MASTER THESIS

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Effects of swimming speed on growth and flesh quality of adult Atlantic salmon (*Salmo salar*) in closed cages

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Abstract

This study investigated how swimming speed may influence the growth performance and flesh quality characteristics of farmed adult Atlantic salmon (*Salmo salar*) in closed cages. Fish (889 g, 41.6 cm) were exposed to water currents corresponding to initial swimming speeds of approximately 0.2 (LOW) and 0.6 BL s^{-1} (HIGH) for five months. Fish in the HIGH group had significantly higher final round weight compared to the LOW group, but no differences on fork length and specific growth rate (SGR) between treatments were found. Fish in the HIGH group also had higher condition factor (CF), relative ventricular mass (RVM), fillet yield than that in the LOW group. However, flesh texture measured instrumentally as maximum shear force and total shear work did not differ between treatments after exposing to water currents for eleven weeks. Other flesh quality characteristics including flesh colour, gaping, water content, lipid content and protein content were not affected by swimming speed as well. In conclusion, higher swimming speed can be used to improve growth performance without compromising flesh quality of farmed adult Atlantic salmon in closed cages.

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1 Introduction

1.1 World aquaculture

Aquaculture refers to the breeding, rearing, and harvesting of plants and animals in all types of water environments (NOAA, n.d.). Global aquaculture production has grown steadily since 1970s. According to the current available statistics from FAO, world aquaculture production reached another high of 90.4 million tonnes (live weight equivalent) in 2012, consisting of 66.6 million tonnes of food fish and 23.8 million tonnes of aquatic algae (FAO, 2014). The world food fish aquaculture production more than doubled from 32.4 to 66.6 million tonnes in the period of 2000 to 2012 (FAO, 2014). 15 aquaculture leading countries produced more than 90% of all farmed food fish in 2012. China is the largest aquaculture production country, accounting for more than 60% of world farmed food fish production in 2012 (FAO, 2014).

The world population is expected to grow by another 2 billion by 2050, with most of the population growth occurring in developing regions. World per capita apparent fish consumption has reached 19.2 kg in 2012, which is almost twice than that in 1960s (9.9kg) (FAO, 2014). Ensuring adequate food and nutrition security to this growing population and growing need are big challenges for meat products. Fish has high potential to meet the meat requirement since they are more efficient in using the feed and processing energy than chicken, cow and pig. Fish is well known by its high quality protein, various vitamins and minerals (Sikorski et al., 1995). Farmed marine fish like Atlantic salmon (*Salmo salar*), is rich in the long chain omega-3 fatty acids, such as DHA and EPA. Consumption of long chain omega-3 fatty acids are beneficial for health and the development of brain (Ruxton et al., 2004). Therefore, aquaculture remains as the best option to meet the increasing demands of meat.

1.2 Atlantic salmon aquaculture

1.2.1 Status

The Atlantic salmon (*Salmo salar*) belongs to the family Salmonidae, is naturally found in the northern Atlantic Ocean and the rivers that flow into the north Atlantic (Shearer, 1992). Atlantic salmon is an anadromous fish that migrates out to the sea after two to five years in a river and then migrates back to its native river to spawn after two to four years in the sea.

Atlantic salmon farming started in the late 1960s in Norway. Global aquaculture production for Atlantic salmon is more than two million tonnes in 2014, predominantly from aquaculture in Norway, Chile, Canada and UK (FAO, 2016). Norway has the largest Atlantic salmon aquaculture production, with 1.26 million tonnes (5.07 billion USD) in 2014 (data from Norwegian Directorate of Fisheries) (NDF, 2014). However, it seems that Norwegian Atlantic salmon aquaculture is facing a challenge of keeping the increase trend (Fig. 1).

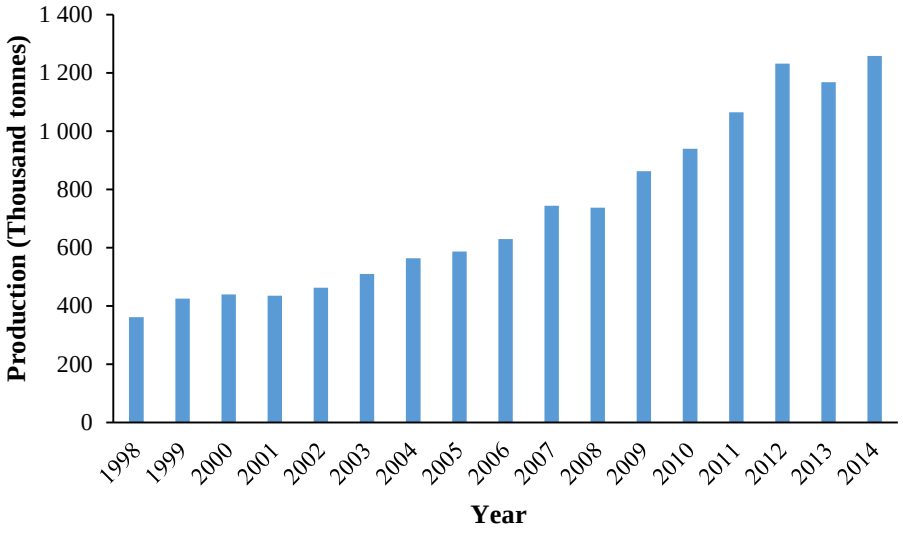

Fig. 1. Production (Sales of slaughtered fish in thousand tonnes round weight) of farmed Atlantic salmon in Norway from 1998 to 2014. Based on data from Norwegian Directorate of Fisheries (NDF, 2014)**.**

1.2.2 Traditional open cage systems

Traditional open cage systems, which are normally located in fjords, bays and open sea, are the most used Atlantic salmon aquaculture systems to date. These systems take advantage of the natural resources such as water and light from the ocean without occupying too much land space. Major components in traditional open cage systems include: 1) Net bag with weights in the bottom to spread the bag 2) A jumping net above the surface fixed to the net bag to prevent fish from escaping 3) Bird net is used to prevent birds from coming into the production unit 4) Floating collar for spreading out the net bag and giving buoyancy to keep the bag in the correct position in the water column 5) Mooring system (Lekang, 2007).

There are three main problems for Atlantic salmon aquaculture in open cage systems currently (Bergheim, 2012). The most common problem is sea lice infection due to the costly treatment, reduced growth, increased feed wastage and reduced market quality of the final product. Sea lice treatments include bath treatment with different medicinal compounds (such as hydrogen peroxide and deltamethrin) and in-feed treatment (emamectin benzoate) (Aaen et al., 2015). Moreover, the use of "cleaner fish" such as lumpfish (*Cyclopterus lumpus*) (Imsland et al., 2014) and wrasse (Leclercq et al., 2014) has become feasible and efficient alternatives to aid in the control of sea lice. Effort has been put to develop vaccines against the salmon sea lice, but effective vaccines haven't been developed yet. The second problem is escaped farmed fish, which would affect wild population through competition, disease and genetic interactions. The third problem is the footprint on the environment (pollution). Elevated discharges of nutrients, excess feed and waste to the marine environment are big concern about open cage aquaculture systems (Mente et al., 2006).

1.2.3 Closed cage systems

Closed cage systems are new technologies that attempt to create restrict interactions between

farmed fish and the external aquatic environment (Thorarensen and Farrell, 2011). The closed cage systems increase the control of water entering and leaving the bag. The largest advantage is that the systems can prevent sea lice infection by pumping water from deeper depth. In addition, it is possible to reduce environmental pollution by pumping and controlling the waste from the system. So far, there are no technology on waste treatment, but there are plans and development ongoing on this topic. Furthermore, the closed cage systems have a high efficiency in preventing fish from escaping.

Open sea cage systems are exposed to the natural water current, closed cage systems have the water enclosed, and it is therefore possible to control the water current within the unit. However, there is limited knowledge on welfare and flesh quality issues from fish subjected to long time exercise in closed cage systems. How the fish react and perform at different water speed are vital factors on deciding the optimal water speed in closed cage systems. Therefore, documentation on what is the optimal water speed for closed cage systems is important before such systems are commercialized.

1.3 Fish muscle structure

Fish striated muscle makes up the fillet, which is the most destined part for most food products. Striated muscle is the largest organ in most of the fish species, contributing approximately 60% of the total body mass (Sänger and Stoiber, 2001). Unlike the mammals which also use the muscle to support the skeletal, fish only use the muscle for movement and as energy storage during periods of food deprivation (Love, 1988).

The myotomal muscle is composed of repeated segment called myotome, which is separated by sheets called myocommata. Myotome is consisted of relatively short lateral muscle fibres. There are mainly two types of muscle fibres in fish muscle, including red (slow) muscle fibres and white (fast) muscle fibres. White muscle fibres are the major part of striated muscle (never

less than 70% of the striated muscle). White muscle fibres have big fibre diameter up to 300 μm, while the diameter of the red fibres is only about 20-50% of that of the white fibres (25-45 μm) (Sänger and Stoiber, 2001). White muscle fibres use anaerobic energy metabolism, while red muscle fibres use aerobic metabolism (Luther et al., 1995). Generally, white muscle is used at high swimming speeds and red muscle is mainly used for sustained energy efficient swimming. The majority of the myotomal muscle occupied by white fibres, which are covered by a thin layer of red muscle fibres. Many species also have a layer of pink intermediate muscle fibres in between white and red muscle fibre compartments (Sänger and Stoiber, 2001). The proportion of red and white fibres is related to the swimming mode and activity level of the fish species (Videler, 1993). Active fish species have higher proportion of red muscle, compare to bentic fish that spend most of their time lying on the bottom. And the proportion of red muscle fibres varies at different position along the body axis of the fish, with the highest percent of red muscle fibres towards tail in most fish species (Videler, 1993).

1.4 Flesh quality and influencing parameters

1.4.1 Texture

Flesh texture is a multi-faced parameter dealing with sensory interpretation of a fish products (Coppes et al., 2002). Textural parameters are frequently used to evaluate fish quality and give an assessment on the shelf life of fish products. Firmness is an essential parameter of fish textural quality that is associated with the human visible acceptability of fish products (Veland and Torrissen, 1999). Firmer fillets are more desirable for consumers (Haard, 1992). Fillet with insufficient firmness can cause downgrading and might not be suited for further industrial processing, resulting in a large economic loss. Study shows this index is largely correlated with the structure of connective tissue and the density of muscle fiber (Johnston et al., 2000).

Collagen is a significant compound in the connective tissue of fresh fish muscle. In fish muscle,

3% to 10% of the muscle protein is collagen, which plays an essential role in maintaining fillet integrity and muscle cohesiveness (Sikorski et al., 1984). A histological study showed that the disintegration of thin collagen fibrils is the reason for fish flesh rapidly soften (Ando et al., 1992). The hydroxylysyl pyridinoline (PYD) is a mature intermolecular cross-link between collagen fibres that contribute to the structure and rigidity of the collagen. Some studies has showed a mature PYD is the most important parameter that affect fish texture (Li et al., 2005; Hagen et al., 2007).

Endogenous enzyme, is a primary factor that cause the biochemical change and quality loss of fish muscle. Post-mortem fish generally have a soft texture, resulting from proteolysis by endogenous proteases (Sriket, 2014). External factors like stress and cold storage have potentially a large impact on enzyme activity and rigor mortis onset, therefor affecting the fish textural quality (Sigholt et al., 1997).

Different texture measurements based on various parameters are carried out to examine the fish flesh quality (Cheng et al., 2014). For consumers, quality index method (QIM) has been implemented in several countries. For industries, “finger method” which mainly indicate the firmness has been used widely to evaluate the texture of fish fillet. For scientific research, different instrumental texture analyses are used to reduce the variation in results from sensory analysis.

1.4.2 Proximate composition

Fish muscle generally consists of approximately 18% protein, about 80% water plus lipid and about 2% other nutrients (carbohydrate, minerals and vitamins).

Fish can be divided into four classes according to their fat content: lean (<2%), low fat (2-4%), medium fat (4-8%) and high fat (>8%) fish species. Marine fish contains high amount of omega-

3 fatty acid including eicosapentaenoic acid (20:5 n-3, EPA) and docosahexaenoic acid (22:6 n-3, DHA), which can help to prevent some diseases (Ashton, 2002; Ruxton et al., 2004). Lipid content can vary according to seasons (Hamre et al., 2003), dietary lipid content (Nanton et al., 2003) and the position within the fillet (Sigurgisladottir et al., 1997). The oxidation of polyunsaturated fatty acid (PUFA) causes the development of off-flavors and aromas by producing volatile lipid oxidation products like aldehydes, alkanes, alkenes, alcohols and organic acids, causing the unpleasant taste and odor. Compared to mammals that rarely have two or more double bounds per fatty acid, fish contains many fatty acids with five or six double bounds, which are more subjected to oxidation (Ashton, 2002).

Proteins are important elements for fish meat quality, regarding to its nutritional value and effects on the sensory properties of fish products. In the fish muscle, the crude protein content is usually in the broad range 11-24% wet weight (Sikorski et al., 1995). Muscle proteins can be divided into three groups (Sikorski et al., 1995). The sarcoplasmic proteins, act as enzymes and oxygen carriers, are normally found in the cell plasma. They will comprise 18-20% of total muscle protein. The myofibrillar proteins give the muscle its fibre-like structure and muscular activity, comprising 65-80% of total protein. The stroma proteins are those making up the connective tissue, surrounding the muscle fibres, comprising about 3-5% of the total protein.

The water content in fish has an important impact on the fish quality, especially for parameters such as dryness and juiciness. Therefore, water content within the fish muscle can have impact on the commercial value and consumer acceptance. The water holding capacity of foods can be defined as the ability to hold its own and added water during the application of forces, pressing, centrifugation or heating. Water binding capacity in fish plays an important role by preventing water from being released from the structure (Zayas, 1997).

1.4.3 Gaping

Fillet gaping happens when the connective tissue fails to hold the muscle segment against the forces pulling the muscle apart (Lavety et al., 1988). Fillet gaping is one of the most important quality issues in Atlantic salmon industry because the unattractive appearance will reduce the final product value (Michie, 2001). The mechanisms behind gaping are still not fully understood, but PYD cross-link concentration has been showed having effects on filleting gaping, as the formation of PYD cross-links increases the strength of the collagen fibres (Hagen and Johnsen, 2016).

Post-mortem processing has a big influence on fillet gaping in Atlantic salmon. Storage temperature that causes fast and strong rigor mortis would increase the risk towards gaping (Lavety et al., 1988). Pre-rigor filleting results in less gaping compared to post-rigor filleting in Atlantic salmon (Skjervold et al., 2001). The fillets were more susceptible to gaping following the rough handling at slaughter, which is known to cause changes of muscle pH (Robb et al., 2000).

Fasting and manipulating feeding regimes and diet are possible strategies to reduce fillet gaping. A study carried out by Hagen and Solberg (2010) has showed fasted Atlantic cod (*Gadus morhua*) performs better texture quality over the fed counterpart. High-fat diet can result in wider myosepta on the fillets and restricted diet can lead to less gaping (Refstie et al., 2001; Johnsen et al., 2013).

1.4.4 Colour

The customers often rely heavily on visual appearance of the products, colour especially, due to the limited opportunity to evaluate the products. In salmonids, flesh colour plays an important role on the price and consumer acceptance of the products. The orange-red colour of farmed

Atlantic salmon is caused by the deposition of the carotenoids in the muscle, with astaxanthin proven to be the most efficient for pigmentation of muscle. It was suggested that carotenoid pigments seem to have other functions than just as a source for colour. For example, astaxanthin could make contributions to the intracellular communication and immune response since it is a precursor of vitamin A (Nickell and Springate, 2001; Davies, 2008). Astaxanthin in muscle is weakly bound to the actomyosin protein-complex by no-specific hydrophobic bounding (Henmi et al., 1990). Moreover, Johnston et al. (2004) hypothesized that the organization of astaxanthin is associated with the regular alignment of actin and myosin proteins, hence the depth in colour also highly depends on the sarcomere alignment.

Farmed Atlantic salmon get the astaxanthin from the feed, which is mainly produced synthetically from a petrochemical source (Lerfall et al., 2016). As farmed Atlantic salmon have to absorb carotenoids exogenously, dietary source and feed composition play important roles in deciding the pigmentation of the fish (Torrissen, 1985; Einen et al., 1999).

1.5 Impact of swimming speed on behavior, growth and flesh quality

For Atlantic salmon aquaculture, fish generally experience water speeds below 20 cm s^{-1} and they are free to express its behaviors within this water speeds range (Johansson et al., 2007). The fish often form a circular and one-way directed swimming pattern under such water current, possibly because fish actively avoiding collision with the cage wall and each other (Føre et al., 2009).

1.5.1 Behavior

Salmonid fish attempt to stay stationary against the water flow and tend to exhibit regular,

synchronized locomotory behaviors and form school when they are exposed to moderate water flow (East and Magnan, 1987; Christiansen and Jobling, 1990). Higher swimming speed can reduce the aggression between fish since they have to hold their station against the water current (East and Magnan, 1987; Christiansen and Jobling, 1990; Adams et al., 1995). The frequency of reduced signs of fin or body damage as a result of reduced aggression in exercised fish may have a potential benefit of lowering the risk of further infections (Jobling et al., 1993). In addition, due to the fact that the energy cost of spontaneous actcities for fish held in still water may be substantial, the reduced aggression in fish swimming at higher speed may have a benefit of reducing energy cost (Christiansen et al., 1991; Adams et al., 1995).

1.5.2 Growth

In general, moderate swimming speed on fish have the potential to stimualte growth, especially in salmonids. A study on yearling hatchery-reared brook charr (*Salvelinus fontinalis*) swimming at different speed of 0.00, 0.85, 1.72 and 2.50 body length per second (BL s^{-1}) shows the highest growth performance happens at 0.85 BL s^{-1} (East and Magnan, 1987). Brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) also show improved growth at moderate swimming speed of 1 BL s^{-1} (Davison and Goldspink, 1977; Houlihan and Laurent, 1987). Both continuous intensity training (0.8 BL s^{-1}) and interval training (0.8 BL s^{-1} 16 h and 1.0 BL s^{-1} 8 h) have been found to increase growth in pre-smolt Atlantic salmon (Castro et al., 2011). Jørgensen and Jobling (1993) found that juvenile Atlantic salmon shows the highest SGRs when fish swimming at 1.5 BL s^{-1} compared to the 1.0, 2.0 BL s^{-1} and non-exercised group. For adult Atlantic salmon, fish swimming at 0.45 BL s^{-1} gained nearly 40% higher weight compared to the non-exercised fish raised in open cages (Totland et al., 1987). However, recently published paper found that fast swimming speed can have negative impact on fish, resulting in a decreased production performance in post-smolt Atlantic salmon (Solstorm et al., 2015).

1.5.3 Proximate composition

Increased swimming speed have potential to change flesh composition and consequently the quality of the fish, even though results about how swimming training affects flesh composition varies among studies. Fish under moderate swimming training tends to contain higher flesh protein content (Davison and Goldspink, 1977; Houlihan and Laurent, 1987; Solstorm et al., 2015). Higher flesh lipid content is found in fish muscle that is trained under moderate swimming speed than untrained fish (Davison and Goldspink, 1977; East and Magnan, 1987; Houlihan and Laurent, 1987; Totland et al., 1987). However, fast swimming speed may also reduce lipid deposition in the muscle in Atlantic salmon (Solstorm et al., 2015). The higher flesh protein content may result from decreased fuelling by protein (Lauff and Wood, 1996). Furthermore, no effects of swimming speed on flesh lipid content and protein content has been observed (Rasmussen et al., 2011).

1.5.4 Fillet firmness

Moderate swimming speed has been shown to induce various effects on fish firmness. Swimming training leads to increased fillet firmness in Atlantic salmon (Totland et al., 1987), sea bream (*Pagrus major*) (Tachibana et al., 1988) and brown trout (Bugeon et al., 2003). On the contrary, Khan et al. (2015) found that firmness and muscle fibre density were significantly lower in the exercised hāpuku (*Polyprion oxygeneios*) than that in the unexercised fish. Such changes may be explained by muscle fibre hypertrophy (enlargement of muscle fibres) leads to lowered muscle fibre density, and may decrease the fillet firmness in salmonids (Bjørnevik et al., 2004; Mørkøre et al., 2009). While other studies shows no significant differences in fillet texture between exercised and unexercised group in rainbown trout (Rasmussen et al., 2011) and Atlantic cod (Bjørnevik et al., 2003).

1.6 Project aims

The aims of this study were to investigate the growth and flesh quality characteristics of Atlantic salmon at two different swimming speeds in a closed cage system. The results will be used to optimize the swimming speed for Atlantic salmon in the closed cage system.

2 Materials and Methods

2.1 Atlantic salmon

The trial was conducted at Norsk Havbrukssenter, Brønnøysund (65.5°N 12.1°E, Nordland county, Norway) during the period from 27 May 2015 to 17 November 2015. The Atlantic salmon used in the experiment originated from Bindalssmolt AS (Nordland, Norway). The fish (S0 autumn smolt) were transferred to sea in November 2014, and were stocked in a closed cage (3000 m^3) at site Møllebogen until 20 May 2015. The fish were then moved by a well boat to Lamholmen and were received in a large closed cage in Norsk Havbrukssenter on 20 May 2015. Prior to the experimental setup, the fish were starved for two days. The fish had an initial mean round weight of 889 g and initial mean fork length of 41.6 cm on 27 May 2015 when they were graded and 1200 fish were evenly distributed into four closed cages. Each sea cage was stocked with 300 salmon, where 250 fish were untagged and 50 fish were PIT tagged with GPT12 Pre-load tags (12.5 mm, 134.2 kHz), using MK25^{TM} Implant Gun (Biomark, Boise, USA).

2.2 Closed cage

The closed cage used in the experiment is 15 m circumference, with an estimated volume of 30 m^3 (Akva Design AS, Brønnøysund, Norway). The basic structure of the cage is similar to a traditional open cage: jumping net, bird net, floating collar and mooring system (Lekang, 2007). However, there are some significant changes on the closed cage (Fig. 2). First change is that a closed bag of dense and flexible tarpaulin wall (Rantex AS, Lundamo, Norway) was used in the closed cage instead of using the net as a bag. Second change is that water is supplied from 25 m deep through a pipe and pumped into the cage. Third change is that the water outlet is located at the center of the bottom, where the dead fish and the remaining waste can be collected and pumped up through a drain pipe. The oxygen and temperature sensors (Akva Group AS,

Trondheim, Norway) are located at 2 m deep and 1 m from the wall. Each cage is set up with a control cabinet where data-collecting IQ Sensor Net 2020 XT (YSI Incorporated, USA) are hooked up, allowing to monitor the water quality in the cage.

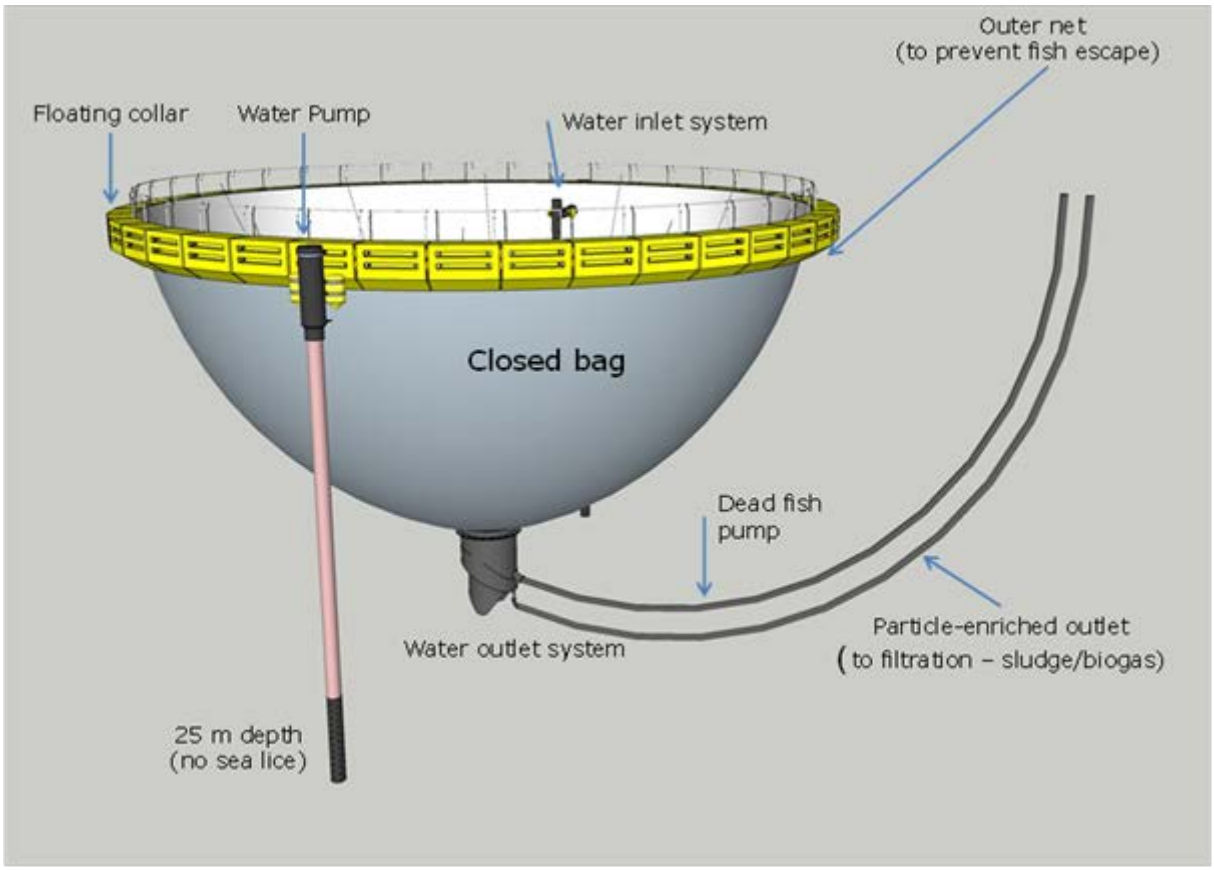

Fig. 2. Model of the closed cage used in the experiment. From Akva Design AS.

2.3 Experimental setup

Two weeks after the fish were distributed to the experimental setup, two water speeds were established (LOW, two cages and HIGH, two cages). The water speed for the LOW group was created only by incoming water through horizontally mounted inlet pipe. The water speed for the HIGH group was established by incoming water through horizontally mounted inlet pipe, with an extra propeller that is opposite to the inlet pipe. The water speed was measured by Flow Rate Sensor LQ2-LE, being connected to Labquest 2 (Vernier Software & Technology, USA).

The water speed was measured just behind the water inlet (A) and the propeller (B) at different depths (10 cm, 1 m and 2 m) (Fig. 3). The water speeds were around 8 cm s^{-1} and 22 cm s^{-1} for LOW and HIGH group respectively, even though variation exist within the cage (Fig. 3). Since the initial fish length was 41.6 cm, the swimming speeds for LOW and HIGH group were approximately 0.2 and 0.6 BL s^{-1} respectively at start of the experiment, decreasing to approximately 0.1 and 0.4 BL s^{-1} at the end of the experiment.

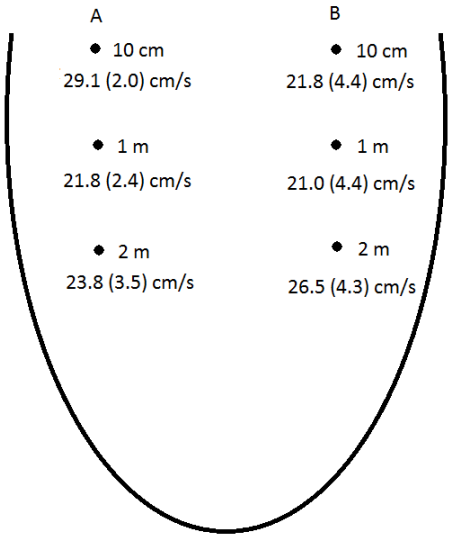

Fig. 3. Mean (SD) water speed at different position in a cage from the HIGH group on July 22th.

All fish were fed Spirit S600-50A 7 mm (Skretting AS, Stavanger, Norway) from 15 June 2015 to 29 July 2015, Premium 1200-50A 9 mm (Skretting AS, Stavanger, Norway) from 29 July 2015 to 14 October 2015, Premium 2500-50A 9 mm (Skretting AS, Stavanger, Norway) from 15 October 2015 to 18 November 2015 to satiation every day, using Betten feeders S1 automatic feeding system (Betten Maskinstasjon AS, Vågland, Norway). Feed and feeding regimes were regulated every week according to commercial standards and manual inspection. Water exchange was continuously, with an estimated water exchange speed of 250-275 L min^{-1} for each cage. Stocking density was approximately 9 kg m^{-3} at the start of the experiment and this increased to a maximum of approximately 25 kg m^{-3} during the experiment. Oxygen saturation

was maintained above 90% through the experiment. Water temperature ranged from 8.7 °C in June to 14.2 °C in August 2015 (Fig. 4).

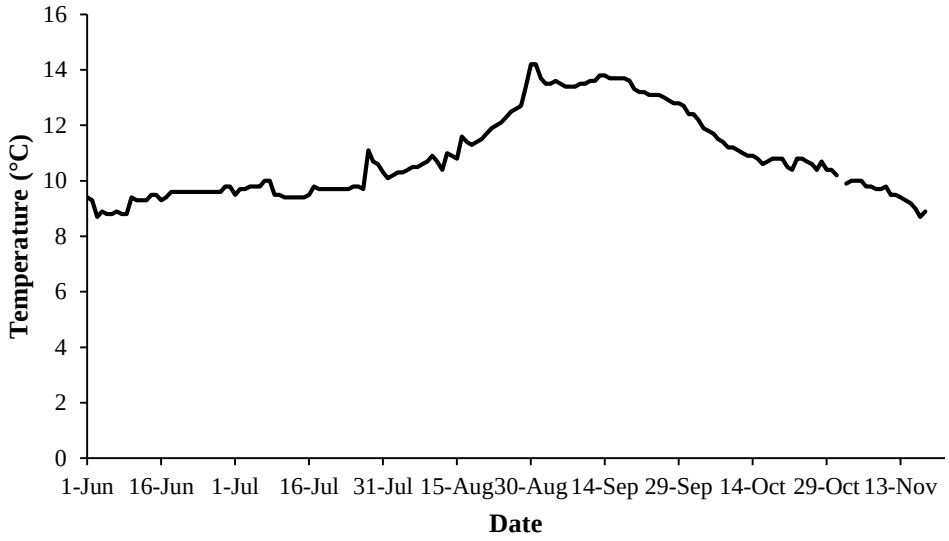

Fig. 4. Water temperature during the experiment.

2.4 Sampling procedure

To see the growth performance, the round weight (± 1 g) and fork length (± 0.5 cm) of all fish were recorded on 27 May 2015 and 17 November 2015, with only 50 fish were measured on 26 August 2015.

Fish were sampled on 10 June, 26 August and 17 November 2015 for the evaluation of flesh characteristics. 15 fish from each cage were sampled for flesh quality characteristics analysis at each sampling point. Fish were collected by purse seine, and randomly taken out by a scoop net. Fish were anesthetized using 1.5-2 gram Tricaine methane sulphonate in a 50 L tank with seawater (30-80 mg/L).

Biomark 601^{TM} Reader (Biomark, Boise, USA) was used to read the PIT tag ID and the tagged fish were not sampled. The sampled fish were killed by a sharp blow to the head immediately

and were bled for half an hour in a 50 L tank with seawater by cutting the gill arches on both sides. The fish were labeled individually. Round weight, fork length, gutted weight, liver weight and heart weight (including the bulbus arteriosus) of each individual were measured. The fish were iced in polystyrene boxes and sent by ferry (Hutigruta) to Faculty of Biosciences and Aquaculture, Nord University (Bodø, Norway) for further analysis. The fish were stored in a cold room (+ 4 °C) awaiting further analysis after arrival at the Nord University.

Five days after slaughter, the fish were filleted and the fillet weight were recorded as the weight of both fillet. Fillet gaping were measured using the whole left fillet. The Norwegian quality cut (NQC, Fig. 5) from the left fillet were cut out and used for colour and texture analysis, and thereafter homogenized in Braun MR530 Turbo-Accesorios homogenizer (Braun, Germany). The homogenized fish were stored at - 40 °C prior to chemical composition analysis.

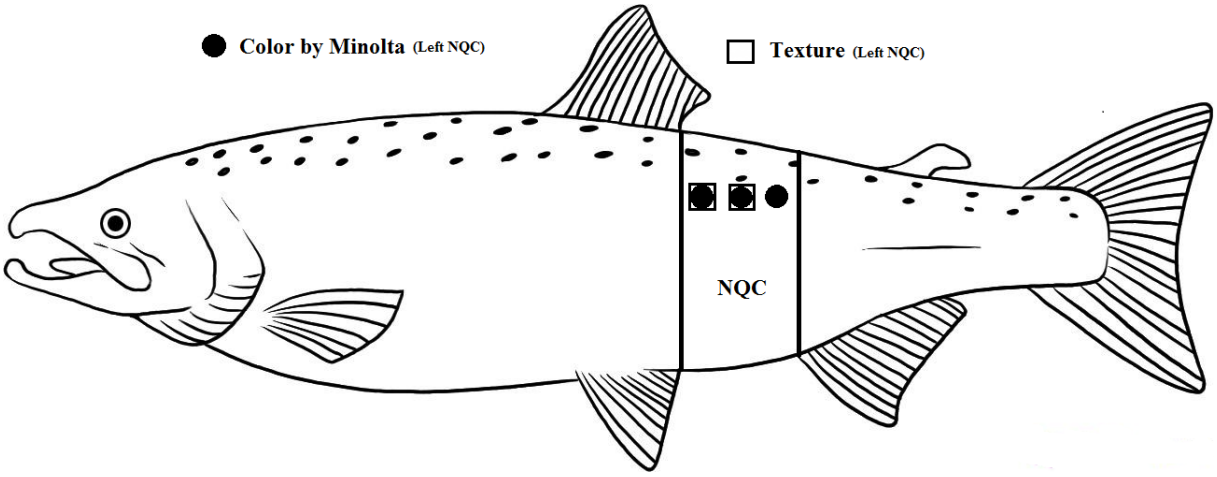

Fig. 5. NQC and sampling sites for texture and colour analysis in the experiment.

2.5 Gaping score assessment

The gaping score was visually evaluated on the whole left fillet in an anterior to posterior

direction, according to a scale from 0-4.0 (Table 1) (Johnsen et al., 2011):

Table 1. Scale of gaping score applied in the study.

Score	Sign
0	no gaping
0.5	1-3 small breaks [< 0.5 cm] in the myoseptum
1.0	4-6 small breaks
1.5	7-9 small breaks or 1-3 medium breaks [0.5-1.5 cm]
2.0	> 10 small breaks or 4-6 medium breaks
2.5	7-9 medium breaks or 1-2 large breaks [> 1.5 cm]
3.0	> 10 medium breaks or 3-5 large breaks
3.5	> 6 large breaks
4.0	extreme gaping = myotomes falling apart

2.6 Colour evaluation

Flesh colour was examined using the DSM SalmoFan^{TM} (DSM, Switzerland) under bright light in a special light cabinet (Ra > 90, colour temperature > 5000 K). SalmoFan evaluation was carried out on the left NQC fillet. To minimize the variation between samples the measurement was performed by the same person. Flesh colour was also measured in triplicate by using Spectrophotometer CM-700d (Konica Minolta, Japan). The measurement was done just above the lateral line on the left NQC (Fig. 5). The L* variable represents lightness (L* = 0 for black, L* = 100 for white), the a* scale represents the red/green (a* positive represents intensive on red colour and a* negative represents intensive on green colour), and b* value represents the yellow/blue (positive and negative respectively) (Hunter and Harold, 1987).

2.7 Instrument texture analysis

Texture analysis was done by using a TA-XT2 PLUS texture analyser with Texture Expert Exceed 2.52 software (Stable Micro System, Surrey, England). The instrument was equipped with a load cell of 50 kg, a knife steel blade with thickness of 3.0 mm and width of 70 mm, a slotted insert platform for muscle blocks. Duplicate measurements were done on each fish by using a standardized block (25 × 25 ×10 mm) from the dorsal part of the left NQC (Fig. 5). The knife blade was pressed downward through the muscle block at a 90 angle to the longitudinal orientation of the muscle block, with a constant test speed of 1 mm/s, cutting through 120 % of the block. A figure was shown on the computer, showing the force needed to cut through the muscle block. The maximum shear force in newton (N) is the maximum resisting force to the cutting of the sampling and the total shear work was calculated as the total work needed to cut through the muscle in millijoules (mJ). Owing to the unfortunate instrumental calibration problems with the instrument, the texture data at final sampling were not included.

2.8 Proximate composition

Chemical composition of post-rigor fillet from the right NQC fillet were determined in duplicate samples. And DA 7200 NIR Analyzer (Perten Instruments, Sweden) was also used to evaluate the chemical composition at the final sampling point.

2.8.1 Water content

Water content was determined in parallels by drying the sample at 105 °C. An aluminium cup was labeled and pre-weighed. Wet weight (5 g) of homogenized fillet was weighed into the cup and placed in an oven for 20 hours at 105 °C. The cup with sample was weighed after drying for determination of dry weight (g). Water content was calculated according to the following formula:

$$\text{Water content (\%)} = 100 \times (\text{Wet weight} - \text{Dry weight}) \times \text{Wet weight}^{-1}$$

2.8.2 Protein content

Protein content was determined by the Kjeldahl method. Homogenized fillet sample was weighed (1 g) into a nitrogen-free Kjeltec paper (GE Healthcare life science whatman, UK) and was added into a glass tube. Two Kjeltabs and 15 ml concentrated sulphuric acid (98% H_2SO_4) were added to the sample tube under fume hood using bottle top dispenser. The tube was then heated at 420 °C on a Foss Tecator 2020 digestor (Foss Analytical AB, Sweden) for 45 minutes. 75 ml distilled water was added after the sample was cooled down. By using a factor of 6.25, the amount of protein was decided by titrating with 0.1999 mol L^{-1} hydrochloric acid in a 1% boric acid indicator solution, with methyl-red and bromcresol-green as indicator by using Kjeltec 2300 (Foss Analytical AB, Sweden).

2.8.3 Lipid content

Lipid content was determined by using homogenized fillet sample extracted in ethyl acetate. Homogenized fillet sample (sample weight: 5 g) and 20 g of water free sodium sulfate were mixed in a porcelain bowl. The mixed powder was transferred into a 100 ml glass bottle, in which 50 ml ethyl acetate was added. The glass bottle was placed on a shaking table for an hour at a speed of 260 shake per minute in a fume hood, 20 ml of the sample was filtrated through a filter paper (VWR international, Belgium). 20 ml filtrated sample was measured into an evaporation cup through glass pipette and was evaporated in a water bath at 100 °C for 20 minutes. The sample was dried at 105 °C for 20 minutes and put into the desiccator to cool down. Then the cup was weighed and lipid weight (g) was calculated. Lipid content was calculated according to the following formula:

$$\text{Lipid content (\%)} = 10300 \times \text{Lipid weight} \times ((40 - 2.17 \times \text{Lipid weight}) \times \text{Sample weight})^{-1}$$

2.9 Calculations

Condition Factor. Fulton's condition factor (CF) was calculated as:

$$CF = 100 \times \text{round weight} \times \text{fork length}^{-3}$$

Specific Growth Rate. Specific growth rate (SGR) was calculated using tagged fish only according to the formula:

$$SGR\ (\%\ day^{-1}) = 100 \times (\ln W_2 - \ln W_1) \times (t_2 - t_1)^{-1}$$

Where W_1 and W_2 represent the individual fish round weights (g) at time t_1 and t_2 (day) respectively.

Hepato Somatic Index. Hepato somatic index (HSI) was calculated as:

$$HSI\ (\%) = 100 \times \text{liver weight} \times \text{round weight}^{-1}$$

Relative Ventricular Mass. Relative ventricular mass (RVM) was calculated according to the formula (Gallaugher et al., 2001):

$$RVM\ (\%) = 100 \times \text{heart weight} \times \text{round weight}^{-1}$$

Fillet yield. Fillet yield was calculated as:

$$\text{Fillet yield}\ (\%) = 100 \times \text{fillet weight} \times \text{round weight}^{-1}$$

2.10 Statistical analyses

Statistics were performed using IBM SPSS Statistics v. 22.0 (IBM Corporation, NY, US). Microsoft Excel 2016 (Microsoft Corporation, WA, US) was used for the graphical illustration of results. A partial least square regression was performed using Unscrambler Ver.10X (Camo Process AS, Oslo, Norway) to predict the flesh water content, protein content, lipid content. Data are presented as mean ± SD, and significance was accepted at $P < 0.05$. Prior to analysis, Shapiro Wilk's W and Levene's tests had been used for checking normality and homogeneity of variance, respectively. Outliers were individually investigated for underlying reasons and the outliers were removed from the data set where methodological causes were detected. Effects of swimming speed on growth performance for overall fish and biometric parameters for sampled fish were analyzed by using one-way ANOVA, followed by a t-test for comparisons when a significant difference was found between the treatments, and the results from these two tests gave the same outcome. A nonparametric Mann-Whitney U test was used when statistical assumptions were not met. A general liner model (GLM) for ANCOVA was used to investigate the effect of swimming speed on HSI, RVM and flesh quality characteristics, with gutted weight as covariate and swimming speed as fixed factor. Relationships between test variables were also analyzed by Pearson's correlation.

3 Results

3.1 Effects on growth performance

Results for overall fish growth performance are presented in Fig. 6. Fish round weight (mean ± SD) increased three-fold from 884 ± 112 g to 2837 ± 468 g and from 894 ± 115 g to 3031 ± 503 g in the LOW group and HIGH group during the five months' trial, respectively. On May 27th and August 26th there were no significant differences between treatments in fish mean round weight (Fig. 6A, $P > 0.05$). However, at the end of the experiment (November 17th), the HIGH group had 6.4% higher mean round weight than the LOW group (Fig. 6A, $P < 0.001$).

Fork length (mean ± SD) on May 27th was 41.5 ± 1.6 cm in the LOW group and 41.7 ± 1.6 cm in the HIGH group, and increased to 59.0 ± 3.7 cm and 58.8 ± 4.5 cm in the LOW group and HIGH group respectively, at the end of the experiment (November 17th). No significant differences in fork length between the treatments were observed throughout the experiment (Fig. 6B, $P > 0.05$).

Calculated mean condition factor increased from 1.23 on May 27th to 1.35 and 1.45 on August 26th in the LOW group and HIGH group, respectively. Mean condition factor was significantly higher in the HIGH group on both August 26th ($P = 0.031$) and November 17th (Fig. 6C, $P < 0.001$).

SGR for individually tagged fish increased from 0.50 ± 0.20% day^{-1} and 0.60 ± 0.10% day^{-1} (May 27th-August 26th) to 0.79 ± 0.19% day^{-1} and 0.82 ± 0.14% day^{-1} (August 26th-November 17th) in the LOW group and HIGH group respectively. During the whole experimental period from May 27th to November 17th, the SGR were 0.66 ± 0.10% day^{-1} in the LOW group and 0.69 ± 0.08% day^{-1} in the HIGH group. No significant differences were found between treatments with regards to mean SGR during the experiment (Fig. 6D, $P > 0.05$).

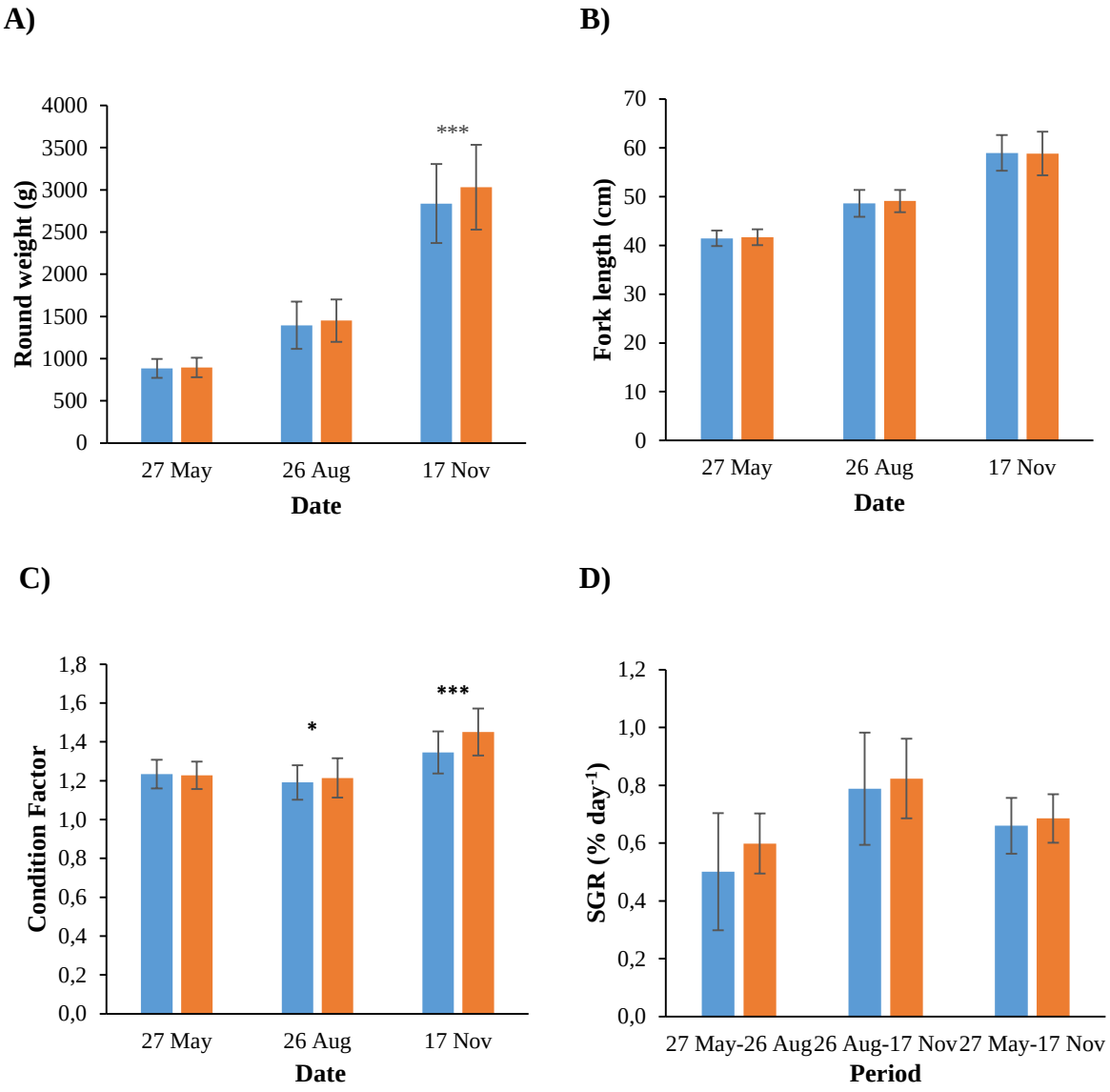

Fig. 6. Round weight (A), fork length (B), condition factor (C) and SGR (D) for Atlantic salmon exposed to water currents corresponding to initial swimming speeds of 0.2 (left column, LOW) or 0.6 BL s^{-1} (right column, HIGH) for five months. Significance differences (ANOVA) between groups at the same sampling time are indicated by asterisks (*) $P < 0.05$ and (***) $P < 0.001$.

3.2 Effects on biometric parameters

Biometry data of the randomly selected fish for flesh quality characteristics analyses are presented in Table 2. Fork length were similar between treatments at all three sampling points ($P > 0.05$). However, fish in the HIGH group had significantly higher round weight ($P = 0.012$), gutted weight ($P = 0.009$) and condition factor ($P = 0.009$) value than the LOW group on November 17th, while no significant differences were found between treatments on both June 10th and August 26th. HSI were significantly higher in the LOW group than the HIGH group only at the start of the experiment ($P = 0.029$). Significant higher RVM was found in the HIGH group at the end of the experiment ($P = 0.048$).

Table 2. Biometry data (mean ± SD) for Atlantic salmon kept at water currents corresponding to initial swimming speeds of 0.2 (LOW) or 0.6 BL s^{-1} (HIGH) for five months. Significant differences (ANOVA and ANCOVA) between groups at the same sampling time are indicated by asterisks (*) $P < 0.05$ and (**) $P < 0.01$.

	June 10th	August 26th	November 17th
Round Weight (g)			
LOW	854 ± 110	1411 ± 289	2866 ± 402*
HIGH	843 ± 100	1485 ± 196	3119 ± 331
Fork Length (cm)			
LOW	41.5 ± 1.6	48.4 ± 2.8	59.4 ± 2.8
HIGH	41.3 ± 1.7	49.2 ± 2.4	59.8 ± 2.1
Gutted Weight (g)			
LOW	779 ± 89	1250 ± 254	2519 ± 351**
HIGH	758 ± 90	1332 ± 200	2748 ± 288
CF[A]			
LOW	1.20 ± 0.07	1.23 ± 0.10	1.36 ± 0.10**
HIGH	1.19 ± 0.06	1.25 ± 0.06	1.46 ± 0.10
HSI[B]			
LOW	0.93 ± 0.10*	0.93 ± 0.09	1.00 ± 0.06
HIGH	0.76 ± 0.09	0.96 ± 0.07	1.04 ± 0.06
RVM[C]			
LOW	0.102 ± 0.011	0.112 ± 0.012	0.111 ± 0.011*
HIGH	0.102 ± 0.014	0.108 ± 0.013	0.118 ± 0.010

[A] Condition factor. [B] Hepato somatic index.

[C] Relative ventricular mass.

3.3 Effects on flesh quality characteristics

3.3.1 Fillet yield

The fillet yield ranged from 64.1 to 67.1% and 65.9 to 66.5 % in the LOW and HIGH group respectively. There were no differences in fillet yield between groups on June 10th and August 26th. However, the fillet yield of the fish in the HIGH group was 3% higher than the fish in the LOW group ($P < 0.001$) on November 17th (Fig. 7).

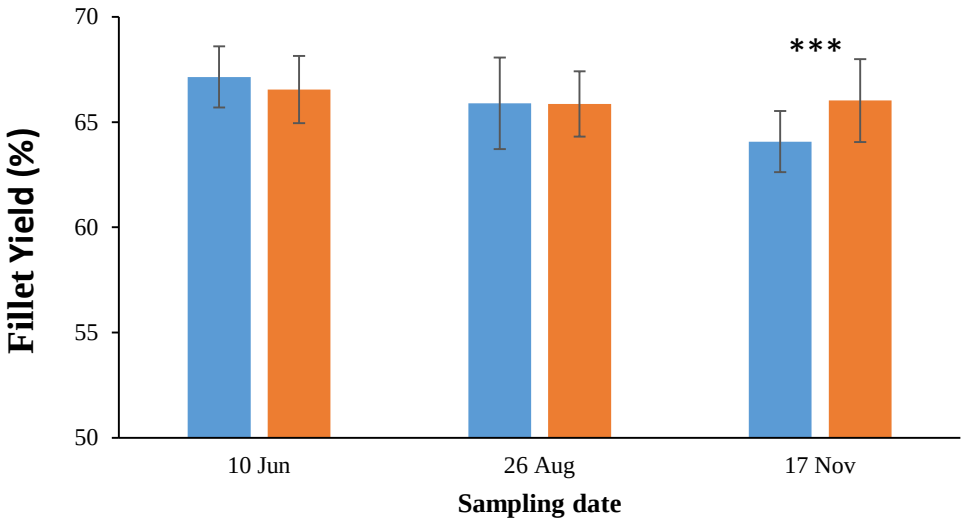

Fig. 7. Fillet yield of Atlantic salmon kept at water currents corresponding to initial swimming speeds of 0.2 (left column, LOW) or 0.6 BL s^{-1} (right column, HIGH) for five months. Significant difference (ANCOVA) between groups at the same sampling time is indicated by (***) $P < 0.001$.

3.3.2 Colour

Flesh colour are presented in Table 3. L* were similar between treatments on June 10th ($P = 0.345$), with significantly higher value in the HIGH group on August 26th ($P = 0.038$). Both a*

and b* were significantly higher in the HIGH group on June 10th (a*: P = 0.040, b*: P = 0.002), but the LOW group had significantly higher a* and b* on August 26th (a*: P = 0.002, b*: P = 0.013). However, no significant differences were observed between treatments with regards to L*, a* and b* at the end of the experiment. No significant differences were found in SalmoFan between treatments throughout the experiment.

3.3.3 Texture and gaping

Flesh maximum shear force and total shear work decreased from June to August (Table 3). Nevertheless, flesh total shear work and maximum shear force were not influenced by swimming speed on June 10th and August 26th (Table 3). Part of the data for the final sampling were missing due to unfortunate instrumental calibration problem. The incidence of fillet gaping was very low across training treatments, with no significant differences between treatments at all three samplings (Table 3).

3.3.4 Proximate composition

The water content and protein content of fish muscle decreased from June to November, whereas the lipid content increased (Table 3). There were no significant differences in water, protein and lipid between treatments during the whole experiment, except for protein in August being significantly higher in the Low group (Table 3, P = 0.014). Lipid content were positively correlated to L* ($r = 0.506$, $P < 0.01$, $n = 60$), a* ($r = 0.305$, $P < 0.05$, $n = 60$), b* ($r = 0.314$, $P < 0.05$, $n = 60$).

Table 3. Flesh quality characteristics of Atlantic salmon kept at water currents corresponding to initial swimming speeds of 0.2 (LOW) or 0.6 BL s^{-1} (HIGH) for five months. Values represent means ± SD and significant differences (ANCOVA) between groups at the same sampling time are indicated by asterisks (*) $P < 0.05$ and (**) $P < 0.01$.

	June 10th	August 26th	November 17th
SalmoFan			
LOW	21.8 ± 0.9	22.5 ± 0.7	24.3 ± 0.8
HIGH	22.2 ± 1.3	22.3 ± 0.9	24.1 ± 0.7
L*			
LOW	40.3 ± 1.7	40.4 ± 1.4*	39.7 ± 1.9
HIGH	39.9 ± 1.3	41.2 ± 1.3	39.5 ± 1.9
a*			
LOW	10.4 ± 1.3*	11.6 ± 1.1**	13.3 ± 1.4
HIGH	10.9 ± 1.2	10.6 ± 1.3	13.7 ± 1.0
b*			
LOW	7.4 ±1.2**	7.4 ± 1.0*	9.5 ± 1.1
HIGH	8.4 ±1.2	6.8 ± 1.1	9.8 ± 1.3
Gaping			
LOW	0.80 ± 0.89	0.15 ± 0.42	0.08 ± 0.32
HIGH	0.53 ± 0.67	0.07 ± 0.17	0.00 ± 0.00
Maximum shear force (N)			
LOW	8.1 ± 1.3	7.4 ± 1.2	-
HIGH	7.7 ± 1.2	7.3 ± 0.8	-
Total shear work (mJ)			
LOW	34.5 ± 5.8	28.8 ± 4.5	-
HIGH	32.3 ± 5.6	29.0 ± 2.9	-
Water (%)			
LOW	68.7 ± 1.1	68.9 ± 1.8	64.9 ± 1.1
HIGH	69.3 ± 1.2	69.0 ± 1.4	64.4 ± 1.0
Protein (%)			
LOW	20.2 ± 0.4	19.5 ± 0.5*	19.1 ± 0.3
HIGH	20.2 ± 0.4	19.2 ± 0.4	19.0 ± 0.2
Lipid (%)			
LOW	10.8 ± 1.3	10.9 ± 1.9	15.8 ± 1.5
HIGH	10.2 ± 1.3	10.8 ± 1.7	16.2 ± 1.3

-. Number are missing due to unfortunate instrumental calibration problem.

4 Discussion

4.1 Water speed

Water speed showed big variation within the closed cage in present study. The homogeneity of the water speed highly depends on the rearing systems. For example, within rectangular tanks, the water speed is generally highest close to the water inlet (Oca et al., 2004). The circular tanks can have over three times higher water speed closer to the outer wall than the center (Oca et al., 2004; Duarte et al., 2011). These systems allow fish to change position and experience different swimming speed. However, experiments that using raceway generally have more uniform water speed, indicating that the fish are forced to swim at a given water speed constantly (Solstorm et al., 2015). Different homogeneity of the water speed could explain some of the inconsistencies between results, since fish distribution is strongly correlated ($r = 0.85$) to water speed (Duarte et al., 2011).

4.2 Effects on growth performance

4.2.1 Growth

The results clearly demonstrate that swimming speed affects growth performance of adult Atlantic salmon, with higher final body round weight in the HIGH group than the LOW group. Positive effects of increased swimming speed on fish growth performance has also been found in both pre-smolt Atlantic salmon (Jørgensen and Jobling, 1993, 1994; Castro et al., 2011) and adult Atlantic salmon (Totland et al., 1987), indicating consistency among studies. However, fast swimming speed of 1.5 BL s^{-1} could have a negative impact on the growth performance of post-smolt Atlantic salmon according to a study from Solstorm et al. (2015), indicating fish swimming at fast speed may use large amount of energy to swim against the water current instead of growing the body mass.

It is not clear whether increased growth with increased swimming speed in Atlantic salmon results from increased food intake or increased food utilization. Jørgensen and Jobling (1993) found that the enhancement of growth in juvenile Atlantic salmon swimming at higher speed was accompanied by improved food utilization. However, Jørgensen and Jobling (1994) found the improved growth with increased swimming speed in juvenile Atlantic salmon was accounted for by a higher food intake, but not food utilization. Our setup did not measure the food intake and food utilization, but similar amounts of feeds were distributed to both treatments, indicating fish in the HIGH group may have better food utilization.

It is also possible that better growth performance was due to less agonistic activity in the HIGH group, which is supported by several studies in salmonids (East and Magnan, 1987; Christiansen and Jobling, 1990; Jørgensen and Jobling, 1993; Adams et al., 1995). Results from Adams et al. (1995) suggested that improved growth in fish swimming at higher speed was a result of lower energetic costs of reduced agonistic activity rather than subordinates got better access to food, which may also explain larger variation of fish final body round weight (standard deviation) in the HIGH group.

Nevertheless, SGR was not improved for fish in the HIGH group in this study. This is in contrast to previous literature, where higher SGR were observed when fish were exercised at higher swimming speed (Jørgensen and Jobling, 1993, 1994). It is known fish growth rate varies among different fish size (Austreng et al., 1987), with larger fish having lower growth rate than smaller fish, making it even more difficult to detect the differences. The fish in our experiment were much larger (~ 900 g) already at the start of the experiment. The higher swimming speed in our study was approximately 0.6 BL s^{-1}, which decreased to approximately 0.4 BL s^{-1}. This relatively low swimming speed might be too weak to generate the differences in SGR.

4.2.2 Condition Factor (CF)

Higher swimming speed gave higher condition factor in this study, indicating salmon in the HIGH group gained more weight relative to the increase in length. This observation is confirmed by other studies that were conducted on Atlantic salmon (Totland et al., 1987; Jørgensen and Jobling, 1994; Castro et al., 2011; Solstorm et al., 2015). Relatively slower growth of vertebral column than muscle growth could be the reason of higher condition factor in the HIGH group (Castro et al., 2011).

4.2.3 Relative Ventricular Mass (RVM)

RVM was higher in the HIGH group compared to the LOW group. This result is in line with previous studies on both pre-smolt (Castro et al., 2013) and post-smolt Atlantic salmon (Solstorm et al., 2015). Higher swimming speed has been shown to increase the stroke volume, cardiac output and maximum power output in rainbow trout (Farrell et al., 1991). Also, molecular study on Atlantic salmon suggested that fish swimming at higher speed may have improved cardiac contractile function (Castro et al., 2013). Thus, greater relative ventricular mass in the HIGH group might result from higher cardiac performance.

4.2.4 Hepato Somatic Index (HSI)

Increase of swimming speed did not affect the HSI in present study. The initial drop in HSI for fish in the HIGH group compared with that in the LOW group at the beginning is likely an artefact. The fact that Atlantic salmon uses mostly the muscle to store energy may suggest weaker effects on liver.

4.3 Effects on flesh quality characteristics

4.3.1 Colour

We found no differences in flesh colour between groups which are in agreement with previous study (Totland et al., 1987), where no significant differences were found in carotenoids content in fish flesh between fish swimming at 0.1 and 0.45 BL s^{-1}.

4.3.2 Texture and gaping

Based on first and second sampling, we conclude that there were no effects of swimming speed on flesh texture, measured as maximum shear force and total shear work. Rasmussen et al. (2011) also found no significant differences on flesh texture between exercised (0.9 BL s^{-1}) and unexercised fish (<0.1 BL s^{-1}), which is in agreement with present results.

Study found that increased swimming speed of 0.45 BL s^{-1} for eight months in adult Atlantic salmon resulted in larger muscle fibre diameter (Totland et al., 1987), which can have a negative impact on flesh texture firmness (Bjørnevik et al., 2004; Mørkøre et al., 2009). The effects of muscle fibre sizes on flesh texture may be hidden by the increase of connective tissue and its collagen crosslinks (PYD). This counterbalance between fibre sizes and connective tissue might explain our conclusion. However, Bugeon et al. (2003) suggested firmer flesh texture may result from stronger connective tissue in fish swimming at 1.0 BL s^{-1} and 2.0 BL s^{-1} compared to standing water, in spite of greater muscle fibre size in exercised fish. Nevertheless, the relatively shorter period (11 weeks vs 8 months) and lower swimming speed (0.6 vs 1.0 BL s^{-1}) in our study compared to Bugeon et al. (2003) might be too weak to cause a significant change in connective tissue. Stronger connective tissue may also explain slightly lower fillet gaping for fish in HIGH group compared to LOW group, although not significant.

Studies on the effects of swimming speed on fish has also found better flesh texture in Atlantic salmon (Totland et al., 1987) and sea bream (Tachibana et al., 1988), but these studies should be explained carefully since important covariate (fish gutted weight) were not included in the statistical analysis. Moreover, flesh texture assessment methods vary between studies, making it difficult to compare the results. We lost the texture data for the last sampling, and thereby any differences in texture between groups at last sampling.

4.3.3 Proximate composition

In present study, no significant differences were found with regards to flesh lipid content, protein content and water content between two experimental groups. This is in line with previous studies on pan-sized rainbow trout (Rasmussen et al., 2011). They suggested that relatively larger fish and slower swimming speed all associate with smaller effects in the flesh composition. In our study, swimming speed in both group (<0.6 BL s^{-1}) were much lower and fish were much larger (~ 900 g). Furthermore, in our study, the water speed differed between different locations in the cage, and there is possibility that the fish would choose to stay at lower water speed in shorter periods to relax. This could also promote access for food, and may explain unchanged flesh chemical composition in the HIGH group. In contrast, Solstorm et al. (2015) using raceway, had the same water speed all over, and the fish had no possibility to rest during the experiment.

Earlier studies on swimming speed are diverging with respect to the flesh lipid content. Some authors find increasing lipid level with increased swimming speed in salmonids (Davison and Goldspink, 1977; East and Magnan, 1987; Houlihan and Laurent, 1987; Totland et al., 1987), whereas others has found decreasing lipid level with higher swimming speed (Solstorm et al., 2015). A decrease in lipid level could be explained by increased lipid metabolism in fish subjected to higher swimming speed (Lauff and Wood, 1996). The reason we did not find decreased flesh lipid content could also be as Rasmussen et al. (2011), who proposed that

unchanged flesh lipid content in fish swimming at higher speed could be the increase of lipid catabolism mainly happens in other tissues than muscle or the applied swimming speed was too low to give increased lipid metabolism.

The increase of the flesh protein content may be due to the relatively lower contribution of protein metabolism in the muscle when fish are forced to swim, which is reflected by the significantly lower flesh lipid content in fish swimming at higher speed (Houlihan and Laurent, 1987; Solstorm et al., 2015). Failure to include gutted weight in the statistical analysis might contribute to the misinterpretation of the results in their study.

No significant difference in muscle water content was also found in Atlantic cod swimming at 0, 0.5 and 1.0 BL s^{-1} (Bjørnevik et al., 2003). However, Bugeon et al. (2003) found that fish exercised at moderate swimming speed of 1.0 BL s^{-1} had significantly lower flesh water content, whilst fish exercised at high swimming speed of 2.0 BL s^{-1} had significantly higher flesh water content. Thus, we suggest that fish exercise at moderate swimming speed might have higher deposition of energy content, but fish exercise at high swimming speed may use more energy content to swim against the water current. In our study, swimming speed in the HIGH group was probably too low to affect the energy content measured in the muscle.

4.4 Correlations

There were significant correlations between lipid content and the perceived colour of raw salmon. High level of flesh lipid content tends to give higher L*, a* and b*. Several studies have also found considerable relations between the perceived colour and lipid content of raw Atlantic salmon fillet (Rørå et al., 1998; Mørkøre et al., 2001). The interaction between flesh colour and lipid content is probably due to the light scattering that is affected by lipid content (Christiansen et al., 1995).

5 Conclusions

This study shows that the increase of swimming speed from 0.2 to 0.6 BL s^{-1} for five months can be used as a tool to enhance the growth of adult Atlantic salmon without compromising flesh quality in closed cages. Higher swimming speed resulted in higher round weight, condition factor, relative ventricular mass and fillet yield. Flesh quality characteristics, including colour, gaping, texture, water content, lipid content and protein content were not affected by swimming speed in present study. A swimming speed of 0.6 BL s^{-1} might be too low to affect flesh quality in Atlantic salmon of this size, and further studies should be carried out at higher swimming speeds. And higher swimming speeds might be challenging due to technical and hydrodynamics challenges.

References

Aaen, S. M., Helgesen, K. O., Bakke, M. J., Kaur, K. & Horsberg, T. E. (2015). Drug resistance in sea lice: a threat to salmonid aquaculture. *Trends in Parasitology,* **31,** 72-81.

Adams, C. E., Huntingford, F. A., Krpal, J., Jobling, M. & Burnett, S. J. (1995). Exercise, agonistic behaviour and food acquisition in Arctic charr, *Salvelinus alpinus*. *Environmental Biology of Fishes,* **43,** 213-218.

Ando, M., Toyohara, H. & Sakaguchi, M. (1992). Post-mortem tenderization of rainbow trout muscle caused by the disintegration of collagen fibers in the pericellular connective tissue. *Nippon Suisan Gakkaishi,* **58,** 567-570.

Ashton, I. P. (2002). Understanding lipid oxidation in fish. *In:* Bremner, H. A. (ed.), *Safety and quality issues in fish processing* (pp. 254-285). Cambridge: Woodhead Publishing.

Austreng, E., Storebakken, T. & Åsgård, T. (1987). Growth rate estimates for cultured Atlantic salmon and rainbow trout. *Aquaculture,* **60,** 157-160.

Bergheim, A. (2012). Recent growth trends and challenges in the Norwegian aquaculture industry. *Latin American Journal of Aquatic Research,* **40,** 800-807.

Bjørnevik, M., Espe, M., Beattie, C., Nortvedt, R. & Kiessling, A. (2004). Temporal variation in muscle fibre area, gaping, texture, colour and collagen in triploid and diploid Atlantic salmon (*Salmo salar* L). *Journal of the Science of Food and Agriculture,* **84,** 530-540.

Bjørnevik, M., Karlsen, Ø., Johnston, I. A. & Kiessling, A. (2003). Effect of sustained exercise on white muscle structure and flesh quality in farmed cod (*Gadus morhua* L.). *Aquaculture Research,* **34,** 55-64.

Bugeon, J., Lefevre, F. & Fauconneau, B. (2003). Fillet texture and muscle structure in brown trout (*Salmo trutta*) subjected to long-term exercise. *Aquaculture Research,* **34,** 1287-1295.

Castro, V., Grisdale-Helland, B., Helland, S. J., Kristensen, T., Jørgensen, S. M., Helgerud, J., Claireaux, G., Farrell, A. P., Krasnov, A. & Takle, H. (2011). Aerobic training stimulates growth and promotes disease resistance in Atlantic salmon (*Salmo salar*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology,* **160,** 278-290.

Castro, V., Grisdale-Helland, B., Helland, S. J., Torgersen, J., Kristensen, T., Claireaux, G., Farrell, A. P. & Takle, H. (2013). Cardiac molecular-acclimation mechanisms in response to swimming-induced exercise in Atlantic salmon. *PLoS ONE,* **8,** e55056.

Cheng, J. H., Sun, D. W., Han, Z. & Zeng, X. A. (2014). Texture and structure measurements and analyses for evaluation of fish and fillet freshness quality: a review. *Comprehensive Reviews in Food Science and Food Safety,* **13,** 52-61.

Christiansen, J. S. & Jobling, M. (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,** 2185-2191.

Christiansen, J. S., Jørgensen, E. H. & Jobling, M. (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, R., Struksnæs, G., Estermann, R. & Torrissen, O. J. (1995). Assessment of flesh colour in Atlantic salmon, *Salmo salar* L. *Aquaculture Research,* **26,** 311-321.

Coppes, Z., Pavlisko, A. & Vecchi, S. D. (2002). Texture measurements in fish and fish products. *Journal of Aquatic Food Product Technology,* **11,** 89-105.

Davies, S. J. (2008). Colouration and flesh quality in farmed salmon and trout. *In:* Lie, Ø. (ed.), *Improving farmed fish quality and safety* (pp. 446-470). Cambridge: Woodhead Publishing.

Davison, W. & Goldspink, G. (1977). The effect of prolonged exercise on the lateral musculature of the brown trout (*Salmo Trutta*). *Journal of Experimental Biology,* **70,** 1-12.

Duarte, S., Reig, L., Masaló, I., Blanco, M. & Oca, J. (2011). Influence of tank geometry and flow pattern in fish distribution. *Aquacultural Engineering,* **44,** 48-54.

East, P. & Magnan, P. (1987). The effect of locomotor activity on the growth of brook charr, *Salvelinus fontinalis* Mitchill. *Canadian Journal of Zoology,* **65,** 843-846.

Einen, O., Mørkøre, T., Rørå, A. M. B. & Thomassen, M. S. (1999). Feed ration prior to slaughter—a potential tool for managing product quality of Atlantic salmon (*Salmo salar*). *Aquaculture,* **178,** 149-169.

FAO (2014). The state of world fisheries and aquaculture. Rome: Food and Agriculture Organization of the United Nations.

FAO. 2016. *Cultured aquatic species information programme Salmo salar* [Online]. Available: http://www.fao.org/fishery/culturedspecies/Salmo_salar/en [Accessed 7 May 2016].

Farrell, A. P., Johansen, J. A. & Suarez, R. K. (1991). Effects of exercise-training on cardiac performance and muscle enzymes in rainbow trout, *Oncorhynchus mykiss*. *Fish Physiology and Biochemistry,* **9,** 303-312.

Føre, M., Dempster, T., Alfredsen, J. A., Johansen, V. & Johansson, D. (2009). Modelling of Atlantic salmon (*Salmo salar* L.) behaviour in sea-cages: a Lagrangian approach. *Aquaculture,* **288,** 196-204.

Gallaugher, P. E., Thorarensen, H., Kiessling, A. & Farrell, A. P. (2001). Effects of high intensity exercise training on cardiovascular function, oxygen uptake, internal oxygen transport and osmotic balance in chinook salmon (*Oncorhynchus tshawytscha*) during critical speed swimming. *The Journal of Experimental Biology,* **204,** 2861-2872.

Haard, N. F. (1992). Control of chemical composition and food quality attributes of cultured fish. *Food Research International,* **25,** 289-307.

Hagen, Ø. & Johnsen, C. A. (2016). Flesh quality and biochemistry of light-manipulated Atlantic cod (*Gadus morhua*) and the significance of collagen cross-links on fillet firmness and gaping. *Food Chemistry,* **190,** 786-792.

Hagen, Ø. & Solberg, C. (2010). Fasting of farmed Atlantic cod (*Gadus morhua* L.) used as tool to improve fillet texture during the summer. *International Journal of Food Science & Technology,* **45,** 2669-2673.

Hagen, Ø., Solberg, C., Sirnes, E. & Johnston, I. A. (2007). Biochemical and structural factors contributing to seasonal variation in the texture of farmed Atlantic halibut (*Hippoglossus hippoglossus* L.) flesh. *Journal of Agricultural and Food Chemistry,* **55,** 5803-5808.

Hamre, K., Lie, Ø. & Sandnes, K. (2003). Seasonal development of nutrient composition, lipid oxidation and colour of fillets from Norwegian spring-spawning herring (*Clupea harengus* L.). *Food Chemistry,* **82,** 441-446.

Henmi, H., Hata, M. & Hata, M. (1990). Combination of astaxanthin and canthaxanthin with fish muscle actomyosins associated with their surface hydrophobicity. *Nippon Suisan Gakkaishi,* **56,** 1821-1823.

Houlihan, D. F. & Laurent, P. (1987). Effects of exercise training on the performance, growth, and protein turnover of rainbow trout (*Salmo gairdneri*). *Canadian Journal of Fisheries and Aquatic Sciences,* **44,** 1614-1621.

Hunter, R. S. & Harold, R. W. (1987). *The measure of appearance* (pp. 411).

Imsland, A. K., Reynolds, P., Eliassen, G., Hangstad, T. A., Foss, A., Vikingstad, E. & Elvegård, T. A. (2014). The use of lumpfish (*Cyclopterus lumpus* L.) to control sea lice (*Lepeophtheirus salmonis* Krøyer) infestations in intensively farmed Atlantic salmon (*Salmo salar* L.). *Aquaculture,* **424–425,** 18-23.

Jobling, M., Baardvik, B. M., Christiansen, J. S. & Jørgensen, E. H. (1993). The effects of prolonged exercise training on growth performance and production parameters in fish. *Aquaculture International,* **1,** 95-111.

Johansson, D., Juell, J. E., Oppedal, F., Stiansen, J. E. & Ruohonen, K. (2007). The influence of the pycnocline and cage resistance on current flow, oxygen flux and swimming behaviour of Atlantic salmon (*Salmo salar* L.) in production cages. *Aquaculture,* **265,** 271-287.

Johnsen, C. A., Hagen, Ø. & Bendiksen, E. Å. (2011). Long-term effects of high-energy, low-fishmeal feeds on growth and flesh characteristics of Atlantic salmon (*Salmo salar* L.). *Aquaculture,* **312,** 109-116.

Johnsen, C. A., Hagen, Ø., Solberg, C., Björnsson, B. T. H., Jönsson, E., Johansen, S. J. S. & Bendiksen, E. Å. (2013). Seasonal changes in muscle structure and flesh quality of 0+ and 1+ Atlantic salmon (*Salmo salar* L.): impact of feeding regime and possible roles of ghrelin. *Aquaculture Nutrition,* **19,** 15-34.

Johnston, I. A., Alderson, R., Sandham, C., Dingwall, A., Mitchell, D., Selkirk, C., Nickell, D., Baker, R., Robertson, B. & Whyte, D. (2000). Muscle fibre density in relation to the colour and texture of smoked Atlantic salmon (*Salmo salar* L.). *Aquaculture,* **189,** 335-349.

Johnston, I. A., Manthri, S., Bickerdike, R., Dingwall, A., Luijkx, R., Campbell, P., Nickell, D. & Alderson, R. (2004). Growth performance, muscle structure and flesh quality in out-of-season Atlantic salmon (*Salmo salar*) smolts reared under two different photoperiod regimes. *Aquaculture,* **237,** 281-300.

Jørgensen, E. H. & Jobling, M. (1993). The effects of exercise on growth, food utilisation and osmoregulatory capacity of juvenile Atlantic salmon, *Salmo salar*. *Aquaculture,* **116,** 233-246.

Jørgensen, E. H. & Jobling, M. (1994). Feeding and growth of exercised and unexercised juvenile Atlantic salmon in freshwater, and performance after transfer to seawater. *Aquaculture International,* **2,** 154-164.

Khan, J. R., Pether, S., Bruce, M., Walker, S. P., Hemar, Y. & Herbert, N. A. (2015). Exercise training reduces the flesh firmness of juvenile hāpuku (*Polyprion oxygeneios*) with a hypertrophic reduction in muscle fibre density. *New Zealand Journal of Marine and Freshwater Research,* **49,** 429-438.

Lauff, R. F. & Wood, C. H. (1996). Respiratory gas exchange, nitrogenous waste excretion, and fuel usage during aerobic swimming in juvenile rainbow trout. *Journal of Comparative Physiology B,* **166,** 501-509.

Lavety, J., Afolabi, O. A. & Love, R. M. (1988). The connective tissues of fish. IX. Gaping in farmed species. *International Journal of Food Science & Technology,* **23,** 23-30.

Leclercq, E., Davie, A. & Migaud, H. (2014). Delousing efficiency of farmed ballan wrasse (*Labrus bergylta*) against *Lepeophtheirus salmonis* infecting Atlantic salmon (*Salmo salar*) post-smolts. *Pest Management Science,* **70,** 1274-1282.

Lekang, O. I. (2007). *Aquaculture engineering* (pp. 183-184). Oxford: Wiley-Blackwell.

Lerfall, J., Bendiksen, E. Å., Olsen, J. V., Morrice, D. & Østerlie, M. (2016). A comparative study of organic- versus conventional farmed Atlantic salmon. I. Pigment and lipid content and composition, and carotenoid stability in ice-stored fillets. *Aquaculture,* **451,** 170-177.

Li, X., Bickerdike, R., Lindsay, E., Campbell, P., Nickell, D., Dingwall, A. & Johnston, I. A. (2005). Hydroxylysyl pyridinoline cross-link concentration affects the textural properties of fresh and smoked Atlantic salmon (*Salmo salar* L.) flesh. *Journal of Agricultural and Food Chemistry,* **53,** 6844-6850.

Love, R. M. (1988). *The food fishes: their intrinsic variation and practical implications.* London: Farrand Press.

Luther, P. K., Munro, P. M. G. & Squire, J. M. (1995). Muscle ultrastructure in the teleost fish. *Micron,* **26,** 431-459.

Mente, E., Pierce, G. J., Santos, M. B. & Neofitou, C. (2006). Effect of feed and feeding in the culture of salmonids on the marine aquatic environment: a synthesis for European aquaculture. *Aquaculture International,* **14,** 499-522.

Michie, I. (2001). Causes of downgrading in the salmon farming industry. *In:* Kestin, S. C. & Warriss, P. D. (eds.), *Farmed fsh quality* (pp. 129-136). Oxford: Wiley-Blackwell.

Mørkøre, T., Ruohonen, K. & Kiessling, A. (2009). Variation in texture of farmed Atlantic salmon (*Salmo salar* L.) relevance of muscle fiber cross-sectional area. *Journal of Texture Studies,* **40,** 1-15.

Mørkøre, T., Vallet, J. L., Cardinal, M., Gomez-Guillen, M. C., Montero, P., Torrissen, O. J., Nortvedt, R., Sigurgisladottir, S. & Thomassen, M. S. (2001). Fat content and fillet shape of Atlantic salmon: relevance for processing yield and quality of raw and smoked products. *Journal of Food Science,* **66,** 1348-1354.

Nanton, D. A., Lall, S. P., Ross, N. W. & McNiven, M. A. (2003). Effect of dietary lipid level on fatty acid β-oxidation and lipid composition in various tissues of haddock, *Melanogrammus aeglefinus* L. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology,* **135,** 95-108.

NDF. 2014. *Grown out: Sale 1994-2014* [Online]. Norway: Norwegian Directorate of Fisheries. Available: http://www.fiskeridir.no/English/Aquaculture/Statistics/Atlantic-salmon-and-rainbow-trout [Accessed 29 October 2015].

Nickell, D. C. & Springate, J. R. C. (2001). Pigmentation of farmed salmonids. *In:* Kestin, S. C. & Warriss, P. D. (eds.), *Farmed fish quality* (pp. 58-75). Oxford: Wiley-Blackwell.

NOAA. n.d. *What is Aquaculture* [Online]. Available: http://www.nmfs.noaa.gov/aquaculture/what_is_aquaculture.html [Accessed 1 May 2016].

Oca, J., Masaló, I. & Reig, L. (2004). Comparative analysis of flow patterns in aquaculture rectangular tanks with different water inlet characteristics. *Aquacultural Engineering,* **31,** 221-236.

Rasmussen, R. S., Heinrich, M. T., Hyldig, G., Jacobsen, C. & Jokumsen, A. (2011). Moderate exercise of rainbow trout induces only minor differences in fatty acid profile, texture, white muscle fibres and proximate chemical composition of fillets. *Aquaculture,* **314,** 159-164.

Refstie, S., Storebakken, T., Baeverfjord, G. & Roem, A. J. (2001). Long-term protein and lipid growth of Atlantic salmon (*Salmo salar*) fed diets with partial replacement of fish meal by soy protein products at medium or high lipid level. *Aquaculture,* **193,** 91-106.

Robb, D. H. F., Kestin, S. C. & Warriss, P. D. (2000). Muscle activity at slaughter: I. Changes in flesh colour and gaping in rainbow trout. *Aquaculture,* **182,** 261-269.

Ruxton, C. H. S., Reed, S. C., Simpson, M. J. A. & Millington, K. J. (2004). The health benefits of omega-3 polyunsaturated fatty acids: a review of the evidence. *Journal of Human Nutrition and Dietetics,* **17,** 449-459.

Rørå, A. M. B., Kvåle, A., Mørkøre, T., Rørvik, K. A., Hallbjoørn, S., Thomassen, S. & Magny, S. (1998). Process yield, colour and sensory quality of smoked Atlantic salmon (*Salmo salar*) in relation to raw material characteristics. *Food Research International,* **31,** 601-609.

Shearer, W. M. (1992). *The Atlantic salmon: natural history, exploitation and future management.* New York: Halsted Press.

Sigholt, T., Erikson, U., Rustad, T., Johansen, S., Nordtvedt, T. S. & Seland, A. (1997). Handling stress and storage temperature affect meat quality of farmed-raised Atlantic salmon (*Salmo Salar*). *Journal of Food Science,* **62,** 898-905.

Sigurgisladottir, S., Torrissen, O., Lie, Ø., Thomassen, M. & Hafsteinsson, H. (1997). Salmon quality: methods to determine the quality parameters. *Reviews in Fisheries Science,* **5,** 223-252.

Sikorski, Z. E., Pan, B. S. & Shahidi, F. (1995). *Seafood proteins.* London: Chapman and Hall.

Sikorski, Z. E., Scott, D. N., Buisson, D. H. & Love, R. M. (1984). The role of collagen in the quality and processing of fish. *Critical Reviews in Food Science and Nutrition,* **20,** 301-343.

Skjervold, P. O., Rørå, A. M. B., Fjæra, S. O., Vegusdal, A., Vorre, A. & Einen, O. (2001). Effects of pre-, in-, or post-rigor filleting of live chilled Atlantic salmon. *Aquaculture,* **194,** 315-326.

Solstorm, F., Solstorm, D., Oppedal, F., Fernö, A., Fraser, T. & Olsen, R. E. (2015). Fast currents reduce production performance of post-smolt Atlantic salmon *Salmo salar*. *Aquaculture Environment Interactions,* **7,** 125-134.

Sriket, C. (2014). Proteases in fish and shellfish: role on muscle softening and prevention. *International Food Research Journal,* **21,** 433-445.

Sänger, A. M. & Stoiber, W. (2001). Muscle fiber diversity and plasticity. *In:* Johnston, I. A. (ed.), *Muscle growth and development* (pp. 187-250). San Deigo: Academic Press.

Tachibana, K., Doi, T., Tsuchimoto, M., Misima, T., Ogura, M., Matsukiyo, K. & Yasuda, M. (1988). The effect of swimming exercise on flesh texture of cultured red sea-bream. *Nippon Suisan Gakkashi,* **54,** 677-681.

Thorarensen, H. & Farrell, A. P. (2011). The biological requirements for post-smolt Atlantic salmon in closed-containment systems. *Aquaculture,* **312,** 1-14.

Torrissen, O. J. (1985). Pigmentation of salmonids: factors affecting carotenoid deposition in rainbow trout (*Salmo gairdneri*). *Aquaculture,* **46,** 133-142.

Totland, G. K., Kryvi, H., Jødestøl, K. A., Christiansen, E. N., Tangerås, A. & Slinde, E. (1987). Growth and composition of the swimming muscle of adult Atlantic salmon (*Salmo salar* L.) during long-term sustained swimming. *Aquaculture,* **66,** 299-313.

Veland, J. O. & Torrissen, O. J. (1999). The texture of Atlantic salmon (*Salmo salar*) muscle as measured instrumentally using TPA and Warner-Brazler shear test. *Journal of the Science of Food and Agriculture,* **79,** 1737-1746.

Videler, J. J. (1993). The structure of the swimming apparatus: muscles. *Fish swimming* (pp. 23-39). London: Chapman and Hall.

Zayas, J. F. (1997). Water holding capacity of proteins. *In:* Zayas, J. F. (ed.), *Functionality of proteins in food* (pp. 76-133). Berlin: Springer.

Appendix: Correlations

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Round weight (g)	1														
2	Fork length (cm)	**,801****	1													
3	Gutted weight (g)	**,996****	**,806****	1												
4	Condition factor	**,381****	-,244	**,367****	1											
5	HSI	**,320***	,124	**,298***	**,333****	1										
6	RVM	,070	,033	,054	,085	-,054	1									
7	SlmoFan	,237	,238	,245	,021	,025	,035	1								
8	L*	,257	**,319***	,252	-,080	,178	,018	-,253	1							
9	a*	,225	,169	,229	,124	,195	,153	,242	,094	1						
10	b*	,072	,056	,083	,061	,151	,236	,034	,191	**,831****	1					
11	Gaping	,076	,113	,075	-,064	-,002	-,082	,092	,252	,055	-,008	1				
12	Water (%)	**-,452****	**-,359****	**-,475****	-,202	-,103	,003	,033	**-,481****	**-,325***	**-,307***	-,128	1			
13	Protein (%)	-,122	-,039	-,117	-,124	,034	-,132	,179	**-,446****	-,131	-,250	-,097	**,599****	1		
14	Lipid (%)	**,388****	**,298****	**,397****	,188	,091	-,015	-,054	**,506****	**,305***	**,314***	.163	**-,948****	**-,731****	1	
15	Fillet yield (%)	,254	-,007	**,293***	**,403****	-,013	,002	-,024	-,185	-,022	-,067	-,037	-,262	-,219	,231	1

**.Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

c. Cannot be computed because at least one of the variables is constant.