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Increased protein-to-lipid ratio in energy dense diets improves slaughter yields and muscle thickness of different weight classes of farmed Atlantic salmon (*Salmo salar* L.)

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ABSTRACT

Two isoenergetic feeding strategies, with emphasis on the grow-out stage (> 1 kg), with dietary high (HP > 1.1) and low protein-to-lipid ratio (LP < 1.0) were tested by using year-old smolt (S1) and under-year-old smolt (S0) Atlantic salmon in two large-scale trials, respectively, and in one small-scale experiment using S1 smolt. This was done to investigate the dietary influence on slaughter yield, muscle fat content, condition factor and thickness of the hypaxial anterior muscle (HAM) in all three trials. In addition, effects on the viscerosomatic index (VSI) was included in the small-scale trial. The initial body weights in the three trials were 100 g, 319 g and 978 g, respectively. At harvest, fish for analyzes were sampled into three weight classes of 4.5 kg, 5.5 kg, 6.5 kg in the large-scale trials, and 2.4 kg, 3.2 kg and 4.0 kg in the small-scale trial. In all three trials, the dietary HP strategy significantly improved slaughter yield ($p < 0.01$). In the large-scale trials, fish of the HP groups had lower muscle fat ($p < 0.05$), higher condition factor (significant in the S1 group: $p < 0.01$) and a trend towards a thicker HAM ($p \leq 0.10$) than the LP groups. In all three trials, there were a significant positive relation between condition factor and HAM. The small-scale trial verified the large-scale trials revealing significantly lower VSI ($p < 0.001$) among the HP groups, partly explaining the high increase in slaughter yield (1.1%) for the HP groups compared to LP groups in the large-scale study. Except for slaughter yield and VSI, weight class significantly influenced all quality traits. Overall, this study indicates that the salmon farming industry, which generally prefers using lipid dense grower feeds, can improve product yields by using isoenergetic feeds with dietary high protein-to-lipid ratio.

1. Introduction

Like in other meat productions, farming Atlantic salmon is about converting feed into edible tissue. In modern salmon farming the primary commodity is fresh head-on gutted salmon which value chain intermediates further process to consumer demanded products. The major energy carriers in feeds for salmon are protein and lipids. Modern commercial salmon grower feeds (made for fish > 1 kg) have most of their energy as lipids, whereas the protein content has decreased over the years, leading to a gradual reduction in the protein-to-lipid ratio in the diet. This dietary strategy has proven to be successful to support good growth and feed utilization (Hillestad et al., 1998; Karalazos et al., 2007, 2011). However, sufficient dietary protein content with a good balance of amino acids is vital to support muscle growth, protein deposition and weight gain (Bureau et al., 2002). Salmon appears to increase fat deposits in both muscle and visceral tissue with increasing lipid content in the feed (Bendiksen et al., 2003; Einen and Roem, 1997; Hillestad et al., 1998; Jobling et al., 2002a). Thus, diets with high and low protein-to-lipid ratios are likely to have divergent influence on the quality characteristics of farmed salmon.

Processing yields greatly influence the economic performance of the value chain for salmon. Therefore, it is important for actors along the value chain to purchase salmon with characteristics that contribute to high yields. Earlier findings have demonstrated that yields are

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influenced by characteristics such as body shape and muscle fat content (Einen, 1998; Mørkøre et al., 2001; Rørå et al., 1998, 2001). Slaughter yield is highlighted as a central quality trait (Rasmussen, 2001), and according to Einen and Roem (1997) and Hillestad et al. (1998), a low-protein/high-fat feeding strategy reduces slaughter yield in salmon. Although these results also seem to be influenced by fish size and feeding rate, lipid dense diets still seem to be the preferred grower feeds within the industry. High slaughter yields are desired since it is the carcass that is the primary source of income for salmon farmers, but these previous findings suggest that the preference of using a low dietary protein-to-lipid strategy leaves an unexploited product yield in the industry.

At harvest, farmed salmon is normally graded into weight classes based on their carcass weight (1-2 kg, 2-3 kg, 3-4 kg and onwards to 9 + kg), often referred to as head-on gutted (HOG) and the various weight classes are priced differently. Historically, salmon price per kg has increased with the increase in weight class (Fish Pool, 2018). Quality characteristics of farmed fish is highly influenced by body weight (Shearer, 1994). However, grouping salmon into different weight classes has rarely been conducted in scientific studies when evaluating dietary effects on quality characteristics and product yield. Quality characteristics such as slaughter yield, fillet yield and fat content can be modulated by starvation or by altering feed rations prior to harvest (Einen et al., 1998, 1999; Wathne, 1995). Today, starvation prior to harvest is done for a short period, mainly to deplete gut content. Although a prolonged starvation period modifies the quality attributes, this is not an optimal production strategy as it also decreases the overall productivity and biomass (Einen, 1998). To optimize the quality, it is necessary to gain knowledge on how the conversion of feed into edible salmon tissue is influenced by dietary composition. It is therefore important that the desired quality characteristics are attained during the feed conversion process itself and not through starvation or feed restriction, so that production losses are avoided.

In the salmon industry, smolts are regularly transported to sea in the spring as year-old smolt (S1) or in the autumn as under-year-old smolt (S0). Given that the smolt weights are relatively similar when transferred to sea, they will reach harvest weights at different times of the year. Because these two smolt types are produced under different circumstances, their growth patterns diverge (Mørkøre and Rørvik, 2001; Roth et al., 2005). However, irrespective of smolt type and time of harvest, the HOG products enter the same markets and follow the normal pricing mechanisms. With the use of lipid dense feeds in modern salmon farming, this paper questions if the potential of farmed salmon destined for further value-added processes is fully utilized. Hence, the main objective of the present study was to evaluate the effects of iso-energetic diets differing in protein-to-lipid ratio on slaughter characteristics of different weight classes of farmed S1 and S0 Atlantic salmon. In an earlier study, we analyzed the dietary influence on specific feeding rate, feed conversion and growth rate (Weihe et al., 2018) which are considered as key performance indicators in salmon production. Since salmon is usually subjected to value adding processes after harvest, by using the same dataset as in Weihe et al. (2018) the present study focuses on slaughter yield, muscle fullness and body shape as key quality attributes. To ensure commercial relevance, the present study used data from two commercial salmon production cycles in addition to data collected through a more controlled study in small-scale.

2. Material and methods

2.1. Experimental design and -diets

Three feeding experiments were conducted using a dietary high protein-to-lipid (HP) and a dietary low protein-to-lipid (LP) feeding strategy in all three trials. Two of the trials were conducted in large-scale commercial seawater facilities using year-old smolt (S1) and under-year-old smolt (S0), and the third feeding trial was carried out in a small-scale facility using S1 smolt. The proximate composition of protein and lipid in the LP diets in all three trials were designed to resemble common commercial diets. The HP diets were designed to have similar energy as the LP diets but with a greater proportion of the energy deriving from protein, increasing the dietary protein-to-lipid ratio.

All the experimental feeds were produced by Havsbrún (Fuglafjørður, Faroe Islands). Because the large-scale trials were conducted in commercial/industrial conditions, multiple batches of feed were produced throughout the experiments whereas in the small-scale trial, two batches per dietary group were used (highlighted with brackets in Table 1). In accordance with standard commercial feed manufacturing, the physical and nutritional quality was monitored throughout the production process. Also, in line with industrial practice, quality specifications and definitions of the feed ingredients were updated quarterly together with the respective raw material prices. Ranked from highest to lowest inclusion level, the main feed ingredients in the large-scale trials were: fishmeal, fish oil, wheat, soy protein concentrate, wheat gluten and sunflower meal. The same ranking in the small-scale trial was: fishmeal, fish oil, rapeseed oil, wheat, wheat gluten and soy protein concentrate. Within all three trials, the HP and LP feeds were supplied with identical vitamin- and mineral premixes. Based on the intended dietary protein and lipid balance, all feeds were composed and produced on a least-cost production strategy.

Feed digestibility was calculated in accordance with Morris et al. (2003), assuming that the apparent digestibility coefficients for protein, lipid and nitrogen free extractives were 0.86, 0.94 (Einen and Roem, 1997) and 0.50 (Arnesen and Krogdahl, 1993), respectively. The chemical composition of the experimental feeds is shown in Table 1. These are based on the weighted mean from each batch supplied to the farming sites. The 3 mm and 4 mm HP diets in the S1 large-scale experiment were intended to contain 52% protein and 24% lipid. The relative large deviation in protein and lipid composition in the 3 mm HP feed was caused by production problems as well as wrongful transport handling which lead to some LP feed being supplied to fish in the dietary HP group. Consequently, fish in the HP group were fed a combination of both HP and LP feed for approximately 4 weeks.

To investigate if feed intake would influence the quality traits, feed intake was measured as specific feeding rate (SFR) in all three experiments. In the large-scale trials, the SFR was measured for the whole experimental periods only, whereas the SFR was split into three feeding periods in the small-scale trial. There were no differences in SFR between the dietary treatments within the large-scale experiments, whereas differences in feeding rate between the dietary groups was observed in the small-scale trial during the initiating autumn period from September to December. An overview of the SFR for all three experiments is given in Table 2.

2.2. Fish material and rearing conditions in the large-scale trials

The S1 and S0 large-scale feeding trials were conducted at commercial farming sites in Lambavík (62°08′N, 06°41′W, Bakkafrost PF) and Sørvágur (62°04′N, 07°22′W, Luna PF), on the east coast and west coast of the Faroe Islands, respectively. Duplicate cages per experimental diet were used on both sites. The S1 trial started when the smolts were stocked in May 2009, whereas the S0 trial started in March 2009 after the smolts had been stocked in October 2008 and fed 3 mm (48% protein, 27% lipid) and 4 mm (46% protein, 30% lipid) feeds until March, similar to the diets described in Dessen et al. (2017). The weight and number of fish in the S1 group at trial initiation was 100 ± 5 g and 66,627 ± 213 (mean ± SEM), respectively, whereas in the S0 smolt group, the weight and number of fish was 319 ± 5 g and 60,371 ± 243 (mean ± SEM), respectively. Feeding and production on both sites followed the routines of the respective fish farming companies Bakkafrost and Luna. An overview of the design is presented

Table 1
Chemical feed compositions (as is) in all three experiments. Brackets demonstrate the number of feed batches used in the experiment per pellet size per dietary treatment. Values are given as weighted means per diet. HP: dietary high protein-to-lipid ratio strategy. LP: dietary low protein-to-lipid ratio strategy.

Experiment (smolt group)	Large-scale S1		Large-scale S0		Small-scale S1	
Diet	HP	LP	HP	LP	HP	LP
Pellet size 3 mm	*(n = 2)*	*(n = 4)*				
Dry matter, g kg^{-1}	933	931				
Crude protein, g kg^{-1}	499	466				
Lipid, g kg^{-1}	256	272				
Ash, g kg^{-1}	94	87				
Starch, g kg^{-1a}	67	86				
DE, MJ kg^{-1b}	20.3	20.5				
Protein-to-lipid ratio	1.95	1.71				
Pellet size 4 mm	*(n = 3)*	*(n = 5)*				
Dry matter, g kg^{-1}	941	934				
Crude protein, g kg^{-1}	521	458				
Lipid, g kg^{-1}	221	287				
Ash, g kg^{-1}	110	86				
Starch, g kg^{-1a}	69	87				
DE, MJ kg^{-1b}	19.6	20.9				
Protein-to-lipid ratio	2.36	1.60				
Pellet size 6 mm	*(n = 2)*	*(n = 7)*	*(n = 2)*	*(n = 9)*		
Dry matter, g kg^{-1}	956	942	941	939		
Crude protein, g kg^{-1}	466	419	444	427		
Lipid, g kg^{-1}	276	324	308	316		
Ash, g kg^{-1}	95	81	82	78		
Starch, g kg^{-1a}	86	89	83	90		
DE, MJ kg^{-1b}	20.8	21.6	21.4	21.5		
Protein-to-lipid ratio	1.69	1.29	1.44	1.35		
Pellet size 9 mm	*(n = 10)*	*(n = 70)*	*(n = 10)*	*(n = 19)*	*(n = 2)*	*(n = 2)*
Dry matter, g kg^{-1}	937	941	940	942	941	943
Crude protein, g kg^{-1}	420	354	402	345	427	354
Lipid, g kg^{-1}	326	359	344	358	321	360
Ash, g kg^{-1}	81	64	80	67	79	71
Starch, g kg^{-1a}	84	96	91	98	85	110
DE, MJ kg^{-1b}	21.6	22.0	21.9	21.8	21.6	21.9
Protein-to-lipid ratio	1.29	0.99	1.17	0.96	1.33	0.98

aStarch content was not analysed in all feed batches. The stated value is the average of the analysed batches
bDigestible energy (DE) was calculated based on the measured proximate feed composition, assuming 23.7, 39.5 and 17.2 MJ kg of protein, lipids and nitrogen-free extractives (NFE), respectively. The apparent digestibility coefficients used for protein, lipid and NFE were 0.86 (Einen and Roem, 1997), 0.94 (Einen and Roem, 1997) and 0.50 (Arnesen and Krogdahl, 1993).

in Fig. 1. See Weihe et al. (2018) for more details about the rearing conditions in the large-scale trials.

2.3. Fish material and rearing conditions in the small-scale trial

The third feeding trial was conducted in 2012 with S1 smolt in small-scale facilities at Nofima's research station at Ekkilsøy (currently owned by Marine Harvest Fish Feed AS) on the west coast of Norway (63°03′N, 07°35′E). At trial initiation, 150 S1 salmon weighing 978 ± 1 g (mean ± SEM) were randomly distributed in six 5 × 5 x 5 m cages in three blocks, and the two dietary treatments were fed to triplicate groups of fish from 27th of September 2012 to 10th of June 2013 divided into three feeding periods: (1) 27th of September to 4th of December, (2) 7th of December to 8th of April, and (3) 11th of April to 10th of June (Weihe et al., 2018). Fish were fed to daily satiation by approximately 10% overfeeding based on the feed consumption from the day before, following a subsequent collection of excess feed which was analyzed for recovery and dry matter as described by Einen et al. (1999) and Helland et al. (1996), respectively. The fish material had previously been stocked in sea as 95 g smolt in April 2012 and were fed high-protein diets in an earlier feeding experiment until September 2012 which is presented in Dessen et al., (2017). During this earlier trial, the salmon had a body weight gain of 850 g, ending up with a body composition of 17.6% protein and 16.0% lipid. Fig. 1 gives an overview of all three feeding experiments, and Weihe et al. (2018) have more details about the rearing conditions in all three trials.

Table 2
Specific feeding rate (SFR) for year-old (S1) and under-year-old (S0) Atlantic salmon in the two large-scale trials as well as in the small-scale trial, fed diets with either high protein-to-lipid ratio (HP) or low protein-to-lipid ratio (LP). Significant differences between the dietary treatments are depicted with *p*-values, whereas non-significance is abbreviated as ns. Data are given as mean ± SEM. (n = 2 in the large-scale trials; n = 3 in the small-scale trial).

		SFR, %		ANOVA	
		HP	LP	P	R^2
Large-scale S1		0.55 ± 0.00	0.56 ± 0.02	ns	–
Large-scale S0		0.51 ± 0.02	0.52 ± 0.02	ns	–
Small-scale S1	Sep - Dec	0.87 ± 0.01	0.93 ± 0.01	0.006	0.88
	Dec - Apr	0.31 ± 0.01	0.33 ± 0.01	ns	–
	Apr - Jun	0.43 ± 0.01	0.44 ± 0.00	ns	–

2.4. Sampling procedure in the large-scale trials

The final sampling in the S0 trial was conducted 8th of April 2010 (~12 months after trial initiation and ~17 months after stocking) which represented the date when the commercial harvest started. In the S1 trial, fish from three experimental units were sampled during 12th-20th of August (~16 months after initiation) whereas the fourth unit was sampled 1st of October (~17 months after initiation). The sampling of fish in each experimental unit was conducted at the first day of

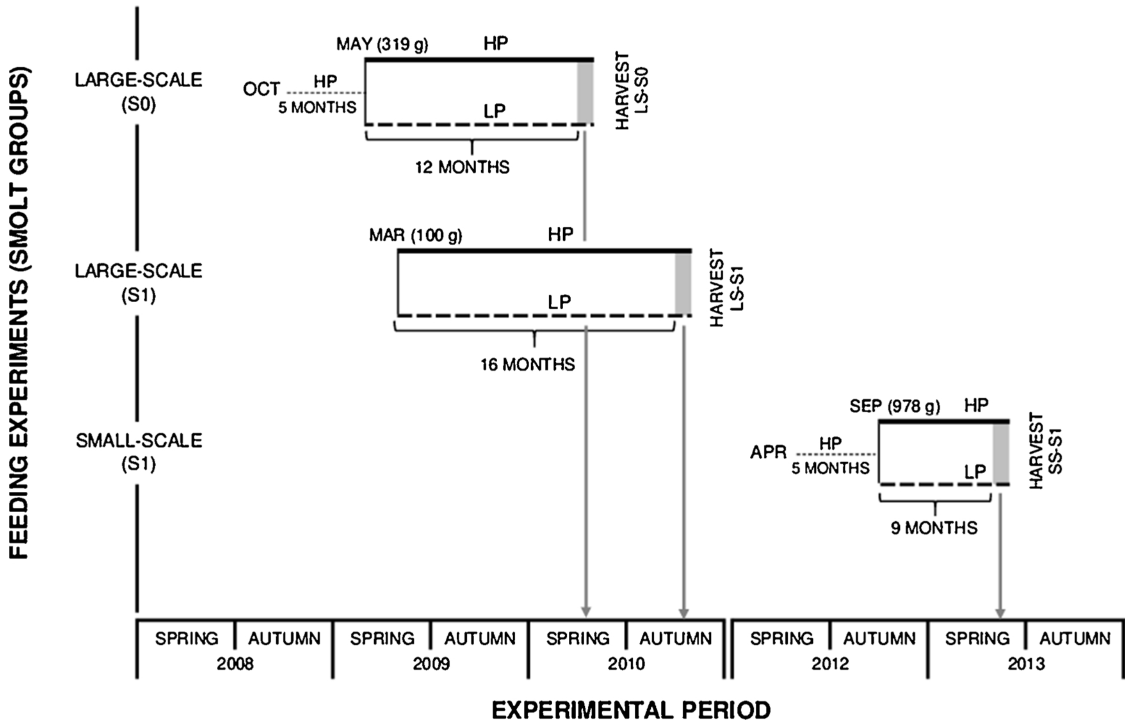

Fig. 1. Schematic overview of the three feeding trials in the experimental design specified with scale size (large-scale or small-scale), smolt group (S1 or S0) and the respective body weight of the salmon and month at trial initiation. The large-scale S0 trial started after the smolt had been in the sea for five months (thin dotted line) fed high-protein feed (HP), whilst this was also the case for the small-scale S1 salmon which had been fed HP feed prior to the trial initiation. For each feeding experiment, the high protein-to-lipid ratio feeding strategy (HP) is marked with a thick black line whereas the low protein-to-lipid ratio feeding strategy (LP) is marked with a black broken line. The shaded area represents the harvesting periods in each experment and highlighted with grey arrowed lines whether this was in the spring or autumn.

harvest of each unit. Here, 10 fish with virtually identical body weight (Tables 3 and 4) within each weight class of 4.5 kg, 5.5 kg and 6.5 kg were sampled (30 fish in total from each cage), aiming to attain equal average body weight for each of the two dietary groups within each weight class. By changing body weight from being a continuous variable to a class variable with 10 fish making up the mean weight of each weight class, it would be easier and more reproducible to visualize potential dietary influence on quality traits. Based on the operative software feeding systems that were used on the farming sites, which continuously estimated body weight development of the fish based on daily feeding quantities, in combination with the fact that the Faroese salmon generally has a harvest weight between 5 kg and 6 kg (Nystøyl, 2018), the chosen weight classes were considered to represent the main weight classes of the overall harvested fish. Larger weight classes yield higher prices per kilo (Fish Pool, 2018), and it is therefore reasonable to assume that salmon producers aim to attain high harvest weights ($>$ 4 kg) compared to lower weights ($<$ 4 kg). Thus, sampling salmon smaller than 4 kg did not seem to be very relevant from a commercial perspective.

The 3 × 10 fish in each experimental unit were sampled from the bleeding tank within the commercial harvesting facilities after the salmon had been killed and bled out using an automated swim-in killing and bleeding system (SI-7 Combo) complying to standard procedures at the commercial harvesting sites. The weights of sampled fish were corrected for 2.7% blood loss in accordance with Einen et al. (1998). First, body weight (BW) and body length (BL: fork length) of each fish was measured. Thereafter, the fish were cut open, cleaned and rinsed with water and carcass weight (CW) recorded. Carcass weight was defined as the weight after the fish was bled and all visceral contents removed, including heart, liver and kidneys. The thickness of the hypaxial anterior muscle (HAM) was measured before muscle samples were taken (Norwegian Quality Cut, NQC, NS 9401, Norwegian Standard, 1994a) for rapid analysis of muscle fat (MFAT).

2.5. Sampling procedure in the small-scale trial

At the end of each feeding period, all fish in the individual experimental cages were taken out and anesthetized in batches with MS-222 (Metacaine 0.1 g L^{-1}; Alpharma, Animal Health Ltd., UK) and subsequently bulk weighed and counted. Ten fish representing the average body weight in each cage were killed with a blow to the head and bled out. These fish were measured for body weight, visceral weight and analyzed for muscle fat.

At the final sampling 11th of June 2013, all fish in the individual experimental cages were anesthetized, bulk weighed and counted. The salmon were harvested over a three-day period, one block for each day. The fish in each block were starved for 3 days prior to harvest. Following the sampling procedure from the large-scale trials, thirty fish in each experimental unit were divided into subgroups of 10 fish, representing the weight classes of 2.4 kg, 3.2 kg and 4.0 kg and given a lethal dose of MS-222 before being individually measured for body weight and length. Thereafter, the sampled fish were cut open and visceral content weighed, followed up with measurements of carcass weight and muscle thickness (HAM), in accordance with the large-scale procedure. Finally, the NQC was cut for rapid analysis of muscle fat.

The seawater temperature during the trial were the coldest compared to the previous fifteen years at this location. Salmon are poikilothermic and therefore the colder temperatures had a negative influence on feed intake and subsequently growth. Thus, salmon in the small-scale experiment did not attain as high body weight as the salmon in the large-scale trials which ultimately resulted in sampling of smaller fish.

2.6. Fish analysis

The fat level (%) was predicted by digital image analyses, as described by Folkestad et al. (2008) by photographing the filleted left

NQC cutlet using the PhotoFish box (PhotoFish, AKVAgroup, Bryne, Norway). The predictions made by the image analyses were calibrated against individual chemical analysis of fat (NS 9402, Norwegian Standard, 1994b) based on a great number of salmon with different body weight (0.5–7.0 kg) and levels of fat (3.6–22.9%). Highly significant correlation between the predicted and measured values for fat are documented ($p < 0.0001$, $R^2 = 0.95$; MSE of 10 fish is 0.5%, Rørvik et al., 2014). This non-invasive method for determination of fat has been used successfully in previous studies of Atlantic salmon (Arge et al., 2012; Dessen et al., 2016; Rørvik et al., 2018). Muscle thickness (HAM) was measured with a slide caliper behind the pectoral fin above the belly flap, according to the section of the fish described by Einen et al. (1998).

2.7. Calculations

Specific feeding rate: SFR = (feed intake during the time period (kg) x average biomass weight during the time period (kg)) × 100^{-1}. Condition factor based on whole body weight: CF_{BW} = body weight (g)/body length (cm)^3. Condition factor based on carcass weight: CF_{CW} = carcass weight (g)/body length (cm)^3. Slaughter yield: SY = carcass weight (g)/body weight (g) × 100. Viscerosomatic index: VSI = visceral mass (g)/body weight (g) × 100.

2.8. Statistical analysis

The results from the large-scale trials were initially analyzed by the General Linear Model (GLM) procedure using dietary treatment (HP and LP, referred to as D) and weight class (4.5 kg, 5.5 kg and 6.5 kg, referred to as WC) as class variables (see Section 2.4) and their interaction (D x WC). The dependent variables were body weight (BW), body length (BL), muscle fat content (MFAT), slaughter yield (SY), condition factor based on body weight (CF_{BW}), condition factor based on carcass weight (CF_{CW}) and hypaxial anterior muscle thickness (HAM). As the statistical analysis showed no significant effects of the interaction term (D x WC) on the traits studied, the data were analyzed using D and WC as the experimental factors (similar to a two-way ANOVA). The small-scale trial was based on a randomized block design and the results were initially analyzed by the GLM using block (1, 2 and 3), D and WC (2.4 kg, 3.2 kg and 4.0 kg) as class variables (see Section 2.5). The dependent variables were the same as in the large-scale trial including viscerosomatic index (VSI) as a quality trait. Because the statistical analysis found no significant effects of block nor the interaction term between D and WC (except for VSI), the small-scale data were analyzed in the same way as the data in the large-scale statistical model. Cages were used as the experimental units, with two replicate cages (n = 2) per dietary treatment in the large-scale trials and three replicates (n = 3) in the small-scale trial.

All results are presented as means ± SEM unless otherwise stated and the proportion of total variation explained by the model is expressed as R^2. The level of significance was chosen as $p \leq 0.05$ whereas $p \leq 0.10$ was considered a trend and significant differences between means were determined by Tukey's HSD tests. The statistical analyses were carried out with the SYSTAT® 13 software package (SYSTAT Software Inc., USA) and Microsoft Office Excel 2016 (Microsoft Corporation, USA).

3. Results

3.1. Large-scale experiments

3.1.1. Body weight and body length

There were highly significant differences in body weight between weight classes, but no differences between the dietary treatments within smolt groups (Table 3,4). Within the S1 smolt group, fish in the dietary LP group was significantly longer compared to the HP group (Table 3).

3.1.2. Muscle fat content and slaughter yield

At harvest, salmon fed the LP diet had significantly higher muscle fat than those fed the HP diet in both smolt groups (Table 3,4). Muscle fat content increased significantly with increase in weight class in the S0 group (Table 4) and a similar trend ($p = 0.07$) was seen in the S1 group.

Within both smolt groups, fish fed the HP diet had significantly higher slaughter yield than those fed the LP diet (Table 3,4), in average 1.1% higher in the S1 group and 1.2% in the S0 group.

3.1.3. Body shape and muscle thickness

Condition factors (CF_{BW} and CF_{CW}) were markedly influenced by weight class in both large-scale experiments (Table 3,4), the biggest fish having the highest CF. In the S1 group, CF_{BW} and CF_{CW} were significantly higher in the HP group than in the fish fed the LP diet (Table 3). This was not observed within the S0 smolt group with regards to CF_{BW} (Table 4), but there was a trend ($p = 0.08$) towards increased CF_{CW} in the HP group (Table 3).

As expected, HAM thickness (mm) increased with increasing weight class (Table 3,4). ANOVA identified a significant influence of weight class together with a trend ($p \leq 0.10$) towards improved HAM thickness in the HP groups (Table 3,4). In all weight classes in both smolt groups, the HAM was numerically higher in the HP group than in the LP group, average 0.33 to 0.37 mm thicker in the HP group, resulting in *p*-values between 0.008 and 0.06 in a simple paired *t*-test analysis. There were positive and significant linear relationships between CF_{BW} and HAM (Fig. 2a, b) in both smolt groups. Based on the presented regression equations, an increase in CF_{BW} by 0.1 improves HAM by 1.8 mm in the S1 smolt group compared to 0.8 mm in the S0 smolt group. This linear relationship was also observed between CF_{CW} and HAM (S1: $p = 0.04$, S0: $p = 0.001$)

Table 3
Quality characteristics at harvest (mean ± SEM, n = 2) of year-old Atlantic Salmon (S1) after being produced in large-scale commercial environment and fed diets with high protein-to-lipid ratio (HP) or low protein-to-lipid ratio (LP). Significant differences between the dietary treatments are depicted with *p*-values, and trends of significance are highlighted with brackets. Non-significance is abbreviated as ns. BW: body weight, BL: body length, MFAT: muscle fat, SY: slaughter yield, CF_{BW}: condition factor based on body weight, CF_{CW}: condition factor based on carcass weight, HAM: thickness of the hypaxial anterior muscle, D: diet, WC: weight class.

LS-S1	HP			LP			ANOVA		
	4.5 kg	5.5 kg	6.5 kg	4.5 kg	5.5 kg	6.5 kg	D	WC	R^2
BW, kg	4580 ± 40	5625 ± 51	6602 ± 17	4649 ± 25	5595 ± 44	6622 ± 69	ns	< 0.001	0.99
BL, cm	71.0 ± 0.3	75.6 ± 0.1	78.9 ± 0.2	71.9 ± 0.2	76.0 ± 0.1	79.8 ± 0.4	< 0.01	< 0.001	0.99
MFAT, %	15.7 ± 0.6	16.2 ± 0.3	17.3 ± 0.4	17.2 ± 0.3	17.8 ± 0.7	18.0 ± 0.3	< 0.01	ns	0.45
SY, %	87.9 ± 0.1	87.8 ± 0.2	87.5 ± 0.2	86.8 ± 0.5	86.6 ± 0.7	86.6 ± 0.9	0.01	ns	0.49
CF_{BW}	1.28 ± 0.00	1.31 ± 0.02	1.35 ± 0.02	1.25 ± 0.00	1.28 ± 0.02	1.31 ± 0.00	< 0.01	< 0.01	0.84
CF_{CW}	1.13 ± 0.00	1.15 ± 0.01	1.18 ± 0.02	1.09 ± 0.00	1.11 ± 0.00	1.13 ± 0.02	0.001	< 0.01	0.86
HAM, mm	9.8 ± 0.2	10.8 ± 0.4	11.3 ± 0.3	9.6 ± 0.0	10.3 ± 0.1	11.0 ± 0.3	(0.10)	0.001	0.82

Table 4
Quality characteristics at harvest (mean ± SEM, n = 2) of under-year-old Atlantic Salmon (S0) after being produced in large-scale commercial environment and fed diets with high protein-to-lipid ratio (HP) or low protein-to-lipid ratio (LP). Significant differences between the dietary treatments are depicted with *p*-values, and trends of significance are highlighted with brackets. Non-significance is abbreviated as ns. BW: body weight, BL: body length, MFAT: muscle fat, SY: slaughter yield, CF_{BW}: condition factor based on body weight, CF_{CW}: condition factor based on carcass weight, HAM: thickness of the hypaxial anterior muscle, D: diet, WC: weight class.

LS-S0	HP			LP			ANOVA		
	4.5 kg	5.5 kg	6.5 kg	4.5 kg	5.5 kg	6.5 kg	D	WC	R^2
BW, kg	4678 ± 35	5692 ± 2	6697 ± 32	4644 ± 22	5651 ± 16	6755 ± 23	ns	< 0.001	0.99
BL, cm	71.6 ± 0.2	76.3 ± 0.0	78.1 ± 0.6	72.4 ± 0.4	76.4 ± 1.4	79.3 ± 0.6	ns	< 0.001	0.93
MFAT, %	16.1 ± 0.1	16.7 ± 0.5	18.2 ± 0.1	16.7 ± 0.1	17.9 ± 0.7	18.8 ± 0.7	0.05	< 0.01	0.80
SY, %	86.4 ± 0.5	86.8 ± 0.0	86.3 ± 0.8	85.7 ± 0.9	85.2 ± 0.2	85.0 ± 0.4	< 0.01	ns	0.51
CF_{BW}	1.28 ± 0.00	1.29 ± 0.00	1.41 ± 0.02	1.23 ± 0.03	1.28 ± 0.08	1.36 ± 0.00	ns	0.01	0.63
CF_{CW}	1.10 ± 0.01	1.12 ± 0.00	1.21 ± 0.01	1.06 ± 0.02	1.09 ± 0.07	1.16 ± 0.00	(0.08)	0.02	0.58
HAM, mm	9.7 ± 0.2	10.1 ± 0.3	10.8 ± 0.3	9.3 ± 0.3	9.8 ± 0.4	10.4 ± 0.4	(0.07)	0.02	0.59

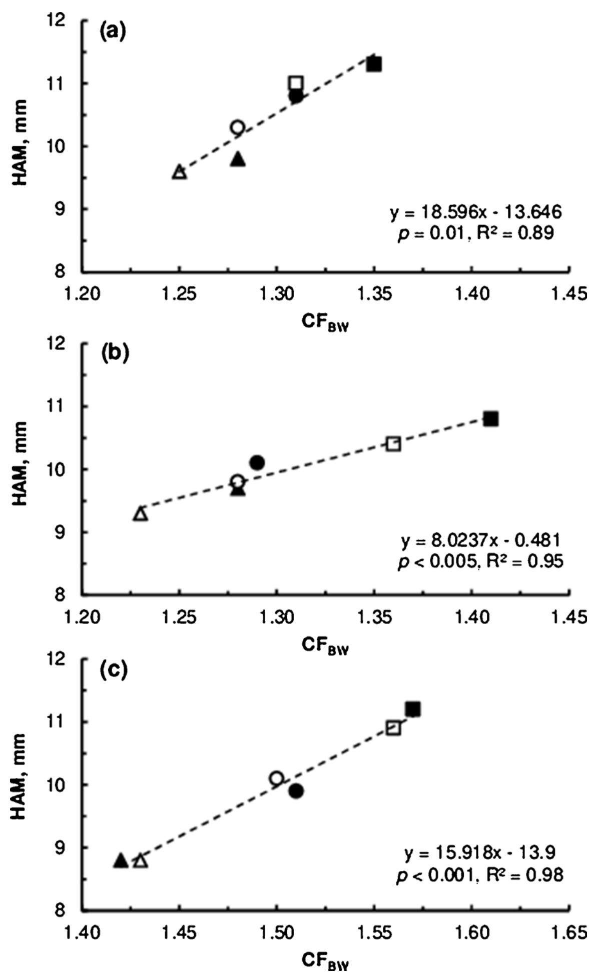

Fig. 2. Thickness of the hypaxial anterior muscle (HAM) in relation to condition factor based on body weight of year-old (a: S1) and under-year-old (b: S0) Atlantic salmon in large-scale production and year-old (c: S1) salmon in small-scale fed diets with either high protein-to-lipid ratio (HP: black symbols) or low protein-to-lipid ratio (LP: white symbols). Triangles, circles and squares represent weight classes, respectively, from lowest to highest in each experiment. Values are retrieved from the data in Table 3,4 and 5. Error margins are depicted in the respective tables.

3.2. Small-scale experiment

3.2.1. Body weight and body length

Body weight and body length were only influenced by weight class. Virtually all the variation in the model was explained by weight class (Table 5).

3.2.2. Fat content, viscerosomatic index and slaughter yield

During the first autumn period from September to December, there was a rapid decrease in VSI and a corresponding increase in muscle fat content for both dietary treatments (Fig. 3). The differences in VSI that emerged in the autumn lasted throughout the study revealing significantly higher VSI for the LP group than for the HP group in April and at harvest in June (Fig. 3, Table 5). At harvest, the muscle fat content varied with weight classes, but was not influenced by diet (Fig. 3, Table 5). However, when leaving out the 2.4 kg weight class, muscle fat content was significantly higher in the LP group than in the HP group ($p = 0.04$, ANOVA).

Corresponding with the large-scale harvest results, salmon fed the HP diet in the small-scale trial had significantly higher slaughter yield compared with the dietary LP group, irrespective of weight class (Table 5), in average 0.6% higher.

3.2.3. Body shape and muscle thickness

Weight class significantly influenced CF_{BW}, CF_{CW} and HAM (Table 5). As in the large-scale study, there was a positive and significant linear relationship between CF_{BW} and HAM (Fig. 2c) as well as between CF_{CW} and HAM ($p < 0.001$). Based on the presented regression equation, an increase in CF_{BW} by 0.1 improves HAM by 1.6 mm. In the small-scale study, numerically higher HAM for HP compared to LP was observed for salmon in the largest weight class only and no significant overall dietary effect was observed.

4. Discussion

Fish weight highly influenced quality characteristics of the harvested salmon. This corresponds with the conclusion from Shearer (1994) and underlines the importance of comparing data from equal sized fish when assessing the dietary influence on quality attributes. When assessing the quality potential in salmon from an industrial point of view, it is important to use harvest weights representative for the industrial practice. In addition, repetition in a controlled small-scale experiment may be necessary in order to validate observations from commercial data and to get more detailed information.

The duration of the experiments was relatively long (≥ 9 months) with an aim to produce fish up to harvest weight, and both feed raw material quality as well raw material prices may vary over such a long period. Although trying to maintain a stable dietary protein and lipid content and thus a steady protein-to-lipid ratio throughout the trial periods, some fluctuations in raw material inclusions in a least-cost formulation were unavoidable. However, this applied to both dietary groups in all three trials, and the repetition of results in the experiments supports that the dietary protein-to-lipid balance has a greater influence on salmon quality characteristics such as slaughter yield, rather than

Table 5
Quality characteristics at harvest (mean ± SEM, n = 2) of year-old Atlantic Salmon (S1) after being produced in small-scale research environment and fed diets with high protein-to-lipid ratio (HP) or low protein-to-lipid ratio (LP). Significant differences between the dietary treatments are depicted with *p*-values, and trends of significance are highlighted with brackets. Non-significance is abbreviated as ns. BW: body weight, BL: body length, MFAT: muscle fat, SY: slaughter yield, VSI: viscerosomatic index, CF_{BW}: condition factor based on body weight, CF_{CW}: condition factor based on carcass weight, HAM: thickness of the hypaxial anterior muscle, D: diet, WC: weight class.

SS-S1	HP			LP			ANOVA		
	2.4 kg	3.2 kg	4.0 kg	2.4 kg	3.2 kg	4.0 kg	D	WC	R^2
BW, kg	2442 ± 31	3208 ± 6	3981 ± 6	2461 ± 22	3207 ± 28	4006 ± 26	ns	< 0.001	0.99
BL cm	55.7 ± 0.3	59.7 ± 0.2	63.4 ± 0.1	55.7 ± 0.5	59.8 ± 0.6	63.6 ± 0.6	ns	< 0.001	0.98
MFAT, %	19.0 ± 0.0	19.9 ± 0.2	20.3 ± 0.0	18.9 ± 0.4	20.7 ± 0.4	21.4 ± 0.3	(0.10)	< 0.01	0.83
SY, %	87.1 ± 0.3	86.4 ± 0.1	86.9 ± 0.1	86.2 ± 0.2	86.2 ± 0.1	86.1 ± 0.1	0.001	ns	0.72
VSI, %	8.2 ± 0.2	8.8 ± 0.1	8.1 ± 0.2	9.3 ± 0.1	9.1 ± 0.1	8.9 ± 0.1	< 0.001	ns	0.75
CF_{BW}	1.42 ± 0.02	1.51 ± 0.01	1.57 ± 0.01	1.43 ± 0.02	1.50 ± 0.04	1.56 ± 0.04	ns	< 0.001	0.82
CF_{CW}	1.23 ± 0.02	1.31 ± 0.01	1.36 ± 0.01	1.23 ± 0.02	1.30 ± 0.04	1.34 ± 0.04	ns	< 0.001	0.81
HAM, mm	8.8 ± 0.1	9.9 ± 0.2	11.2 ± 0.3	8.8 ± 0.2	10.1 ± 0.2	10.9 ± 0.2	ns	< 0.001	0.94

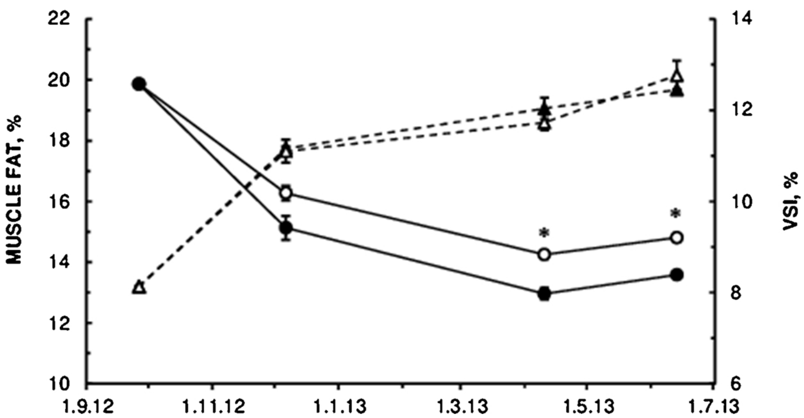

Fig. 3. Development in muscle fat content (triangles/broken line, y-axis) and viscerosomatic index (circles/solid line, z-axis) in year-old (S1) Atlantic salmon fed diets with either high protein-to-lipid ratio (HP: black symbols) or low protein-to-lipid ratio (LP: white symbols) in the small-scale trial. Values are presented as means ± SEM (n = 3). Values in June are based on the harvest data from Table 3. Asterisks denote significant ($p < 0.05$) differences between dietary treatments.

minor changes in raw material inclusion rates.

Overall, the present results demonstrate that high dietary protein-to-lipid ratio has a positive influence on key quality attributes. In compliance with earlier studies (Hillestad and Johnsen, 1994; Wathne, 1995; Einen and Roem, 1997; Hillestad et al., 1998; Einen et al., 1998), the presented results highlight that slaughter yield is clearly improved when the protein content in grower feed is increased above levels typically used in the industry over the last years. This improvement was evident in all three trials, despite the differences between them in smolt type, initial body weight, trial duration, rearing environment and management. The findings in the small-scale trial correspond with the results from Einen and Roem (1997), who found that the slaughter yield of salmon reared from 1 to 3 kg decreased with decreasing dietary protein-to-lipid level. Similar results have also been shown to be valid for post-smolt salmon up to nearly 1 kg (Dessen et al., 2017). In contrast to our findings, Einen and Roem (1997) found no influence of dietary protein-to-lipid ratio on slaughter yield for salmon reared from 2.5 to 5 kg. High slaughter yield is not only an expression of bigger muscle density. Elevated visceral fat deposition also contributes to slaughter yield differences between fish of equal body weights. This was depicted in the present small-scale trial. In this study, salmon deposited large amount of fat in the muscle and a relatively smaller proportion in the viscera first autumn in sea and about the same fat levels were observed in muscle for both the HP and LP groups, but significanlty lower VSI for the HP group. Hence, the deposition in the muscle appears irrespective of the fat content of the feed, whereas the decrease in visceral fat deposition appears partly relative to the fat content of the feed. The latter may also be affected by a significantly higher SFR in the LP group during the initiating autumn period. However, as the relative differences in dietary fat is about twice the difference in SFR (12.1% vs. 6.9%), the main explanation is probably the reduced dietary fat for the HP group. Increased VSI is usually related to higher visceral fat deposition (Hillestad et al., 1998; Bendiksen et al., 2003; Jobling et al., 1998, 2002b). Thus, the combination of both higher VSI and muscle fat content in the LP group indicates that there is an excess of lipid content in the LP diets. The results of Dessen et al. (2017) demonstrated how VSI in fish fed a HP diet in the autumn plateaued whilst muscle fat content still increased, whereas LP fed salmon during the same period deposited fat in both muscle and viscera, which ultimately increases both muscle fat and VSI and consequently reduces slaughter yield. The autumn represents the period with highest sea temperatures, high feed intake and high growth (Dessen et al., 2017; Weihe et al., 2018). Thus, the accumulation of dietary energy during this part of the year seems to be highly influenced by the season and the positive influence of a HP diet is greater and more evident in the latter part of the year compared to the spring season. Seasonal differences must therefore be accounted for in future studies when assessing feed influences on fish quality.

The present large-scale results of higher condition factor, significant correlation inn all groups between CF_{BW} and HAM, combined with a trend to greater HAM thickness and lower muscle fat content, indicate that a HP feeding strategy stimulates muscle development in salmon and that this, in combination with reduced VSI, is the main reason for the improvement in slaughter yields and overall product outcome. The results from the small-scale trial complemented the observations in the large-scale trial and depict that lipid dense diets increase the overall fat content in salmon, and this corresponds with earlier work (Einen and Roem, 1997; Hillestad et al., 1998; Jobling et al., 2002a; Bendiksen et al., 2003).

The majority of fish species grow continuously throughout their lives and the muscle growth is a combined effect of recruitment of more muscle fibers (*hyperplasia*) and increased size (*hyperthrophia*) of already existing fibers (Kiessling et al., 2006). Bearing in mind that proteins and amino acids are the building blocks in muscles, continuous muscle growth in farmed salmon will depend on the availability of dietary protein. With some exceptions, the development in CF_{BW} and muscle fat content typically correlates throughout the production cycle (Mørkøre and Rørvik, 2001; Alne et al., 2011). Rørå et al. (1998) indicated that fish with high fat content induced a higher degree of trimming of the fillet, consequently reducing fillet processing yields. Thus, high CF_{BW} based on increased fat content and not improved muscle development might be undesirable. The belly flaps below the HAM section is the fillet region with the highest fat content (Einen et al., 1998). These are typically cut of during fillet processing, and an increased degree of trimming will reduce the final weight and value of the fillet. Therefore, the relationship between HAM and CF_{BW} and reduced muscle fat in the HP group, indicate that an HP feeding strategy might induce higher fillet yields and subsequent greater economic value during processing.

The results in the large-scale and small-scale trials would probably have been more overlapping if the large-scale S0 trial had been initiated when the smolts were stocked in sea, and the small-scale S1 trial had been somewhat prolonged in time so that the experimental fish would reach bigger harvest weight. Also, it may be questioned if the 2.4 kg weight class in the small-scale S1 trial, which represented the smallest and most slowly growing part of the fish is representative to determine feed induced quality differences between the dietary treatments. Despite being smaller in body weight, salmon in the small-scale trial generally had higher muscle fat content and condition factors than the commercially produced salmon in large-scale. A potential explanation for this is the typical excess feeding conducted in small-scale trials (with subsequent feed collection), which ensures that all fish are fed to satiation. Further, an eight-times smaller perimeter of the small-scale cages compared to the commercial large-scale cages likely generates different behaviors (Huntingford et al., 2012). In contrast, commercial farmers avoid overfeeding to avoid additional feed costs.

In conclusion, this paper found that energy-dense diets with a high (> 1.1) protein-to-lipid ratio (HP) significantly improves slaughter yield in Atlantic salmon and generates more primary product for further trade and processing, compared with isoenergetic diets with low (< 1) protein-to-lipid ratio. In addition, muscle fat content can be significantly reduced by increasing protein on the expense of lipids. When adjusted for body weight of the fish, condition factor and muscle thickness are also positively influenced by HP diets. The overall results also highlight the importance of basing quality comparisons between different dietary treatments on fish of equal sizes.

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References

Helland, S.J., Grisdale-Helland, B., Nerland, S., 1996. A simple method for the measurement of daily feed intake of groups of fish in tanks. Aquaculture 139, 157–163. https://doi.org/10.1016/0044-8486(95)01145-5.

Nystøyl, R., 2018. Trender – Produksjon & Marked Atlantisk Laks – 2018. Oral presentation at The Faroese Aquaculture Conference 2nd of March 2018. Retrieved from website, last accessed 29th of August 2018. http://industry.fo/kunning/tiltoek/hildin-tiltoek/aliraðstevnur-2008-2018/aliraðstevnan-2018.

Alne, H., Oehme, M., Thomassen, M.S., Terjesen, B.F., Rørvik, K.-A., 2011. Reduced growth, condition factor and body energy levels in Atlantic salmon Salmo salar L. during their first spring in the sea. Aquac. Res. 42, 248–259. https://doi.org/10.1111/j.1365-2109.2010.02618.x.

Arge, R., Thomassen, M.S., Berge, R.K., Zambonino-Infante, J.L., Terjesen, B.F., Oehme, M., Rørvik, K.-A., 2012. Reduction of early sexual maturation in male S0 Atlantic salmon (*Salmo salar* L.) by dietary supplementation of tetradecylthioacetic acid (TTA). Aquac. Res. 45, 922–933. https://doi.org/10.1111/are.12036.

Arnesen, P., Krogdahl, Å., 1993. Crude and pre-extruded products of wheat as nutrient sources in extruded diets for Atlantic salmon (*Salmo salar*, L) grown in sea water. Aquaculture 118, 105–117. https://doi.org/10.1016/0044-8486(93)90284-6.

Bendiksen, E.A., Berg, O.K., Jobling, M., Arnesen, A.M., Masoval, K., 2003. Digestibility, growth and nutrient utilisation of Atlantic salmon parr (Salmo salar L.) in relation to temperature, feed fat content and oil source. Aquaculture 224 (03), 283–299. https://doi.org/10.1016/S0044-8486. 00218-7.

Bureau, D.P., Kaushik, S.J., Cho, C.Y., 2002. Bioenergetics. In: Halver, J.E., Hardy, R.W. (Eds.), Fish Nutrition. Academic Press, New York, pp. 1–59.

Dessen, J.-E., Arge, R., Thomassen, M.S., Rørvik, K.-A., 2016. Differences in fat accumulation between immature male and female Atlantic salmon *Salmo salar* after dietary administration of tetradecylthioacetic acid. J. Fish Biol. 89, 2085–2097. https://doi.org/10.1111/jfb.13113.

Dessen, J.-E., Weihe, R., Hatlen, B., Thomassen, M.S., Rørvik, K.-A., 2017. Different growth performance, lipid deposition, and nutrient utilization in in-season (S1) Atlantic salmon post-smolt fed isoenergetic diets differing in protein-to-lipid ratio. Aquaculture 473, 345–354. https://doi.org/10.1016/j.aquaculture.2017.02.006.

Einen, O., 1998. Product Quality in Atlantic Salmon – Influence of Dietary Fat Level, Feed Ration and Ration Before Slaughter. Doctor Scientarum Thesis 1998:27. Agricultural University of Norway, Ås.

Einen, O., Roem, A.J., 1997. Dietary protein/energy ratios for Atlantic salmon in relation to fish size: growth, feed utilization and slaughter quality. Aquac. Nutr. 3, 115–126. https://doi.org/10.1046/j.1365-2095.1997.00084.x.

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

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 179, 149–169. https://doi.org/10.1016/S0044-8486(99)00126-X.

Fish Pool, 2018. Nasdaq Salmon Index. Website, last accessed 29th of August 2018. http://fishpool.eu/price-information/reports/nasdaq-salmon-index-archive/.

Folkestad, A., Wold, J.P., Rørvik, K.-A., Tschudi, J., Haugholt, K.H., Kolstad, K., Mørkøre, T., 2008. Rapid and non-invasive measurements of fat and pigment concentrations in live and slaughtered Atlantic salmon (Salmo salar L.). Aquaculture 280, 129–135. https://doi.org/10.1016/j.aquaculture.2008.04.037.

Hillestad, M., Johnsen, F., 1994. High-energy/low-protein diets for Atlantic salmon: effects on growth, nutrient retention and slaughter quality. Aquaculture 124, 109–116. https://doi.org/10.1016/0044-8486(94)90366-2.

Hillestad, M., Johnsen, F., Austreng, E., Åsgård, T., 1998. Long-term effects of dietary fat level and feeding rate on growth, feed utilization and carcass quality of Atlantic salmon. Aquac. Nutr. 4, 89–97. https://doi.org/10.1046/j.1365-2095.1998.00051.x.

Huntingford, F., Hunter, W., Braitwathe, V., 2012. Movement and orientation. In: Huntingford, F., Jobling, M., Kadri, S. (Eds.), Aquaculture and Behavior. Wiley-Blackwell, Oxford, pp. 87–120.

Jobling, M., Koskela, J., Savolainen, R., 1998. Influence of dietary fat level and increased adiposity on growth and fat deposition in rainbow trout, *Oncorhynchus mykiss* (Walbaum). Aquac. Res. 29, 601–607. https://doi.org/10.1046/j.1365-2109.1998.00251.x.

Jobling, M., Larsen, A.V., Andreassen, B., Olsen, R.L., 2002a. Adiposity and growth of post-smolt Atlantic salmon Salmo salar L. Aquac. Res. 33, 533–541. https://doi.org/10.1046/j.1365-2109.2002.00738.x.

Jobling, M., Larsen, A.V., Andreassen, B., Olsen, R.L., 2002b. Fat dynamics of Atlantic salmon Salmo salar L. smolt during early seawater growth. Aquac. Res. 33, 739–745. https://doi.org/10.1046/j.1365-2109.2002.00712.x.

Karalazos, V., Bendiksen, E.Å., Dick, J.R., Bell, J.G., 2007. Effects of dietary protein, and fat level and rapeseed oil on growth and tissue fatty acid composition and metabolism in Atlantic salmon (Salmo salar L.) reared at lower water temperatures. Aquac. Nutr. 13, 256–265. https://doi.org/10.1111/j.1365-2095.2007.00471.x.

Karalazos, V., Bendiksen, E.Å., Bell, J.G., 2011. Interactive effects of dietary protein/lipid level and oil source on growth, feed utilisation and nutrient and fatty acid digestibility of Atlantic salmon. Aquaculture 311, 193–200. https://doi.org/10.1016/j.aquaculture.2010.11.022.

Kiessling, A., Ruohonen, K., Bjørnevik, M., 2006. Muscle fibre growth and quality in fish. Arch. Tier. Dummers 49, 137–146.

Mørkøre, T., Rørvik, K.-A., 2001. Seasonal variations in growth, feed utilization and product quality of farmed Atlantic salmon (Salmo salar) transferred to seawater as 0+ or 1+ smolts. Aquaculture 199, 145–157. https://doi.org/10.1016/S0044-8486(01)00524-5.

Mørkøre, T., Vallet, J.L., Cardinal, M., Gomez-Guillen, M.C., Montero, P., Torrisen, O.J., Nortvedt, R., Sigurgisladóttir, S., Thomassen, M.S., 2001. Fat content and fillet shape of Atlantic salmon: relevance for processing yield and quality of raw and smoked products. J. Food Sci. 66, 1348–1354. https://doi.org/10.1111/j.1365-2621.2001.tb15213.x.

Morris, P.C., Beattie, C., Elder, B., Finlay, J., Gallimore, P., Jewison, W., Lee, D., Mackenzie, K., McKinney, R., Sinnott, R., Smart, A., Weir, M., 2003. Effects of the timing of the introduction of feeds containing different protein and lipid levels on the performance and quality of Atlantic salmon, Salmo salar, over the entire seawater phase of growth. Aquaculture 225, 41–65. https://doi.org/10.1016/S0044-8486(03)00277-1.

Norwegian Standard, 1994a. NS 9401, *Atlantic Salmon. Reference Sampling for Quality Measurements*. Norwegian Standards Association, Oslo, Norway.

Norwegian Standard, 1994b. NS 9402, Atlantic salmon. Measurement of Colour and Fat. Norwegian Standards Association, Oslo, Norway.

Rasmussen, R.S., 2001. Quality of farmed salmonids with emphasis on proximate composition, yield and sensory characteristics. Aquac. Res. 32, 767–786. https://doi.org/10.1046/j.1365-2109.2001.00617.x.

Rørå, A.M.B., Kvåle, A., Mørkøre, T., Rørvik, K.-A., Steien, S.H., Thomassen, M.S., 1998. Process yield, colour and sensory quality of smoked Atlantic salmon (Salmo salar) in relation to raw material characteristics. Food Res. Int. 31, 601–609. https://doi.org/10.1016/S0963-9969(99)00034-4.

Rørå, A.M.B., Mørkøre, T., Einen, O., 2001. Primary processing (Evisceration and filleting). In: Kestin, S.C., Warris, P.D. (Eds.), Farmed Fish Quality. Blackwell Science, Oxford 249-26.

Rørvik, K.-A., Rørvik, S., Salberg, T., Larsson, T., 2014. Hvor rød er laks? (How red is salmon?). Norsk Fiskeoppdrett 11, 54–58.

Rørvik, K.-A., Dessen, J.-E., Åsli, M., Thomassen, M.S., Hoås, K.G., Mørkøre, T., 2018. Low body fat content prior to declining day length in the autumn significantly increased growth and reduced weight dispersion in farmed Atlantic salmon Salmo salar L. Aquac. Res. 49, 1944–1956. https://doi.org/10.1111/are.13650.

Roth, B., Johansen, S.J.S., Suontama, J., Kiessling, A., Leknes, O., Guldberg, B., Handeland, S., 2005. Seasonal variation in flesh quality, comparison between large and small Atlantic Salmon (Salmo salar) transferred into seawater as 0+ or 1+ smolts. Aquaculture 250, 830–840. https://doi.org/10.1016/j.aquaculture.2005.05.009.

Shearer, K.D., 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture 199, 63–88. https://doi.org/10.1016/0044-8486(94)90444-8.

Wathne, E., 1995. Strategies for Directing Slaughter Quality of Farmed Atlantic Salmon (Salmo Salar) With Emphasis on Diet Composition and Fat Deposition. Doctor Scientarium thesis 1995:6. Agricultural University of Norway, Ås. Norway.

Weihe, R., Dessen, J.-E., Arge, R., Hatlen, B., Thomassen, M.S., Rørvik, K.-A., 2018. Improving production efficiency of farmed Atlantic salmon (Salmo salar L.) by isoenergetic diets with increased dietary protein-to-lipid ratio. Aquac. Res. 49, 1441–1453. https://doi.org/10.1111/are.13598.