered to be the most important water quality parameter in aquaculture production. It is difficult to specify critical dissolved concentrations because the response to low DO is a continuum of effects that are influenced by exposure time, the size and health of the fish, water temperature, and several other environmental factors (Jobling, 1994, 2010; Lekang, 2007; MacIntyre et al., 2008; Harmon, 2009). When considering the DO supply to the fish in the rearing units it is essential to remember that fish require more oxygen in warm water than in cool, because metabolic rate increases as temperature is increased. Fish that are well-fed will require more oxygen than those that are fasting, as a result of the increase in metabolic rate that accompanies feeding, and small fish use more oxygen per unit weight than larger fish. This means that the amount of DO to be supplied to a rearing unit will not only depend upon the number of fish present, but also upon their size and feeding state, and upon water temperature (Jobling, 1994, 2010; Lekang, 2007; MacIntyre et al., 2008).

As is the case for other fish species the oxygen consumption of Arctic charr varies with body weight, feeding and growth rates, activity levels and swimming speed, water temperature, and stress levels. For juvenile Arctic charr (30–100 g) held at temperatures of 6–10°C oxygen consumption will usually fall within the range 100–200 mg O_2 kg^{-1} h^{-1} (Christiansen et al., 1991; Jørgensen et al., 1993). Fish that are feeding well and have good growth rates have an average oxygen consumption above 150 mg O_2 kg^{-1} h^{-1}, and shortly after the completion of a meal oxygen demand may be 40–50% above the average.

The transfer of oxygen from the water to the blood over the gills is passive, and depends on the partial pressure that the gas contributes to the total pressure. When oxygen concentrations and partial pressures are low (hypoxia), the fish can compensate by increasing water flow over the gills, increasing functional gill surface area (lamellar recruitment) and/or can reduce oxygen demand by decreasing activity or by reducing the amount of food eaten (Jobling, 1994, 2010). The latter has the consequence of reducing the rate of growth. There may not be any negative effects on feeding and growth when DO falls from 100 to 70% saturation, but below 70% saturation both feed intake and growth generally decline (Table 1). Recent results indicate that Arctic charr can tolerate DO down to 60% saturation without any reduction in growth rate, but at 60% saturation feed conversion was poorer than at higher DO (Beuvard & Thoraresen, unpublished data). In cases where there is a risk that the fish may be exposed to hypoxic water, remedial measures can include supplementary oxygenation, reducing or stopping feeding, and lowering water temperature; the latter to reduce the metabolic rates of the fish and, thereby, reduce oxygen demand.

Super saturation of water with oxygen (hyperoxia) is not usually a problem, but it can sometimes arise during handling and transport when it is common practice to oxygenate the water (Lekang, 2007; MacIntyre et al., 2008; Harmon, 2009). This reduces water needs, which may be favourable and even necessary under some conditions. By removing nitrogen before adding oxygen, the total gas saturation may be kept under 100% even though the DO content *per se* is increased (Lekang, 2007).

Carbon dioxide (CO_2)

Production of carbon dioxide is directly related to oxygen consumption, since it is an end product of aerobic metabolism in tissues, and CO_2 that is carried from the tissues in the blood diffuses over the gills into the water that surrounds the fish (Jobling, 1994). The dynamics of the reactions of CO_2 with water are complex, and they are influenced by pH and alkalinity (Summerfelt et al., 2000; MacIntyre et al., 2008). The CO_2 in the water will be present as free, dissolved carbon dioxide gas, carbonic acid (H_2CO_3), and bicarbonate (HCO_3') and carbonate (CO_3'') ions:

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3' \leftrightarrow 2H^+ + CO_3''$$

As hydrogen ions are released, the pH of the water is reduced, i.e. acidity increases, and this determines the amount of each component present. At a pH of below 6, free CO_2 will dominate, at a pH of 7–9 bicarbonate is the dominant form, and at pH 11 the carbonate ion makes up the highest percentage. Thus, to avoid accumulation of free CO_2 the pH of the water should be held above 6. The pH should also be kept stable because changes in pH initiate complex water quality changes that may cause harm to the fish, especially their gills. Salmonids can tolerate pH within the range 5–9, and water with a pH between 6.5 and 8.5 seems suitable for good production (Jobling, 1994; MacIntyre et al., 2008).

If the concentration of free CO_2 in the water increases to a level where it interferes with the ability of the fish to excrete CO_2 then CO_2 can accumulate in the blood and the pH of the blood will be lowered (acidosis). This, in turn, reduces the affinity of haemoglobin to bind oxygen and can result in a life-threatening situation (Jobling, 1994; MacIntyre et al., 2008). The fact that carbon dioxide has been used as an anaesthetic and for killing fish attests to the ability of this gas to interfere with, and disrupt, physiological functions. The anaesthetic effects of CO_2 are observed at total concentrations of 150–200 mg l^{-1}, but there is a risk of blood acidosis and reduced growth following prolonged exposure to much lower concentrations (20 and 45 mg l^{-1}, respectively).

Although carbon dioxide is highly soluble in water, the concentrations present as free gas are usually low (1–6 mg l^{-1}) even though total levels may be 50–60 mg l^{-1}. Sometimes, high concentrations of free CO_2 can occur in fish rearing units, particularly in recirculating water systems (RAS) when there has been inadequate degassing (Colt, 2006; Colt et al., 2009). In Arctic charr culture, levels of CO_2 should be kept below 10 mg l^{-1} when the alkalinity of the water is less than 100 mg l^{-1}, and below 15 mg l^{-1}at higher alkalinities (Table 1) (Johnston, 2002).

Ammonia, nitrite and nitrate

Ammonia (NH_3) is the primary waste metabolite produced when amino acids present in feed proteins are deaminated and catabolized. The fish excrete the majority of their nitrogenous wastes over the gills as ammonia (NH_3), some ammonia is converted to the ammonium ion (NH_4^+) and is excreted in this form, and there is also some production and excretion of urea (Jobling, 1994). The excreted ammonia is usually rapidly diluted to non-toxic concentrations in the surrounding water, and some of the ammonia is also ionized to the ammonium ion. Within fish rearing units, ammonia can also arise as the result of decomposition of uneaten feed, but this will usually be much less than the amounts excreted by the fish.

The proportions of total ammonia nitrogen (TAN) present as ammonia and the ammonium ion depend upon pH, temperature, and salinity (Jobling, 1994; Colt, 2006; Lekang, 2007; MacIntyre et al., 2008). The proportion of the most toxic form, ammonia, increases as pH and water temperature are increased. At high external ammonia concentrations there is a slowing of the rate of outward diffusion of ammonia over the gills of the fish and blood ammonia concentrations may start to rise (Jobling, 1994, 2010; MacIntyre et al., 2008). Ammonia toxicity manifests as increased ventilation rates, muscle spasms and erratic swimming, loss of equilibrium, convulsions, and eventually death of the fish (Jobling, 1994; MacIntyre et al., 2008).

In intensive closed or semi-closed rearing systems, there is often accumulation of nitrogenous compounds and metabolites, such as ammonia (NH_3), nitrite (NO_2'), and nitrate (NO_3'), even when there is frequent water exchange (Colt, 2006; Lekang, 2007; MacIntyre et al., 2008; Colt et al., 2009). High concentrations of ammonia and nitrite in the water are potentially toxic, can induce stress and lead to fish mortality if remedial measures are not taken. Control over ammonia concentrations can be achieved by a combination of measures. These include reducing the amounts of waste feed to a minimum to limit nitrogen input, regulation of carbon dioxide concentration and pH to reduce the proportion of TAN present as NH_3 and maintaining control over fish stocking densities to ensure that rates of ammonia excretion are not excessive. When fish are held in intensive rearing systems the water is usually treated to remove ammonia (Colt, 2006; Lekang, 2007; Colt et al., 2009).

The removal of ammonia from water generally occurs through the conversion of ammonia (NH_3) to nitrite (NO_2'), and then to nitrate (NO_3') by bacteria. In intensive re-use or recirculation systems (RAS) nitrite concentrations may become elevated. This occurs when rates of oxidation of ammonia to nitrite exceed the rates of oxidation of nitrite to nitrate. Increases in nitrite concentrations are of concern because nitrite is toxic to fish, and there may be negative effects on the fish at concentrations as low as 0.1 mg l^{-1} (Jensen, 2003; Lekang, 2007; MacIntyre et al., 2008). Nitrite is toxic to salmonids at relatively low concentrations, because it reduces the oxygen transport capacity of the blood. Nitrite oxidizes the iron in the haemoglobin (Hb with Fe^{2+}) resulting in the formation of methaemoglobin (metHb with Fe^{3+}). When blood metHb content is high the blood is brown, rather than red. MetHb does not have the ability to bind to oxygen, so the formation of metHb leads to a decrease in the oxygen-carrying capacity of the blood and this is the cause of nitrite toxicity (Jensen, 2003; MacIntyre et al., 2008; Jobling, 2010). Factors that affect either oxygen availability or the oxygen demand of the fish change the levels of nitrite that are toxic. Thus, nitrite is more toxic when fish are held under hypoxic conditions (when oxygen concentrations are low), or when they have high metabolic rates. Addition of common salt (sodium chloride, NaCl) to the water may be used as a mitigation measure, because chloride ions will reduce the rate at which nitrite is taken up over the gills of fish in freshwater. Brackish water and seawater contain high concentrations of chloride ions, and this reduces the toxicity of nitrite to fish held in saline water.

Safe levels of ammonia, nitrite, and nitrate for Arctic charr are unknown. However, based on the experience of using recirculating aquaculture systems (RAS) to farm Arctic charr, and the recommendations for Atlantic salmon (*Salmo salar*) and other salmonids, ammonia levels in fresh water should not exceed 0.015 mg l^{-1}, and TAN should be below 1 mg l^{-1}. Nitrite should preferably be below 0.1 mg l^{-1} and not be allowed to exceed 0.2 mg l^{-1} (MacIntyre et al., 2008; Skybakmoen et al., 2009). For Arctic charr held in seawater, safe levels will be somewhat higher (Johnston, 2002). Nitrate will probably not be a threat to most of the life-history stages, but exposure of eggs to nitrate can result in developmental problems in salmonids. Therefore, a maximum of 1 mg l^{-1} nitrate is probably advisable in water used for egg incubation (MacIntyre et al., 2008).

Suspended solids

Suspended solids are particles that have a diameter greater than 1 µm. They are complexes of organic materials, such as faeces, uneaten feed and mucus, bone fragments, inorganic particulate matter, such as clay and soil sediments, and microbial communities composed of micro-organisms, cellular debris, and organic polymers (Lekang, 2007; MacIntyre et al., 2008). Particles in the size range 1–100 µm are super colloidal and those that are larger than 100 µm are settleable solids. Exposure of fish to suspended solids can give gill damage, abrade the skin, induce stress, and reduce feeding (MacIntyre et al., 2008). Chronic exposure to low levels of suspended solids, in the form of waste feed and faeces, gave rise to gill irritation and precipitated an outbreak of bacterial gill disease in juvenile Arctic charr (Siikavuopio et al., 2009b). According to Johnston (2002), suspended solids from waste feed and faeces should not exceed 15 mg l^{-1} over the background present in the inflow water, and there is a general recommendation that total suspended solids in rearing units for salmonids should be kept below 25 mg l^{-1} if possible (MacIntyre et al., 2008).

Water currents

Sustained exercise invoked by inducing the fish to swim against a current, results in improved growth of Arctic charr (Table 2) (Christiansen & Jobling, 1990; Christiansen et al., 1992; Jobling, 1995). The reasons for the growth improvement are probably complex and multifactorial. One hypothesis is that active swimming induces muscle hypertrophy and protein synthesis at the expense of fat deposition, which results in increased weight gain. A second possibility is that the increased growth is the result of a decrease in aggressive behaviour. In standing water or at low current speeds, the charr swim in a disorganised manner and seem to engage in more aggressive interactions than when swimming against a current. Dominant fish attempt to hold territories, preferably nearby feeding stations. In contrast, at higher water current speeds, the fish orientate against the current and start to school. The fish are then evenly distributed and less occupied with social interactions and aggressive behaviour, and this results in less fin damage

Table 2 Manipulation of rearing conditions influences welfare, growth, and size dispersion of farmed charr (adapted from Jobling, 1995)

	Fish with bite marks (%)	Growth metric	
		Growth rate (SGR, %d^{-1})	Variation (CV, %)
Current speed			
0	77	0.50	246
6.5 cm s^{-1} (0.5 BL s^{-1})	79	0.61	115
13 cm s^{-1} (1 BL s^{-1})	51	0.85	65
19.5 cm s^{-1} (1.5 BL s^{-1})	50	0.86	63
26 cm s^{-1} (2 BL s^{-1})	14	1.44	42
Stocking density			
15 kg m^{-3}	26	0.13	401
60 kg m^{-3}	6	1.00	50
120 kg m^{-3}	13	1.07	42

Specific growth rate (SGR) = [(ln Final weight − ln Initial weight)/Time (days))] × 100

Coefficient of variation (CV) = (Standard deviation/Population mean weight) × 100

(Table 2) (Christiansen & Jobling, 1990; Jobling, 1995). The water current also helps to distribute the feed more evenly in the water column, and gives feeding opportunities to all of the fish. The consequences of this are homogeneous growth and a reduction in size dispersion (Table 2) along with improved feed utilization. As the fish prefer to hold the same position in the tank when schooling, due to their rheotactic response, the water current speed also becomes the swimming speed of the fish.

The threshold swimming speed to induce schooling seems to be between 0.5 and 1 body length per second (BL s^{-1}) and, for small, juvenile charr, growth increases up to speeds in excess of 1.75 BL s^{-1}- (Table 2) (Christiansen & Jobling, 1990; Jobling, 1995). Having circumferential water currents in tanks can, therefore, serve several purposes; self-cleaning of the tank, distribution of feed, reduction of aggression, and fin damage as a result of schooling, providing exercise for the fish and the promotion of good growth and feed utilization. Water currents are necessary for the self-cleaning of most tank systems, and circular tanks require a minimum water flow of 4–6 cm s^{-1}, which is below the threshold that gives growth and fish welfare benefits. It is not possible to create a circular water current in a net cage, but if stocked at appropriate densities the charr will form schools.

Stocking density

Stocking density may influence the behaviour of fish in a number of ways. On one hand, problems associated with the formation of social (dominance) hierarchies may be reduced as stocking density increases (Grant, 1997). On the other hand, for some species, there may be problems relating to stress, fin damage, and health when stocking density is high. Arctic charr tolerate high densities without any apparent negative effects on feed intake and growth (Jørgensen et al., 1993), and low densities should be avoided because they can lead to increased social interactions, aggression, fin damage, depressed growth, and size disparity (Table 2) (Jobling, 1995; Siikavuopio & Jobling, 1995). Arctic charr are robust with regard to high stocking densities, and growth is better than at low density when stocking densities are higher than 60 kgm^{-3} (Table 2). The upper limit is uncertain, but it seems that stocking densities of at least 150 kg m^{-3} may not be problematic (Jørgensen et al., 1993). The recommended rearing density is 60–150 kgm^{-3}(Jobling et al., 1993; Jobling, 1995; Siikavuopio & Jobling, 1995; Johnston, 2002). At these densities the charr form schools, thereby reducing aggression and agonistic behaviour, growth is improved, the proportion of fish with fin damage is reduced, and the population is more homogeneous (Table 2).

Photoperiod and light regime

The three characteristics of light that may influence the performance of fish in culture are quality, quantity, and duration. Light quality refers to the spectral characteristics of the light with respect to wavelength, light quantity is illuminance or light intensity, and light duration is the photoperiod, or the ratio of hours of light to hours of darkness during a 24-h period. It is the effects of photoperiod on fish physiology and behaviour that have been studied most, with relatively few studies covering the influences of light spectral quality and intensity (Jobling, 2010). Salmonids are generally considered to be visual feeders, locating their food by sight, but Arctic charr can feed and grow in the dark when they are given the opportunity to pluck food items from the bottom (Jørgensen & Jobling, 1990). Feeding in darkness may have an additional advantage in that the negative effects of rearing at low stocking densities can be mitigated or even eliminated (Jørgensen & Jobling, 1993).

Photoperiod is known to influence several physiological and behavioural responses that are of interest when farming fish (Jobling, 1994, 2010). For example, the manipulation of photoperiod may be used to influence the timing of parr-smolt transformation in salmonids. Thermal and photoperiod manipulations (photo-thermal manipulations) are often used in combination to induce the fish to undergo parr-smolt transformation much earlier than would be the case in the wild (McCormick, 2013). Photo-thermal manipulation may also be used to influence the reproductive cycle, to accelerate or delay the timing of oocyte growth and egg production. Exposure of fish to continuous or extended periods of light has been used to delay the onset of puberty to ensure that the fish reach market size before they become sexually mature (Taranger et al., 2010). It is of particular interest that increased growth is often observed when fish are exposed to long days, i.e. continuous or extended periods of light. Extended photoperiods may promote feeding and growth via stimulation of the hypothalamic-pituitary axis leading to increased production and secretion of growth hormone and induction of an anabolic state.

In the wild, Arctic charr experience considerable seasonal changes in photoperiod as a result of living at high latitudes and the charr seems well-adapted to exploit the associated changes in resource availability (Johnson, 1980; Jørgensen & Johnsen, 2014). Changes in photoperiod are known to influence feeding, growth, salinity tolerance, sexual maturation, and the reproductive cycle of Arctic charr held in captivity (Mortensen & Damsgård, 1993; Tveiten et al., 1996; Damsgård et al., 1999; Johnsen et al., 2000; Frantzen et al., 2004; Knudsen et al., 2015). Several of these seasonal changes in biological responses probably involve the entrainment of endogenous circannual rhythms by the prevailing photoperiod, possibly using patterns of melatonin secreted from the pineal gland as an important hormonal mediator (Jørgensen & Johnsen, 2014). For example, Sæther et al. (1996) presented evidence that temporal changes in food intake and growth of Arctic charr held in captivity are probably driven by endogenous rhythms, because seasonal cycles persisted when the fish were exposed to a combination of constant photoperiod (12L:12D) and temperature (4°C).

In general, food intake and growth of Arctic charr increase during early summer under conditions of increasing day length, i.e. during the transition from a short photoperiod to a long photoperiod, and are highest in summer (Tveiten et al., 1996; Damsgård et al., 1999; Johnston, 2002; Knudsen et al., 2015). It is a change from short to long photoperiod that seems to trigger the increase in feeding and growth, rather than exposure to more hours of daylight *per se*. For example, Mortensen & Damsgård (1993) demonstrated that juvenile Arctic charr cultivated under constant short- or long-day conditions grew at comparable rates, while growth rates of fish that experienced short-day conditions followed by long-day conditions were significantly higher. Enhanced growth, relative to fish held under a continuous light regime (24L:0D), was observed in Arctic charr that were exposed to 6-week periods of short days (8L:16D) during either the autumn or winter and then returned to a 24L:0D photoperiod (Gunnarsson et al., 2012, 2014). Maturation rates were little affected by the short photoperiod treatments, indicating that application of a short photoperiod (8L:18D) over a limited time (6 weeks) might be incorporated into a production cycle to promote growth without inducing increased rates of sexual maturation.

Handling, transport, and harvesting

Fish are handled when they are moved within the farm during the production cycle, for example from one tank or cage to another. At harvest, the fish are moved from the farm to the slaughterhouse, and this can often involve transport over quite long distances by road transport or air freight, or in well boats (Lekang, 2007;

Table 3 Some problems experienced in charr farming and possible remediation measures

Environmental and rearing factors	Mitigation or remedial measure
Water quality e.g. oxygen, ammonia, nitrite, pH, suspended solids	Water treatment (Oxygenation, Bio-filtration, Disinfection) Water exchange rates
Interactions with conspecifics	Tank design, colour, and water flow characteristics
	Adjustment of stocking densities
	Feeding routines
Attack by predators	Preventive measures, e.g. protective nets, scaring devices
Diseases, pathogens, and parasites	Water treatment; filtration and disinfection (UV, Ozone)
	Good fish welfare, e.g. stocking densities, feeding routines
	Nutritionally balanced, high-quality, formulated feeds
	Vaccination
Handling and transport	Sedation
	Appropriate water quality, e.g. dilute saline, pH, oxygen
Harvest and slaughter	Minimum crowding and handling times
	Minimize transport times
	Effective stunning and exsanguination methods

Robb, 2008; Harmon, 2009). Intensively farmed salmonids, including Arctic charr, may therefore be subjected to a number of procedures that are potentially stressful and can give rise to animal welfare issues. The discussion that follows provides a brief general overview of these procedures and problems that may arise.

Handling and internal transport of fish within the farm may relate to regulation of stocking density, size grading and sorting, weight sampling, and vaccination (Lekang, 2007; Harmon, 2009).This will almost inevitably involve crowding the fish into a restricted volume of water, followed by netting and transfer to a transport tank, or by pumping the fish from one rearing unit to another. Crowding may lead to the damage or death of some fish due to insufficient dissolved oxygen as a result of high levels of activity being displayed by fish that have been crowded into too small a volume. If nets are used, increased activity by crowded fish may result in skin abrasions and scale loss, eye and snout damage and bruising (Lines & Spence, 2012).

Harvesting involves fasting the fish to empty the gut, crowding and capture, transport to the slaughterhouse and finally stunning and killing (Robb, 2008; Lines & Spence, 2012). Fasting lowers the metabolic rate, reduces oxygen consumption, and reduces the rate at which ammonia and carbon dioxide build up in the water. Fasting also ensures that the fish have an empty gut, and this prevents the accumulation of faeces in tanks during transport, and eliminates the risk of faecal contamination during processing; contamination of the processed fish with faecal matter can result in reduced shelf life. Crowding is usually a prerequisite in harvesting. For fish grown in net cages, this is achieved by slowly lifting part of the cage or by inserting a second net into the water. In ponds, raceways, and tanks, it is achieved using a seine net to encircle the fish or by introducing moving partitions or grids into the rearing unit. Once crowded, the fish are moved by pumping or brailing. When pumping distances are long hazards can arise as a result of poor water quality or overcrowding (Lekang, 2007; Robb, 2008; Lines & Spence, 2012). Fish are then transported from the farm to the slaughterhouse, and it is difficult to transport fish without imposing significant stress on them (Harmon, 2009).

Once at the slaughterhouse, the fish are stunned and killed. Large numbers of fish are often killed in a short period, and this requires special considerations. Previously it was common practice to kill fish by asphyxiation in air or in ice slurry. To deprive fish of oxygen as a method of slaughter is neither efficient nor humane. Similarly, the beheading or bleeding of the fish while still conscious is not humane. Immersion in water infused with carbon dioxide is a well-established method for killing fish, but the slow onset of insensibility and behavioural indications of distress have resulted in this method of killing being prohibited in some countries. Percussive stunning results in rapid and permanent insensibility if the blow is strong enough and is correctly applied. Similarly, electrical stunning can result in rapid, prolonged insensibility if the correct electrical parameters are used and they are applied in a manner that avoids pre-stun shocks. Electrical stunning can be carried out both in water (wet stunning) and out of water (dry stunning).

What is clear is that fish are subject to negative influences, and may become stressed, at each stage of the harvesting process; crowding, transport, stunning, and killing. Improved techniques need to be developed to avoid as many of the stressors as possible, and these need to be incorporated into industry guidelines and codes of practice (Robb, 2008; Harmon, 2009; Lines & Spence, 2012).

Conclusions

The purpose of this review has been to give an overview of the water quality requirements (e.g. oxygen, carbon dioxide, ammonia, and nitrite) and other important abiotic and biotic factors (e.g. temperature, water currents, stocking density) that affect aquaculture production of Arctic charr. Knowledge about threshold limits for dissolved gases and some other water quality parameters is scarce and needs further investigation. By comparison, knowledge about thermal requirements and biotic factors that influence production of Arctic charr is better. Commercial producers of Arctic charr may experience problems at all stages of the rearing process; there is knowledge about remediation and mitigation measures that can be applied to solve some of these problems (Table 3), but many challenges remain. In addition, there is a need to develop clear guidelines and codes of practice to cover the entire production cycle, including all aspects of the harvesting process.

References

Árnason, T., S. Gunnarsson, A. K. Imsland, H. Thorarensen, H. Smáradóttir, A. Steinarsson, A. Gústavsson, M. Johansson & B. T. Björnsson, 2014. Long-term rearing of Arctic charr *Salvelinus alpinus* under different salinity regimes at constant temperature. Journal of Fish Biology 85: 1145–1162.

Arnesen, A. M., E. H. Jørgensen & M. Jobling, 1993a. Feed intake, growth and osmoregulation in Arctic charr, *Salvelinus alpinus* (L.), following abrupt transfer from freshwater to more saline water. Aquaculture 114: 327–338.

Arnesen, A. M., E. H. Jørgensen & M. Jobling, 1993b. Feed intake, growth and osmoregulation in Arctic charr, *Salvelinus alpinus* (L.), transferred from freshwater to saltwater at 8°C during summer and winter. Fish Physiology and Biochemistry 12: 281–292.

Arnesen, A. M., E. H. Jørgensen & M. Jobling, 1994. Feed-growth relationships of Arctic charr transferred from freshwater to saltwater at different seasons. Aquaculture International 2: 114–122.

Branson, E. J., 2008. Fish Welfare. Blackwell Publishing, Oxford.

Brännäs, E. & B. S. Wiklund, 1992. Low temperature growth potential of Arctic charr and rainbow trout. Nordic Journal of Freshwater Research 67: 77–81.

Christiansen, J. S. & M. Jobling, 1990. The behaviour and the relationship between food intake and growth of juvenile Arctic charr, *Salvelinus alpinus* L., subjected to sustained exercise. Canadian Journal of Zoology 68: 2184–2191.

Christiansen, J. S., E. H. Jørgensen & M. Jobling, 1991. Oxygen consumption in relation to sustained exercise and social stress in Arctic charr (*Salvelinus alpinus* L.). Journal of Experimental Zoology 260: 149–156.

Christiansen, J. S., Y. S. Svendsen & M. Jobling, 1992. The combined effects of stocking density and sustained exercise on the behaviour, food intake and growth of juvenile Arctic charr (*Salvelinus alpinus* L.). Canadian Journal of Zoology 70: 115–122.

Colt, J., 2006. Water quality requirements for reuse systems. Aquacultural Engineering 34: 143–156.

Colt, J., B. Watten & M. Rust, 2009. Modeling carbon dioxide, pH, and un-ionized ammonia relationships in serial reuse systems. Aquacultural Engineering 40: 28–44.

Damsgård, B., A. M. Arnesen & M. Jobling, 1999. Seasonal patterns of feed intake and growth of Hammerfest and Svalbard Arctic charr maturing at different ages. Aquaculture 171: 149–160.

Didlecadet, D., F. Dufresne, N. R. Le Francois & P. U. Blier, 2006. Applying microsatellites in two commercial strains of Arctic charr (*Salvelinus alpinus*): potential for a selective breeding program. Aquaculture 257: 37–43.

Delabbio, J. L., B. D. Glebe & A. Sreedharan, 1990. Variation in growth and survival between two anadromous strains of Canadian Arctic charr (*Salvelinus alpinus*) during long-term saltwater rearing. Aquaculture 85: 259–270.

Duston, J., T. Astatkie & S. B. Murray, 2007. Effect of salinity at constant 10°C on grow-out of anadromous Arctic charr from Labrador. Aquaculture 273: 679–686.

Eliassen, R. A., H. K. Johnsen, I. Mayer & M. Jobling, 1998. Contrasts in osmoregulatory capacity of two Arctic charr, *Salvelinus alpinus* (L.), strains from northern Norway. Aquaculture 168: 255–269.

Elliott, J. M. & J. A. Elliott, 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. Journal of Fish Biology 77: 1793–1817.

Eriksson, L.-O., A. Alanärä, J. Nilsson & E. Brännäs, 2010. The Arctic charr story: development of subarctic freshwater fish farming in Sweden. Hydrobiologia 650: 265–274.

Frantzen, M., A. M. Arnesen, B. Damsgård, H. Tveiten & H. K. Johnsen, 2004. Effects of photoperiod on sex steroids and gonad maturation in Arctic charr. Aquaculture 240: 561–574.

Gillet, C., 1991. Egg production in an Arctic charr (*Salvelinus alpinus* L.) brood stock: effects of temperature on the timing of spawning and the quality of eggs. Aquatic Living Resources 4: 109–116.

Gillet, C., B. Breton, T. Mikolajczyk, P. Bodinier & A. Fostier, 2011. Disruption of the secretion and action of 17, 20β-dihydroxy-4-pregnen-3-one in response to a rise in temperature in Arctic charr, *Salvelinus alpinus.* Consequences on oocyte maturation and ovulation. General and Comparative Endocrinology 172: 392–399.

Grant, J. W. A., 1997. Territoriality. In Godin, J.-G. J. (ed), Behavioural Ecology of Teleost Fishes. Oxford University Press, Oxford: 81–103.

Gunnarsson, S., A. K. Imsland, S. I. Siikavuopio, J. Árnason, A. Gústavsson & H. Thorarensen, 2012. Enhanced growth of farmed Arctic charr (*Salvelinus alpinus*) following a short-day photoperiod. Aquaculture 350–353: 75–81.

Gunnarsson, S., M. Johansson, A. Gústavsson, T. Árnason, A. Árnason, H. Smáradóttir, B. T. Björnsson, H. Thorarensen & A. K. Imsland, 2014. Effects of short-day treatment on long-term growth performance and maturation of farmed Arctic charr *Salvelinus alpinus* reared in brackish water. Journal of Fish Biology 85: 1211–1226.

Hammer, J., 1984. Ecological characters of different combinations of sympatric populations of Arctic charr in Sweden. In Johnson, L. & B. L. Burns (eds), Biology of the Arctic charr. Proceedings of the International Symposium on Arctic charr, Winnipeg, Manitoba, May 1981. University of Manitoba Press, Winnipeg: 35–63.

Hammar, J., 2014. Natural resilience in Arctic charr, *Salvelinus alpinus*: life history, spatial and dietary alterations along gradients of interspecific interactions. Journal of Fish Biology 85: 81–118.

Harmon, T. S., 2009. Methods for reducing stressors and maintaining water quality associated with live fish transport in tanks: a review of the basics. Reviews in Aquaculture 1: 58–66.

Janhunen, M., J. Piironen & N. Peuhkuri, 2010. Parental effects on embryonic viability and growth in Arctic charr *Salvelinus alpinus* at two incubation temperatures. Journal of Fish Biology 76: 2558–2570.

Jensen, F. B., 2003. Nitrite disrupts multiple physiological functions in aquatic animals. Comparative Physiology and Biochemistry 135A: 9–24.

Jeuthe, H., E. Brännäs & J. Nilsson, 2013. Effects of egg size, maternal age and temperature on egg viability of farmed Arctic charr. Aquaculture 408: 70–77.

Jeuthe, H., E. Brännäs & J. Nilsson, 2015. Thermal stress in Arctic charr *Salvelinus alpinus* broodstock: a 28 year case study. Journal of Fish Biology 86: 1139–1152.

Jobling, M., 1994. Fish Bioenergetics. Chapman & Hall, London.

Jobling, M., 1995. Feeding of charr in relation to aquaculture. Nordic Journal of Freshwater Research 71: 102–112.

Jobling, M., 2010. Fish culture: the rearing environment. In Le François, N. R., M. Jobling, C. Carter & P. Blier (eds), Finfish Aquaculture Diversification. CABI, Wallingford: 33–60.

Jobling, M., E. J. Jørgensen, A. M. Arnesen & E. Ringø, 1993. Feeding, growth, and environmental requirements of Arctic charr: a review of aquaculture potential. Aquaculture International 1: 20–46.

Jobling, M., H. K. Johnsen, G. W. Pettersen & R. J. Henderson, 1995. Effect of temperature on reproductive development in Arctic charr, *Salvelinus alpinus* (L.). Journal of Thermal Biology 20: 157–165.

Jobling, M., H. Tveiten & B. Hatlen, 1998. Cultivation of Arctic charr: an update. Aquaculture International 6: 181–196.

Jobling, M., A. M. Arnesen, T. Benfey, C. Carter, R. Hardy, N. R. Le François, R. O'Keefe, J. Koskela & S. G. Lamarre, 2010. The Salmonids (Family: Salmonidae). In Le François, N. R., M. Jobling, C. Carter & P. Blier (eds), Finfish Aquaculture Diversification. CABI, Wallingford: 234–289.

Johnsen, H. K., R. A. Eliassen, B.-S. Sæther & J. S. Larsen, 2000. Effects of photoperiod manipulation on development of seawater tolerance in Arctic charr. Aquaculture 189: 177–188.

Johnson, L., 1980. The Arctic charr, *Salvelinus alpinus*. In Balon, E. K. (ed), Charrs, Salmonid Fishes of the Genus Salvelinus. W. Junk, The Hague: 15–98.

Johnston, G., 2002. Arctic charr aquaculture. Fishing News Books, Oxford.

Jonsson, B. & N. Jonsson, 2001. Polymorphism and speciation in Arctic charr. Journal of Fish Biology 58: 605–638.

Jørgensen, E. H. & M. Jobling, 1990. Feeding modes in Arctic charr, *Salvelinus alpinus* L: the importance of bottom feeding for the maintenance of growth. Aquaculture 86: 379–385.

Jørgensen, E. H. & M. Jobling, 1993. Feeding in darkness eliminates density-dependent growth suppression in Arctic charr. Aquaculture International 1: 90–93.

Jørgensen, E. H., J. S. Christiansen & M. Jobling, 1993. Effects of stocking density on food intake, growth performance and oxygen consumption in Arctic charr (*Salvelinus alpinus*). Aquaculture 110: 191–204.

Jørgensen, E. J. & H. K. Johnsen, 2014. Rhythmic life of the Arctic charr: adapted to life at the edge. Marine Genomics 14: 71–81.

Klemetsen, A., 2013. The most variable vertebrate on earth. Journal of Ichthyology 53: 781–791.

Klemetsen, A., P.-A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connel & E. Mortensen, 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12: 1–59.

Knudsen, R., H. Johnsen, B.-S. Sæther & S. I. Siikavuopio, 2015. Divergent growth patterns between juveniles of two sympatric Arctic charr morphs with contrasting depth gradient niche preferences. Aquatic Ecology 49: 33–42.

Larsson, S., 2005. Thermal preference of Arctic charr, Salvelinus alpinus, and brown trout, Salmo trutta, implications for their niche segregation. Environmental Biology of Fishes 73: 89–96.

Lekang, O.-I., 2007. Aquaculture Engineering. Blackwell Publishing, Oxford.

Lines, J. A. & J. Spence, 2012. Safeguarding the welfare of farmed fish at harvest. Fish Physiology and Biochemistry 38: 153–162.

Lyttikäinen, T., J. Koskela & I. Rissanen, 1997a. Thermal resistance and upper lethal temperatures of underyearling Lake Inari Arctic charr. Journal of Fish Biology 51: 515–525.

Lyttikäinen, T., J. Koskela & I. Rissanen, 1997b. The influence of temperature on growth and proximate body composition of underyearling Lake Inari arctic charr (*Salvelinus alpinus* (L.)). Journal of Applied Ichthyology 13: 191–194.

MacIntyre, C. M., T. Ellis, B. P. North & J. F. Turnbull, 2008. The influences of water quality on the welfare of farmed rainbow trout. In Branson, E. J. (ed), Fish welfare. Blackwell Publishing, Oxford: 150–184.

McCormick, S. D., 2013. Smolt physiology and endocrinology. In Farrell, A. P. & C. J. Brauner (eds), Euryhaline fishes. Academic Press, New York: 199–244.

Mortensen, A. & B. Damsgård, 1993. Compensatory growth and weight segregation following light and temperature manipulation of juvenile Atlantic salmon (*Salmo salar* L.) and Arctic charr (*Salvelinus alpinus* L.). Aquaculture 114: 261–272.

Nilsson, J., E. Brännäs & L.-O. Eriksson, 2010. The Swedish Arctic charr breeding programme. Hydrobiologia 650: 275–282.

Ojima, D., R. J. Pettersen, J. Wolkers, H. K. Johnsen & E. H. Jørgensen, 2009. Growth hormone and cortisol treatment stimulate seawater tolerance in both anadromous and landlocked Arctic charr. Comparative Biochemistry and Physiology 53A: 378–385.

Rikardsen, A. H., J. E. Thorpe & J. B. Dempson, 2004. Modelling the life-history variation of Arctic charr. Ecology of Freshwater Fish 13: 305–311.

Robb, D. H. F., 2008. Welfare of fish at harvest. In Branson, E. J. (ed.), Fish welfare. Blackwell Publishing, Oxford: 217–242.

Siikavuopio, S. I. & M. Jobling, 1995. The effects of stocking density on survival and growth of wild-caught Arctic charr. Nordic Journal of Freshwater Research 71: 419–423.

Siikavuopio, S. I., R. Knudsen, A. Winger & R. Kristoffersen, 2009a. Is winter period a severe bottleneck of anadromous riverine Arctic charr parr? Ecology of Freshwater Fish 18: 126–131.

Siikavuopio, S. I., S. Skybakmoen & B.-S. Sæther, 2009b. Comparative growth study of wild- and hatchery produced Arctic charr (*Salvelinus alpinus* L.)in a cold-water recirculation system. Aquacultural Engineering 41: 122–126.

Siikavuopio, S. I., R. Knudsen & P. A. Amundsen, 2010. Growth and mortality of Arctic charr and European whitefish reared at low temperature. Hydrobiologia 650: 255–263.

Siikavuopio, S. I., A. Foss, B.-S. Sæther, S. Gunnarsson & A. K. Imsland, 2013. Comparison of the growth performance of offspring from cultured versus wild populations of Arctic charr, *Salvelinus alpinus* (L.), kept at three different temperatures. Aquaculture Research 44: 995–1001.

Siikavuopio, S. I., B.-S. Sæther, H. Johnsen, T. Evensen & R. Knudsen, 2014. Temperature preference of juvenile Arctic charr originating from different thermal environments. Aquatic Ecology 48: 313–320.

Skybakmoen, S., S. I. Siikavuopio & B.-S. Sæther, 2009. Coldwater RAS in an Arctic charr farm in Northern Norway. Aquacultural Engineering 41: 114–121.

Staurnes, M., T. Sigholt, G. Lysfjord & O. A. Gulseth, 1992. Difference in seawater tolerance of anadromous and landlocked populations of Arctic charr (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences 49: 443–447.

Summerfelt, S. T., B. J. Vinci & R. H. Piedrahita, 2000. Oxygenation and carbon dioxide control in water reuse systems. Aquacultural Engineering 22: 87–108.

Sæther, B.-S., H. K. Johnsen & M. Jobling, 1996. Seasonal changes in food consumption and growth of Arctic charr exposed to either simulated natural or a 12:12 LD photoperiod at constant water temperatures. Journal of Fish Biology 48: 1113–1122.

Sæther, B.-S., S. I. Siikavuopio, H. Thorarensen & E. Brännäs, 2013. Status of Arctic charr (*Salvelinus alpinus*) farming in Norway, Sweden and Iceland. Journal of Ichthyology 53: 833–839.

Taranger, G. L., M. Carrillo, R. W. Schulz, P. Fontaine, S. Zanuy, A. Felip, F.-A. Weltzien, S. Dufour, Ø. Karlsen, B. Norberg, E. Andersson & T. Hansen, 2010. Control of puberty in farmed fish. General and Comparative Endocrinology 165: 483–515.

Thyrel, M., I. Berglund, S. Larsson & I. Näslund, 1999. Upper thermal limits for feeding and growth of Arctic charr. Journal of Fish Biology 55: 199–210.

Tveiten, H., H. Johnsen & M. Jobling, 1996. Influence of maturity status on the annual cycles of feeding and growth in Arctic charr reared at constant temperature. Journal of Fish Biology 48: 910–924.