Improving production efficiency of farmed Atlantic salmon (*Salmo salar* L.) by isoenergetic diets with increased dietary protein-to-lipid ratio

Rúni Weihe[1,2*], Jens-Erik Dessen[2,3], Regin Arge[2,4], Magny Thomassen[2], Bjarne Hatlen[5] and Kjell-Arne Rørvik[2,3]

[1] Havsbrún, Bakkavegur 48, FO-530 Fuglafjørður, Faroe Islands

[2] Department of Animal and Aquaculture Sciences, Norwegian University of Life Sciences, NO-1432 Ås, Norway

[3] Nofima, NO-1432 Ås, Norway

[4] Fiskaaling, Við Áir 11, FO-430 Hvalvík, Faroe Islands

[5] Nofima, NO-6600 Sunndalsøra, Norway

Keywords: Atlantic salmon, isoenergetic diets, dietary protein-to-lipid ratio, carcass weight, nutrient retention, seasonal variation

*Corresponding author: Rúni Weihe; Havsbrún P/F, Bakkavegur 48, 530 Fuglafjørður, Faroe Islands; Tel: +298 41 44 64; e-mail: ruw@havsbrun.fo

Abstract

The effects of isoenergetic diets with high (HP) and low (LP) protein-to-lipid ratios on feeding rate (SFR), feed conversion (FCR), growth (TGC) and relative- and absolute nutrient retention were investigated using both whole body weight (BW) and carcass weight (CW) to assess the production efficiency. Three different feeding trials in seawater were conducted: two large-scale trials with yearling smolt (S1) and under-yearling smolt (S0) and one small-scale with S1 smolt). The initial body weights in the trials were 105 g, 319 g, and 978 g, respectively, and the fish were fed and monitored until they reached harvest weights. In all three trials, the dietary HP group attained significantly higher ($P < 0.05$) CW at harvest based on fish with equal BW. Also, fish fed the HP diets significantly improved FCR ($P < 0.05$) when based on CW. In the small-scale trial, fish fed HP diet, especially during late autumn and spring, significantly ($P < 0.001$) improved FCR_{BW} and FCR_{CW}. Improved FCR coincided with significantly higher ($P < 0.05$) relative energy retention in the dietary HP group. In all three trials, the HP groups had significantly higher ($P < 0.05$) TGC with regards to both BW and CW. Taken together, the present studies indicate that growth performance and feed utilization in modern salmon farming has the potential to be further improved by increasing the dietary protein-to-lipid ratio. In addition, dietary influence is more precisely assessed when using carcass as the weight denominator when analyzing feed utilization and growth performance.

Introduction

In modern aquaculture production of Atlantic salmon, the dietary protein-to-lipid ratio generally decreases inversely with increasing body weight. Small salmon, like parr and smolt, are usually fed a diet with relative high protein content (> 40 %) and low lipid content (< 30 %). The commercial practice, especially in Norway, has been to give the salmon high-fat diets (≥ 35 % lipid, ≤ 35 % protein) from a body weight of approximately 1 kg (grower diets), while the protein content is reduced so that protein derived energy is spared in favour of fat. A historical retrospective from the Norwegian aquaculture industry displays an approximately four times increase in lipid inclusion in the feed for salmon since the start of the industry in the 1970's (Tacon & Metian 2009; Torrisen, Olsen, Toresen, Hemre, Tacon, Asche, Hardy & Lall 2011). Thus, during the relative short lifespan of the salmon farming industry, the dietary protein-to-lipid ratio in the grower diets have changed from near 5 to 1. With a shift towards higher content of lipid, the feeds have necessarily become denser in energy.

High-fat diets have previously been demonstrated to have beneficial effects on key production parameters such as growth rate and feed conversion ratio (Hillestad, Johnsen, Austreng & Åsgård 1998; Karalazos, Bendiksen, Dick & Bell 2007; Karalazos, Bendiksen & Bell 2011). But studies have also indicated that high dietary fat intake may result in increased lipid content in both muscle and intestinal tissues of salmonids (Hillestad & Johnsen 1994; Jobling 1998, Jobling 2001; Refstie, Storebakken, Baeverfjord & Roem 2001; Jobling, Larsen, Andreassen & Olsen 2002). This may be undesirable since body lipids may act as a negative feedback signal on feed intake and thus impair growth (Silverstein, Shearer, Dickhoff & Plisetskaya 1999; Johansen, Ekli & Jobling 2002; Johansen, Sveier & Jobling 2003). Also, increased fat deposition in the visceral tissues may reduce the overall production yield.

Salmonids are poikilothermic, meaning that their feed intake and growth is highly influenced by water temperatures (Brett 1979; Jobling 1997). Both sea temperatures and day length vary throughout the year, and previous experiments have demonstrated that Atlantic salmon responds greatly to the seasonal changes with regards to energy demand, feed intake, nutrient retention and growth (Måsøval, Åsgård, Wathne, Shearer, Staurnes & Sigholt 1994; Mørkøre & Rørvik 2001; Lysfjord, Jobling & Solberg 2004; Hemre & Sandnes 2008; Oehme, Grammes, Takle, Zambonino-Infante, Refstie, Thomassen & Rørvik 2010; Alne, Oehme, Thomassen, Terjesen & Rørvik 2011). In general, these studies seem to depict a high production efficiency during the autumn, which coincides with decreasing day lengths and peak sea temperatures in the salmon producing countries situated in the North Atlantic Ocean such as Norway, the British Isles, and the Faroe Islands.

In general, it is a goal for all producers of animal proteins to increase utilization of feed resources. Thereto, a high turnover rate of production is crucial in most businesses. This is especially momentous in animal farming when the production areal is limited. The Faroese aquaculture industry encounters significant limitations in biomass growth due to the relative limited coastline of the Faroe Islands (1117 km), and virtually all potential farming areas are presently utilized. Currently, lack of well-established farming technology makes it difficult to farm salmon in exposed areas that surrounds the islands. Thus, the only realistic, short-term possibility for biomass increase for the Faroese aquaculture industry is through higher growth rate of salmon (shorter production cycle from sea transfer to harvest) and increased carcass-to-body weight yield.

Since final carcass is the primary tradable commodity, carcass weight and not only body weight, should be considered as the weight denominator when evaluating the dietary effects on feed conversion and growth performance. Thus, using the carcass weight as a biometric measurement of dietary effects, a more complete picture, both nutritional and economical, may be achieved when assessing overall feed efficiency in salmon production. Previous experiments have displayed high carcass-to-body weight yields (≥ 90 %) (Hillestad & Johnsen 1994; Wathne 1995; Einen & Roem 1997; Einen, Waagen, Thomassen 1998; Hillestad *et al.* 1998). Although there might be a lack of detailed definition of carcass weight in these studies, these results may indicate that the carcass-to-body weight ratio have been somewhat higher compared to some of the yields (~ 83 %) recently observed in the industry (Waagbø, Berntssen, Danielsen, Helberg, Kleppa, Berg Lea, Rosenlund, Tvenning, Susort, Vikeså & Breck 2013). Therefore, it may be questioned whether the changes seen in the dietary protein-to-lipid composition has been in favour of obtaining high carcass growth throughout the marine production phase of salmon. In this context, diets with low protein-to-lipid ratios may not utilize the full potential of carcass growth in salmon, and thus the industry has not been assessing what protein-to-lipid composition is needed to achieve a more optimal production throughout the whole seawater phase, especially in the grow-out phase from approximately 1 kg until harvest. During this phase of production, the dietary protein-to-lipid ratio is at the lowest, however, most of the weight gain is generated as the fish is harvested between 4-6 kg (Nystøyl 2017).

The aim of the present work was, consequently, to examine the effects of different dietary protein-to-lipid ratios on feed utilisation and fish growth rate using both whole body weight and carcass weight in assessing the feed effects on overall production efficiency. In addition, the effect of seasonal influence on biometric performance was examined together with the potential interaction of dietary effects.

Material and methods

Experimental design

Three dietary high protein-to-lipid ratio (HP) and three lower protein-to-lipid ratio (LP) feeding strategies were first tested in two different commercial large-scale farming sites in the Faroe Islands with yearling (S1) and under-yearling smolt (S0) following a small-scale (SS) trial which was conducted in Norway using S1 smolt. In all three experiments, the protein and lipid contents in the LP diets were designed to resemble those of a typical commercial diet for the respective sizes of fish, whereas the HP diets had higher protein and lower lipid contents. The total energy from lipid, protein and carbohydrates were targeted to be equal in the HP and LP diets for each pellet size.

Compared with large-scale feeding experiments in commercial conditions in general, small-scale trials ensure more accurate measurements of feed intake, biomass and equal slaughter time. Therefore, the present small-scale trial was conducted to test the reproducibility and validity of the dietary influences as well as to complement the observations from the large-scale experiments with a more scientific approach with regards to feed intake, feed utilization and dietary retention of nutrients.

Experimental diets

All feeds were produced by Havsbrún (Fuglafjørður, Faroe Islands). Multiple batches of feed were produced throughout the large-scale experimental period and two feed batches per dietary treatment were produced for the small-scale trial (Table 1). The main dietary raw materials used in the large-scale experiments, ranked from highest to lowest inclusion level, were fishmeal, fish oil, wheat, soy protein concentrate, wheat gluten, and sunflower meal. In the small-scale experiment the ingredients used were, fishmeal, fish oil, rapeseed oil, wheat, krill meal and porcine blood meal. In the small-scale trial, sunflower meal was not used in any of the diets. For all three trials, premixes containing pigments, minerals and vitamins were included in the diets to fulfil the minimum nutritional requirements in accordance with the National Research Council (1993, 2001). The estimated feed digestibility was calculated in compliance with Morris, Beattie, Elder, Finlay, Gallimore, Jewison, Lee, Mackenzie, McKinney, Sinnott, Smart & Weir (2003) assuming apparent digestibility coefficients for protein and lipid to be 0.86 and 0.94 (Einen & Roem 1997), respectively, and 0.50 for nitrogen free extractives (Arnesen & Krogdahl 1993). The feed production process included standard manufacturing routines regarding the control of physical pellet quality as well as the monitoring and control of proximate feed composition. Table 1 states the proximate composition of the experimental diets. These were based on the weighted mean from each feed batch supplied to the fish farming sites. The 3 mm and 4 mm HP diets in the S1 large-scale were intended to be the same (52 % protein and 24 % lipid). The relative large compositional deviation of the 3 mm HP feed was caused by manufacturing problems in addition to wrongful handling of feed during transport, which resulted in the dietary HP fish group being supplied with some 3 mm LP feed instead of HP feed. Thus, the dietary HP group was fed a combination of both HP and LP feed for approximately 4 weeks.

Fish and facilities – large-scale trials

In the large-scale S1 trial, salmon smolt were supplied by Bakkafrost hatchery station in Glyvradalur and transferred to the Bakkafrost commercial seawater site at Lambavík (62°08´N, 06°41´W), Faroe Islands, during April 2009. Duplicate 128 m circumference cages with a water volume of 18 500 m^3 were used for rearing the fish per dietary treatment. Mean number of fish per net pen was 66 627 (SEM = 213). The fish were subjected to 1000 W artificial light (L:D 24:0) from 10 December 2009 until 21 March 2010. We identified an error regarding the body weight measurement of the stocked fish five months after the trial initiation which caused unequal starting weights between the dietary treatments, showing that the dietary LP group was 8 % bigger (LP = 104 ± 10 g vs. HP = 96 ± 2 g, n = 2). To achieve equal starting weights per dietary treatment, a triplicate cage, also fed HP diet since sea transfer, was included. This was considered necessary to achieve reliable data to examine dietary influence based on comparable fish groups with equal starting weights. Thus, mean body weight at sea transfer for the fish group fed the LP diet was 104 g (SEM = 10, n = 2) versus 105 g (SEM = 10, n = 3) after adjustment of the HP fed smolt group. Feeding of the fish in the experimental cages started in week 19 (May 2009). There was a great algal bloom during the period July-August 2009 at the S1 trial site causing a severe decrease in feeding rate within both dietary treatments. The average sea water temperature through the S1 experimental period was 8.5°C with a maximum and minimum of 11.1°C and 5.7°C, respectively (Fig. 1A). Salmon fed HP feed had an average production period of 452 ± 11 days and 3752 ± 109 day degrees, whereas the production duration of the dietary LP group was 477 ± 27 days and 3971 ± 266 day degrees.

S0 smolt from Luna’s hatchery station in Fútaklettur had been transferred to Luna´s commercial sea farming site in Sørvágur (62°04´N, 7°20´W), Faroe Islands, in October 2008. In March 2009, when the feeding trial started, the fish had a mean body weight of 319 g (SEM = 5, n = 4) with a mean number of 60 392 fish per cage (SEM = 245). Duplicate cages per dietary treatment of 24 m x 24 m, with a water volume of 6 912 m^3 were used in the beginning of the trial. In June 2009, all the fish were transferred by towing the cages approximately 1 km southwest across the fjord (62°04´N, 07°22´W) and restocked in 128 m circumference cages with a water volume of 18 500 m^3, maintaining the same experimental groups. The transportation time was approximately 3.5 hours per cage. The S0 experimental fish were subjected to 1000 W artificial light (L:D 24:0) from 14

December 2009 until 15 March 2010. The average sea water temperature through the S0 experimental period was 8.4°C where the peak temperature was 10.7°C and the lowest temperate was 5.8°C. The average production period for the dietary HP group was 429 ± 6 days and 3597 ± 42 day degrees whilst the dietary LP group had a production period of 439 ± 11 days and 3688 ± 97 day degrees, respectively. Figure 1A gives an overview of the temperature and day length in both large-scale trials.

Four different pellet sizes were used within the dietary treatments in the S1 large-scale experiment, whereas two pellet sizes were used within the dietary treatments in the S0 large-scale trial (Table 2). The pellet sizes were adjusted to fit the fish weight according to the guidelines of the feed manufacturer.

Fish and facilities – small-scale trial

The small-scale experiment with S1 post-smolt was conducted at Nofima's research station at Ekkilsøy (currently owned by Marine Harvest Fish Feed AS) on the west coast of mid Norway (63°03´N, 07°35´E) in 2012. One hundred and fifty post smolt salmon weighing 978 g (SEM = 1, n = 6) were randomly distributed in each of six cages measuring 5 m x 5 m x 5 m. Prior to this, the fish had been transferred to sea as yearling (S1) smolt (95 g) in April 2012 from Salmar's hatchery station in Straumsnes, and then been involved in an earlier feeding trial (Dessen, Weihe, Hatlen, Thomassen & Rørvik 2017) and fed the same high-protein diets through three different periods from April to September. During the last period from 23 July to 24 September in this pre-trial, the post-smolt grew 658 g, ending up with a final body weight of 926 g and a whole-body composition of 17.6 % protein and 16.0 % fat.

The experimental diets (HP and LP 9 mm, Table 1) used in the small-scale trial were fed to triplicate groups of fish from 27 September 2012 until trial termination on 10 June 2013. The trial was split into three feeding periods representing three different seasons; 1: 27 September – 4 December (late autumn), 2: 7 December – 8 April (winter), and 3: 11 April – 10 June (spring), respectively (Fig. 1B). Fish were fed to satiation daily using automatic feeders four times a day from 27 September to 25 October. Subsequently, until trial termination in June, the fish were fed three rations per day. The daily feed rations were approximately 10 % in excess of the feed eaten the day before. Waste feed was collected daily as described by Einen, Mørkøre, Rørå & Thomassen (1999) and analysed for recovery of dry matter as described by Helland, Grisdale-Helland & Nerland (1996). The average sea water temperature in the three experimental periods was 9.4°C (612 day degrees), 4.1°C (490 day degrees) and 7.1°C (427 day degrees), respectively. Figure 1B illustrates the changes in temperature and day length during the small-scale trial.

Sampling procedures large-scale

Fish from the experimental cages were harvested following standardized routines of the farming respective companies (Bakkafrost and Luna). This included a starvation period of 3 to 5 days prior to slaughter, and the average harvesting time per cage in the S1 and S0 trials was two and four weeks, respectively. In the S1 large-scale trial, the fish were transported with well boat to the Bakkafrost harvesting facilities in Klaksvík (62°23´N, 06°59´W) during the period from week 28 (July) to week 41 (November) 2010. The experimental S0 fish were harvested at Luna´s harvesting facility in Sørvágur (62°07´N, 07°32´W) from week 17 (April) to week 25 (June) 2010 after dragging the experimental cages approximately 2 km from the production site to the harvesting facilities at the head of the fjord. At both harvesting facilities, the salmon were killed and bleed using an automated swim-in system (SI-7 Combo, killing and bleeding machine) and subsequently transported to a bleeding tank with a water temperature between 0°C and -1°C to bleed out.

At the first day of slaughter of each experimental cage in the S1 trial, 30 fish were sampled and divided into three weight classes á 10 fish of 4.5 kg, 5.5 kg and 6.5 kg average weight, respectively. All the sampled fish were handpicked from the bleeding tank at the harvesting facilities. In one experimental unit (cage no. 4) in the large-scale S1 trial fed HP feed, only 10 fish respectively of 4.5 kg and 5.5 kg were sampled. In the S0 experiment, 30 fish from all experimental cages were sampled 8 April (week 14), and divided into the mentioned weight classes. All samples in both large-scale experiments were recorded and measured for body weight, length and carcass weight. Carcass weight was defined as the weight after removal of blood, viscera, heart and kidneys. The measured body weights were corrected for 2.7 % blood loss in accordance with Einen, Waagan & Thomassen (1998) to calculate live weight at slaughter.

During the harvest period, the total number of fish and gutted biomass were recorded and harvest reports were generated for each experimental unit and the body weight of fish and biomass within each cage was calculated. We chose to use the carcass-to-body weight ratio per cage, measured at first day of harvest, to convert the carcass weights in the harvest reports to whole body weight and biomass within each experimental cage. The harvest reports depict a difference within the smolt groups regarding the number of production days in the experimental units and thus a difference in day degrees were used to achieve about the same body weight within dietary treatments at harvest.

Sampling procedures small-scale

At the end of each feeding period (Fig. 1B), all fish within each experimental unit were anaesthetized (MS 222 metacaine 0.1g L^{-1}, Alpharma, Animal Health, Hampshire, UK) and bulk-weighed for determination of specific feeding rate (SFR), growth rate (presented as thermal growth coefficient, TGC) and feed conversion (FCR). When sampling fish in the first two periods, ten fish representing the average body weight in each unit were stunned with a blow to the head and bled out. These fish were then individually weighed, length measured and gutted, and carcass weight registered. In line with the large-scale trials at trial termination, 30 fish from each cage were collected and divided into three weight classes. Because the experimental fish did not grow as big as the fish in the large-scale trials, the three groups of ten fish were divided in subgroups of 2.4 kg, 3.2 kg and 4.0 kg. Also, an additional 10 fish (not bled) representing the mean body weight per experimental unit were sampled for whole body analysis of protein, fat and energy to calculate both relative and absolute retention of dietary nutrients. The fish were starved for 4 days prior the sampling in December whereas the fish were starved for 3 days prior to the samplings in April and June. At each sampling, all fish with obvious signs of wounds, runts, or sexual maturity were removed (weights and number of these fish was recorded).

Feed chemical analyses

In all three experiments, the feeds were analysed for moisture (drying loss at 103°C to stable weight; ISO 6496), ash (combustion at 550°C, ISO 5984), crude protein (N x 6.25, combustion according to the Kjeldahl principle, ISO 5983) and crude fat was analysed using pre-extraction and post-extraction in petroleum ether after HCL hydrolysis (98/64/EC). In the large-scale trials total- and gelatinised starch was analysed as d-glucose following enzymatic cleavage with gluco-amylase after full gelatinisation by cooking with NaOH. In the small-scale trial, the total starch content was analysed as glucose after enzymatic hydrolysis employing the Megazyme K-TSTA 07/11 kit (Megazyme International, Ireland) in accordance with AOAC method 996.11. The energy content was determined by using a Parr 6400 Oxygen Bomb Calorimeter (Parr Instrument Company, USA) following the NS-EN 14918:2009 standard. Nitrogen free extractives (NFE) was calculated as dry matter – (protein + lipid + ash).

Fish chemical analyses

Homogenates of whole fish samples were analyzed for crude protein and energy as described for feeds. Whole body crude fat was analyzed using a semi-automatized Soxhlet extractor (Tecator Soxtec Avanti 2055) with petroleum ether as the extracting solvent. Whole body energy content was assessed by bomb calorimetry (Parr, Moline, IL, USA).

Calculations

SFR together with FCR and TGC based on whole body weight (FCR_{BW}, TGC_{BW}) were measured in all three trials in accordance with the calculations in Dessen *et al.* (2017) in addition to the calculations of nutrient retention in the small-scale trial. The overall SFR, TGC, FCR and retention means in the small-scale trial, were calculated as the weighted arithmetic mean of the three seasons to balance the values in relation to their relative contribution to the weight gain. In the large-scale trials, the calculations were based on the data given by the production programme FarmControl (AKVA Group, Norway) which was used on both farming sites, whereas the calculations in the small-scale trial were based on the bulk weighings of the experimental fish at the end of each feeding period. Feed conversion based on carcass weight (FCR_{CW}) in the large-scale trials was calculated as: feed eaten (kg) x (biomass increase (kg) + biomass of dead fish (kg) x 0.83)$^{-1}$ where 0.83 is a standard estimation of carcass-to-body weight ratio within the industry to calculate the carcass weight of the dead fish. In the small-scale trial, the measuared carcass-to-body weight ratio was used for each feeding period. Growth based on the gutted biomass (TGC_{CW}) was calculated as the TGC_{BW} using carcass weight (CW) instead of whole body weight.

Statistical analysis

In the large-scale trials, data was analysed by two-way analysis of variance (ANOVA) with interaction using the general linear model (GLM) procedure, in which the two class variables were dietary treatment (D; HP and LP) and smolt group (SG; S1 and S0), and the dependent variables were SFR, FCR, TGC, BW and CW. Two-way ANOVA was also used to analyse the data in the small-scale trial based on a randomized block design, using season (S), diet (D) and the potential interaction between season and diet as class variables to assess their influence on the production performance. If only two means were compared, Student's *t*-test was applied to test dietary differences within season (small-scale experiment) and smolt group (large-scale experiment). Only significant models are presented and the proportion of total variation explained by the model is expressed as R^2, which was calculated as between-group sum of squares divided by the total sum of squares (type III). All analyses were conducted using SYSTAT® 13 software package (SYSTAT Software Inc., USA) and SAS software package (SAS institute Inc., 1990). Fish cage mean was used as the experimental unit. Results are presented as mean ± SEM if not otherwise stated. $P \leq 0.05$ was chosen as level of significance and $P \leq 0.10$ was considered as a trend.

Results

Large-scale experiments

Mortality

In the S1 trial, cages fed the HP diet had a lower (P = 0.03) mortality rate (4.5 ± 0.1 %) compared with the LP fed fish (6.3 ± 0.3 %). In January and February 2010, the number of dead fish was considerably higher than in the rest of the trial period. Most of the dead fish in this period had visible wounds and damages derived from seal predation. No mortality differences between dietary treatments within the S0 smolt group were detected (HP: 2.2 ± 0.4 % vs. LP: 1.6 ± 0.1 %).

Feed intake, feed conversion and growth performance

The S1 smolt group had a significantly higher feeding rate than the S0 group, but there were no differences between the dietary treatments within the smolt groups (Table 3).

FCR_{BW} was significantly higher in the S1 than in the S0 smolt group (Table 3). There was also strong trend (P = 0.06) towards higher FCR_{BW} in fish fed the LP diet than those fed the HP diet. This trend became significant between the dietary treatments when assessing the feed conversion based on carcass weight (Table 3). Thus, the 5.4 % and 3.3 % improvement in FCR_{BW} for the salmon provided with HP feed in the S1 and S0 groups, respectively, increased to 7.3 % and 4.8 % when carcass weight was used as the conversion weight denominator. There were no significant interaction effects of smolt group and diet on FCR_{BW} or FCR_{CW}.

Salmon fed the HP diet grew significantly faster both in terms of body weight (TGC_{BW}) and carcass weight (TGC_{CW}) (Table 3). The dietary influence on carcass growth within both smolt groups may be visualised by the significant higher carcass weight within the dietary HP groups of the sampled fish at harvest which had virtually equal body weight as the dietary LP groups (Fig. 2).

Small-scale experiment

Mortality

Three fish died in the dietary HP group, and no mortality was registered within the fish fed LP diet throughout the trial.

Feed intake, feed conversion and growth performance

Diet, season and their interaction significantly explained 99 % of the variation in feed intake during the trial (Table 4). Both dietary fish groups had the highest feeding rates during late autumn where the fish fed LP feed had significantly higher SFR than dietary HP group. Feed intake decreased in all the experimental units during the winter period, following a SFR increase during the spring season until harvest in June.

Throughout the trial, both dietary treatments had an increase in FCR_{BW} and FCR_{CW} and decrease in TGC_{BW} and TGC_{CW} with increasing body weight (Fig. 4A, Table 4). Overall, both season and diet significantly influenced feed conversion ratios as well as growth rates. Based on the overall weighted mean, the dietary HP group had significantly better feed conversion and growth rate measured with both whole-body weight and carcass weight (Table 4). During the late autumn period, salmon fed the HP diet attained both lower FCR and higher TGC compared to the LP fed salmon, resulting in significant body weight differences between the dietary treatments in December (Fig. 3A and 3B). During the winter period, the dietary HP group had numerically better FCR based on both BW and CW and maintained a significant higher CW (Fig. 3B), whilst there were virtually no differences in TGC between the dietary treatments. From April and onwards, the dietary HP fish group had significantly lower feed conversion ratios and numerically better growth rates than the dietary LP group. Thus, fish fed the HP feed attained significantly higher BW and CW than fish fed LP feed at trial termination (Fig. 3A and 3B). Corresponding with the results in the large-scale trials, the relative differences between the dietary treatments in feed utilisation became more apparent when FCR and TGC were calculated with basis on CW (Table 4). Within dietary treatments, a significant negative linear relationship between FCR_{BW} and TGC_{BW} was observed in the dietary HP group, and a virtual significant relationship was detected for the LP group as well (Fig. 4A). There was no significant interaction between season and diet on FCR or TGC.

Nutrient retention

Overall, the dietary LP group had significantly higher RnR_P whilst no difference was observed for AnR_P (Table 4). Despite the numerical higher RnR_P for the dietary LP group during the winter and spring feeding periods, season had not a significant influence on RnR_P or AnR_P. The season x diet interaction had no significant influence on protein retention.

Both RnR_L and AnR_L were highest during the late autumn and decreased throughout the trial period and were significantly influenced by season (Table 4). The overall weighted mean of RnR_L was virtually significantly higher ($P = 0.07$) for the dietary HP group whereas there were no differences in the AnR_L. In the winter period, the dietary LP group had significantly higher AnR_L, but except for this observation, there were no significant dietary differences between the dietary treatments within season. No significant interaction effects of season and dietary treatment were observed on lipid retention. Within the dietary LP group, a near significant negative linear relationship was observed between the absolute retention of lipid and FCR_{BW}, whilst a similar and steeper pattern was observed within the dietary HP group although not significant (Fig. 4B). A significant positive linear relationship was detected between AnR_L and TGC_{BW} (Fig. 5A), and an overall negative linear relationship between AnR_L and FCR_{BW} (Fig. 6A).

Comparable with the results of lipid retention, both RnR_E and AnR_E were highest during the late autumn and decreased throughout the trial (Table 4). Together with a block influence ($P < 0.01$) the HP fed salmon had significantly higher RnR_E during the late autumn whilst the differences in AnR_E were not observed. During the spring season, both RnR_E and AnR_E were significantly higher for the dietary HP group. The dietary LP group had numerically higher energy retention, both relative and absolute, during the winter season. Trends ($P = 0.10$) were observed for the season x diet interaction in both RnR_E and AnR_E. Analogues with AnR_L results, there was an overall positive linear relationship between AnR_E and TGC_{BW} (Fig. 5B), and an overall negative linear relationship between AnR_E and FCR_{BW} (Fig. 6B).

Discussion

Several studies have previously explored the effects of dietary protein and lipid content on fish growth performance (Hillestad & Johnsen 1994; Einen & Roem 1997; Hillestad *et al.* 1998; Azevedo, Leeson, Cho & Bureau 2004; Karalazos *et al.* 2007; Karalazos et al. 2007) but virtually all studies consider fish performance on live fish weight basis only. Because fresh, head-on gutted salmon (HOG) is the primary commodity in the industry, achieving a certain defined harvest weight is a central production focus. Thus, evaluateing the dietary protein-to-lipid influence on fish performance based on carcass weight is vital, so that it can be better understood how dietary combinations influence the growth of the product as well as the growth of the fish. The present study documents that dietary influences may not be detected unless the biometric performance is assessed on carcass weight. This was clearly demonstrated with the sampling of the dietary fish groups which had equal body weights at harvest but had significantly different carcass weights, and thus illustrating how different protein-to-lipid ratios influence the weight gain of whole body and carcass differently.

Regardless of whether the growth rate is calculated based on whole body weight or carcass weight, all presented experiments demonstrated that increased dietary protein-to-lipid ratios contributed to significantly improved growth, becoming even more evident when based on carcass weight. Corresponding with the recommendations from Einen & Roem (1997), the presented results display that DP:DE ratios > 16 g MJ^{-1} improves fish growth and increases the carcass growth in relation to whole body growth. This stands in contrast with the dietary composition used in the modern salmon farming industry (Tacon & Metian 2009; Torrisen *et al.* 2011; Ytrestøyl, Aas & Åsgåard 2015) where the general increase in dietary energy is derived from higher proportions of lipid. Therefore, it is likely that within the farming industry, the intake of fat might be excessive and that this fat is to a greater extent deposited into visceral tissue (Hillestad & Johnsen 1994; Jobling 1998, Jobling 2001; Refstie, Storebakken, Baeverfjord & Roem 2001; Jobling, Larsen, Andreassen & Olsen 2002) and thus not converted into tradeable carcass. Proteins and amino acids are the major organic compounds in fish tissue (Wilson 2002, National Research Council 2011) and like most fish species, salmon continue growing through most of the life (Kiessling, Ruohonen & Bjørnevik 2006). Therefore, sufficient amount of dietary proteins and amino acids are necessary to support optimal salmon growth and to convert feed into tradeable carcass. According to Einen, Holmefjord, Åsgård & Talbot (1995) a satisfying growth rate for well performing farmed salmon has a TGC_{BW} of 3.3. Unfortunately, the sea temperature in the winter period in the small-scale trial was the lowest recorded in a fifteen-year long period. In poikilotherms, lower temperatures impair feed intake and restrict availability of nutrients which ultimately decreases metabolic processes (Kestemont & Baras 2001; Bureau, Kaushik & Cho 2002). Thus, the record low temperature has likely hindered potential feed effects within both treatments.

Within both smolt groups in the large-scale studies, salmon fed the dietary HP feeds had both shorter production period and higher harvest weight than the LP fed salmon. Due to differences in time of slaughter and day degrees, dietary influence on the final body weight differences can be objectively assessed and estimated by using the TGC_{BW} formula. This was performed by using the same initial body weight within in each smolt group (S1: 105 g, S0: 319 g), the obtained TGC_{BW} (S1: HP = 3.18 vs LP = 2.98, S0: HP = 3.16 vs LP = 3.09) for each dietary treatment together with the same total day degrees used in the production of the dietary LP groups (S1: 3971, S0: 3688), respectively. The calculation demonstrated that the dietary HP group attained an increased body weight of 685 g and 261 g relatively to the LP group, in the S1 and S0 smolt group, respectively. Hence, considering the presented results together with the recommendation from Einen & Roem (1997) indicate that the overall production of salmon carcass in the farming industry has a great potential to improve by increasing the protein-to-lipid ratio throughout the whole production period whilst maintaining an overall high-energy dense feed composition.

The FCR_{BW} tended towards being lower for the HP groups compared to the LP groups in the large-scale trials, but by the improvements in carcass weight among the HP groups the difference became significant when assessed as FCR_{CW}. Dessen *et al.* (2017) also made such an observation, which again highlights the importance of considering carcass weight as the weight denomitor when assessing feed influence on biometric fish performance. Nonetheless, the dietary improvements for the HP groups, in the large-scale trials all FCR's were generally high compared to the overall average conversion rates in the Faroese salmon industry (Nystøyl 2017). A reason for this might be that there has been some overfeeding. In commercial production, great effort is put into controlling feeding quantities so that no feed is wasted. The opposite is applicable in small-scale experiments, where overfeeding is used to ensure that all fish is fed to satiation with a subsequent collection of the uneaten feed (Helland *et* al. 1996; Einen *et al.* 1999). The differences in dietary effect on FCR between the HP and LP treatments correspond in all three experiments, and the relative improved influence of the HP diet are considered valid since the large-scale results were reproduced in the small-scale experiment.

Within the small-scale trial, both dietary treatments had the best biometric performances during the late autumn. Corresponding with the presented results, this is a period associated with fast growth (Mørkøre & Rørvik 2001) and high retention of dietary energy, whereof most is derived from fat (Alne *et al.* 2011). However, there were no significant differences in either relative or absolute retention of nutrients between the dietary treatments during the autumn, suggesting that the higher

FCR in the dietary LP group was related to higher feed intake. Previous studies have indicated an inverse relationship between inclusion rates of protein and lipid and the relative retention of these nutrients, respectively (Hillestad & Johnsen 1994; Einen & Roem 1997; Hillestad *et al.* 1998; Bendiksen *et al.* 2003; Karalazos *et al.* 2007), but this was not observed within any of the three feeding periods. Nonetheless, the dietary LP group had an overall significantly higher RnR_P and the dietary HP group had nearly overall significantly higher RnR_L ($P = 0.07$). Despite this, there were no differences between the dietary groups in the absolute retention of either protein or lipid and no correlations of relationship identified between the AnR_P and growth performance. This might indicate that the salmon needs a relative stabile intake of protein, and because the dietary LP group had lower protein content in the diet, the group had to compensate by moderately increasing the feed intake to ensure necessary proteins for maintenance, whereas the dietary HP group had sufficient proteins to increase carcass weight beyond maintenance requirements. However, apart from the late autumn, the were no dietary differences in feed intake in any of the three periods, stressing that feed responses are a results of feed composition, intake and utilization, especially in periods with high lipid retention. The latter may be visualized by improved FCR for the dietary HP group in late autumn period and revealing an overall relation between FCR and the absolute retention of lipids, and overall strong correlations between FCR and TGC within both dietary treatments.

Although the S1 salmon fed HP diets in January-February was exposed to predator attacks, the mortality rates in the large-scale trials were generally low and consistent with the rates observed within the Faroese salmon industry (Nystøyl 2017). Dietary related differences in mortality was not observed in any of the three experiments.

In summary, high dietary protein-to-lipid ratios ($\geq$ 1.2) throughout the whole production period of Atlantic salmon significantly improves both growth and feed utilization compared to an isoenergitic diet with lower protein-lipid-ratio ($\leq$ 1). A high protein-to-lipid feeding strategy induces greater carcass weight gain, and the improvements in feed conversion and growth rate become larger and more evident when calculated based on carcass weight. The fish performance is also greatly influenced by season whereof autumn seems the period where feed utilization and growth have the highest potential to be optimised. Thus, the presented study indicates that it is possible to attain faster growth and improved feed conversion in modern Atlantic salmon industry, by increasing the current dietary protein-to-lipid ratios, especially during the autumn.

Acknowledgements

We would like to thank the staff at the Bakkafrost and Luna farming sites in Lambavík and Sørvágur, especially the site managers Sunvard Joensen and Jógvan Páll Ole Jacobsen, respectively. Also, we would like to thank for the excellent technical assistance provided by the staff from the former Nofima research station at Averøy (currently the Marine Harvest research station), with special thanks to Sissel Nergård. A great appreciation is sent to The Faroese Research Council, Statoil Faroes and Havsbrún PF who financed this work.

Figure legends

Figure 1 A) Weekly seawater temperature (°C) for the large-scale S0 trial (solid black line) and the large-scale S1 trial (broken black line) displayed on the x-axis. B) Daily seawater temperature (solid black line) during the S1 small-scale experiment is displayed on the y-axis where the sampling periods that identify the three feeding periods is noted above the figure. Average day length per week (hours) for the large- and small-scale experiments, are illustrated with broken grey line displayed on the z-axis.

Figure 2 Average body weight and carcass weight of S1 (A) and S0 (B) Atlantic salmon in the large-scale trial sampled on the harvest line with respect to achieving identical weight classes of 4.5, 5.5, and 6.5 kg, respectively. Grey and white bars illustrate the dietary HP and LP fish groups, respectively. Brackets denote significant differences between dietary treatments. Values are presented as means ± SEM.

Figure 3 Average body weight (A) and carcass weight (B) of Atlantic salmon fed isoenergetic diets with high (HP: grey bars) and low (LP: white bars) protein-to-lipid ratio in the small-scale trial. Brackets denote significant differences between dietary treatments together within sampling periods. Values are presented as means ± SEM, n = 3.

Figure 4 Relationships between feed conversion (FCR_{BW}) and growth (TGC_{BW}) responses (A), and absolute retention of dietary lipid and feed conversion (FCR_{BW}) (B) in Atlantic salmon fed isoenergetic high dietary protein-to-lipid ratio (HP: shaded squares) and low dietary protein-to-lipid ratio (LP: open circles) during late autumn, winter and spring in the small-scale trial. Values are presented as means ± SEM, n = 3.

Figure 5 Growth response (TGC_{BW}) in relation to the absolute retention of dietary lipid (A) and dietary energy (B) in Atlantic salmon fed isoenergetic high dietary protein-to-lipid ratio (HP: shaded squares) and low dietary protein-to-lipid ratio (LP: open circles) throughout three seasons in the grow-out period, respectively late autumn, winter and spring. Values are presented as means ± SEM, n = 3.

Figure 6 Relationships between feed conversion (FCR_{BW}) and absolute retention of dietary lipid (A) and dietary energy (B) in Atlantic salmon fed isoenergetic high dietary protein-to-lipid ratio (HP: shaded squares) and low dietary protein-to-lipid ratio (LP: open circles) during late autumn, winter and spring in the small-scale trial. Values are presented as means ± SEM, n = 3.

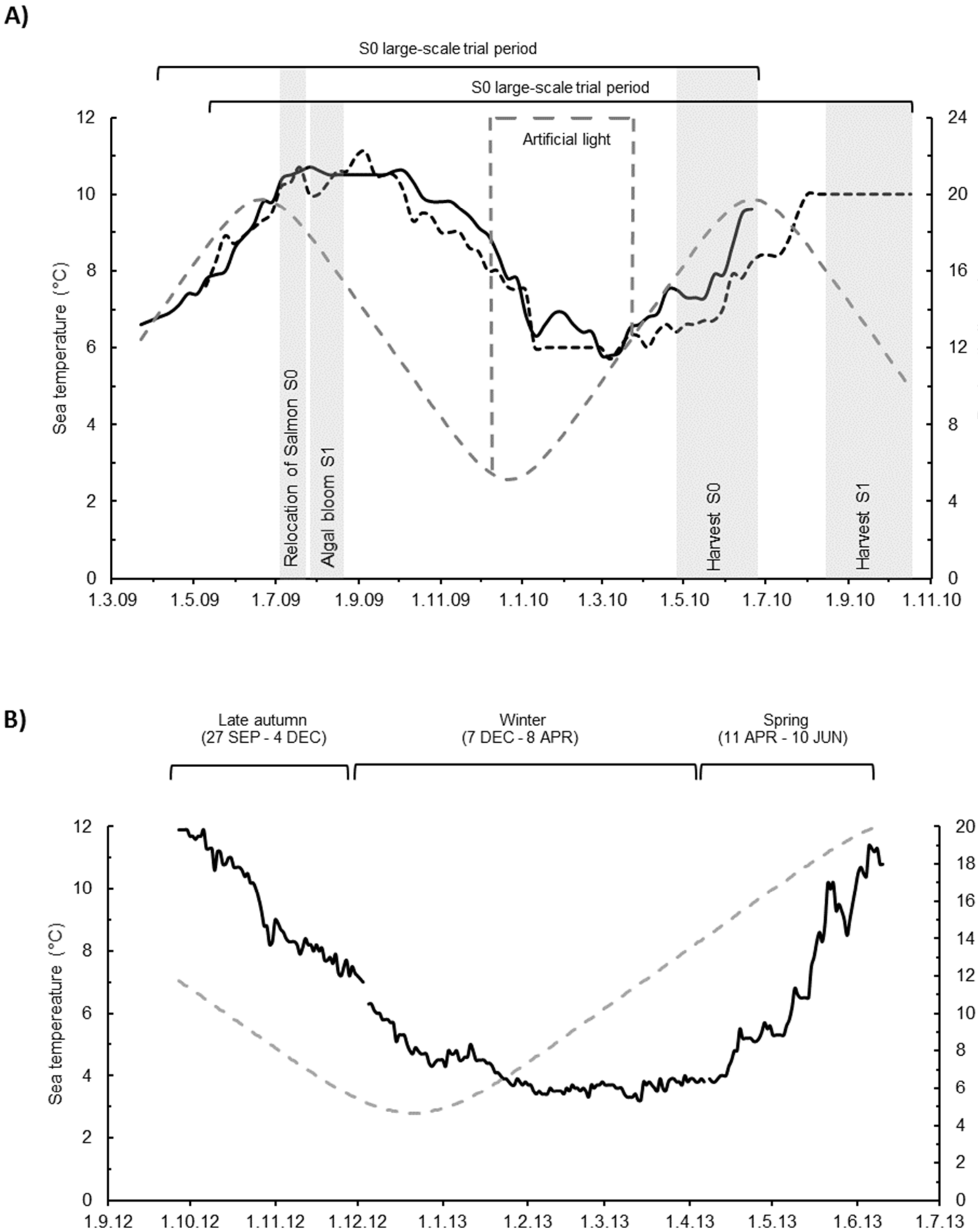

Figure 1 A) Weekly seawater temperature (°C) for the large-scale S0 trial (solid black line) and the large-scale S1 trial (broken black line) displayed on the y-axis. B) Daily seawater temperature (solid black line) during the S1 small-scale experiment is displayed on the y-axis where the sampling periods that identify the three feeding periods is noted above the figure. Average day length per week (hours) for the large- and small-scale experiments, are illustrated with broken grey line displayed on the z-axis.

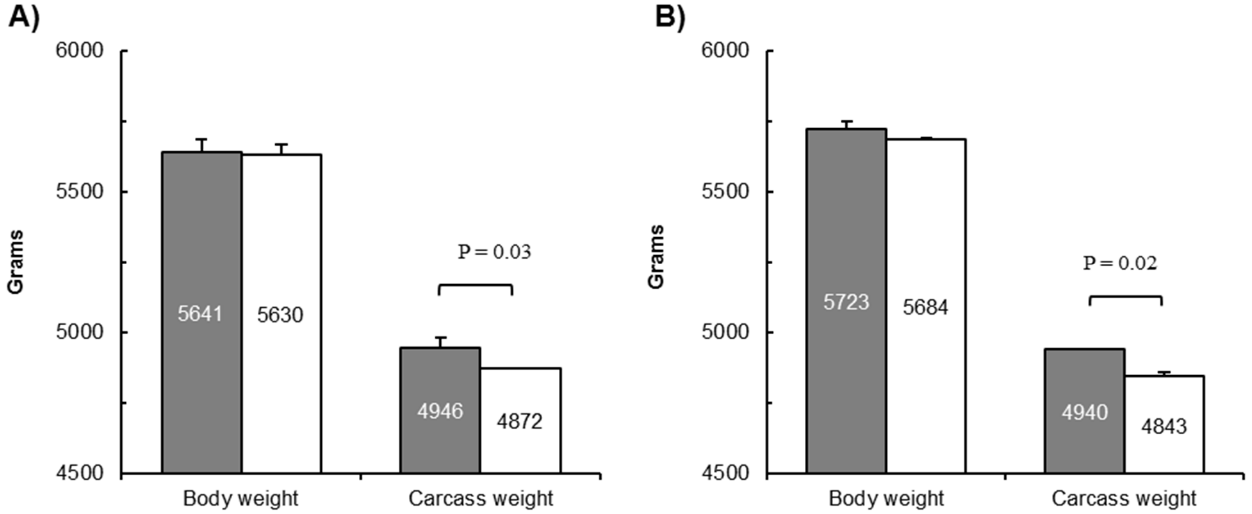

Figure 2 Average body weight and carcass weight of S1 (A) and S0 (B) Atlantic salmon in the large-scale trial sampled on the harvest line with respect to achieving identical weight classes of 4.5, 5.5, and 6.5 kg, respectively. Grey and white bars illustrate the dietary HP and LP fish groups, respectively. Brackets denote significant differences between dietary treatments. Values are presented as means ± SEM.

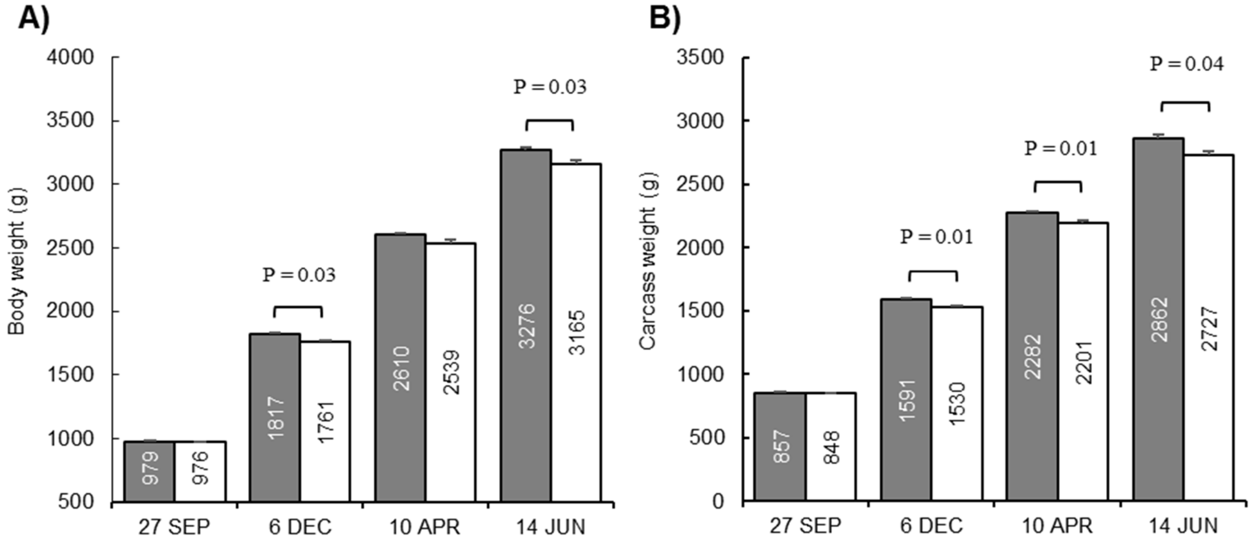

Figure 3 Average body weight (A) and carcass weight (B) of Atlantic salmon fed isoenergetic diets with high (HP: grey bars) and low (LP: white bars) protein-to-lipid ratio in the small-scale trial. Brackets denote significant differences between dietary treatments within sampling periods. Values are presented as means ± SEM, n = 3.

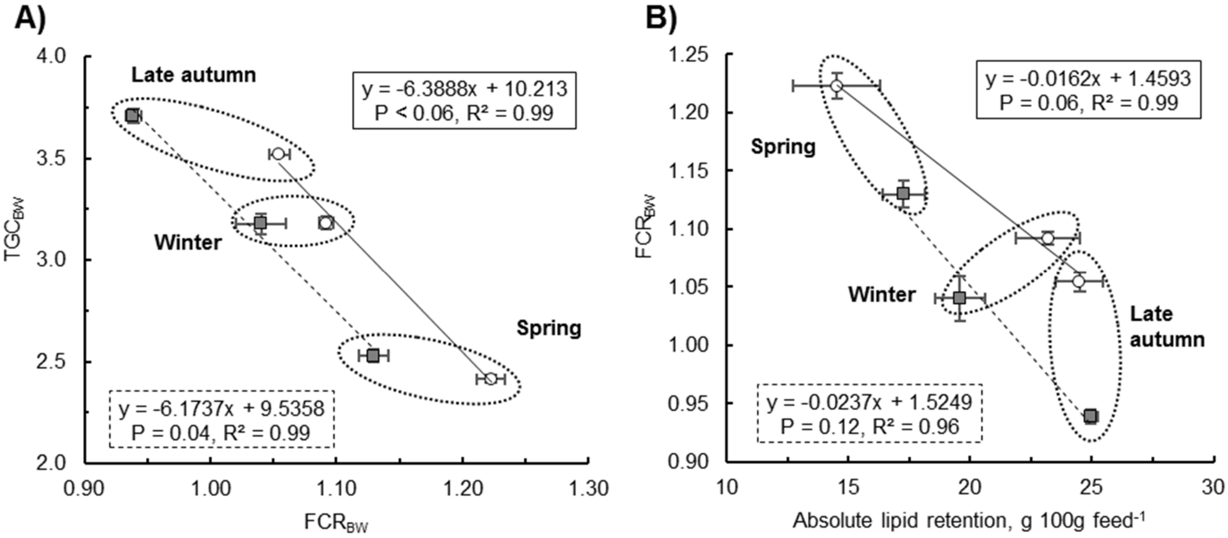

Figure 4 Relationships between feed conversion (FCR_{BW}) and growth (TGC_{BW}) responses (A), and absolute retention of dietary lipid and feed conversion (FCR_{BW}) (B) in Atlantic salmon fed isoenergetic high dietary protein-to-lipid ratio (HP: shaded squares) and low dietary protein-to-lipid ratio (LP: open circles) during late autumn, winter and spring in the small-scale trial. Values are presented as means ± SEM, n = 3.

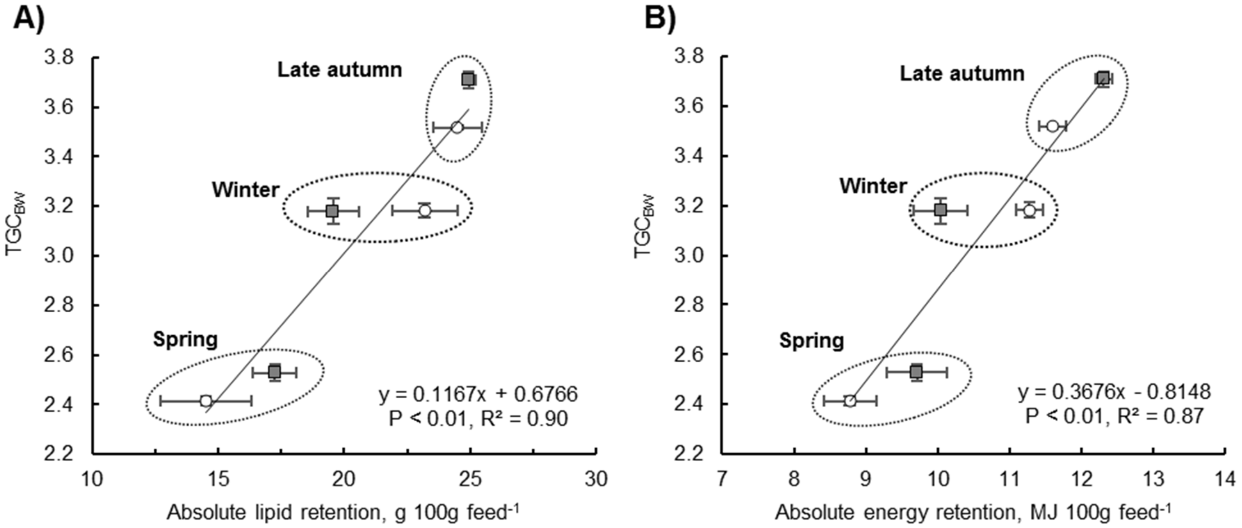

Figure 5 Growth response (TGC$_{BW}$) in relation to the absolute retention of dietary lipid (A) and dietary energy (B) in Atlantic salmon fed isoenergetic high dietary protein-to-lipid ratio (HP: shaded squares) and low dietary protein-to-lipid ratio (LP: open circles) throughout three seasons in the grow-out period, respectively late autumn, winter and spring. Values are presented as means ± SEM, n = 3.

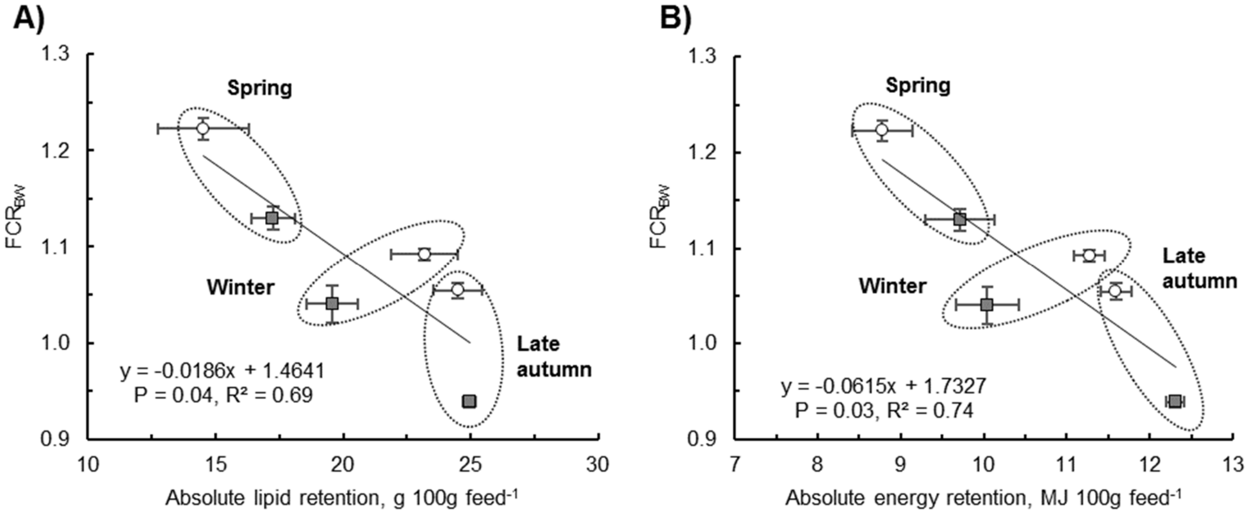

Figure 6 Relationships between feed conversion (FCR$_{BW}$) and absolute retention of dietary lipid (A) and dietary energy (B) in Atlantic salmon fed isoenergetic high dietary protein-to-lipid ratio (HP: shaded squares) and low dietary protein-to-lipid ratio (LP: open circles) during late autumn, winter and spring in the small-scale trial. Values are presented as means ± SEM, n = 3.

Table 1 Proximate feed compositions (wet weight) used 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.

Smolt group	Large-scale S1		Large-scale S0		Small-scale S1	
Diet	HP	LP	HP	LP	HP	LP
Pellet size 3 mm	*(n = 4)*	*(n = 2)*				
Dry matter, %	93.3 ± 0.1	93.1 ± 0.2				
Crude protein, %	49.9 ± 0.7	46.6 ± 0.3				
Lipid, %	25.6 ± 1.4	27.2 ± 0.2				
Ash, %	9.4 ± 0.5	8.7 ± 0.2				
Starch, %*	6.7 ± 0.1	8.6 ± 0.2				
DP. %**	42.4 ± 0.6	40.0 ± 0.2				
DE, MJ/kg**	20.3 ± 0.4	20.5 ± 0.0				
DP:DE, g/MJ**	20.9 ± 0.7	19.5 ± 0.1				
Protein-to-lipid ratio	1.95	1.71				
Pellet size 4 mm	*(n = 5)*	*(n = 2)*				
Dry matter, %	94.1 ± 0.1	93.4 ± 0.2				
Crude protein, %	52.1 ± 1.4	45.8 ± 0.3				
Lipid, %	22.1 ± 1.8	28.7 ± 0.6				
Ash, %	11.0 ± 0.2	8.6 ± 0.3				
Starch, %*	6.9 ± 0.2	8.7 ± 0.3				
DP. %**	44.8 ± 1.2	39.4 ± 0.3				
DE, MJ/kg**	19.6 ± 0.4	20.9 ± 0.2				
DP:DE, g/MJ**	22.9 ± 1.0	18.9 ± 0.3				
Protein-to-lipid ratio	2.36	1.60				
Pellet size 6 mm	*(n = 7)*	*(n = 2)*	*(n = 2)*	*(n = 7)*		
Dry matter, %	95.6 ± 0.1	94.2 ± 0.1	94.1 ± 0.3	93.9 ± 0.2		
Crude protein, %	46.6 ± 0.5	41.9 ± 0.2	44.4 ± 0.3	42.7 ± 0.5		
Lipid, %	27.6 ± 0.4	32.4 ± 0.2	30.8 ± 0.7	31.6 ± 0.4		
Ash, %	9.5 ± 0.4	8.1 ± 0.2	8.2 ± 0.2	7.8 ± 0.1		
Starch, %*	8.6 ± 0.7	8.9 ± 0.0	8.3 ± 0.4	9.0 ± 0.0		
DP. %**	40.1 ± 0.5	36.1 ± 0.2	38.2 ± 0.3	36.7 ± 0.5		
DE, MJ/kg**	20.8 ± 0.1	21.6 ± 0.1	21.4 ± 0.2	21.5 ± 0.1		
DP:DE, g/MJ**	19.3 ± 0.1	16.7 ± 0.1	17.9 ± 0.3	17.1 ± 0.2		
Protein-to-lipid ratio	1.69	1.29	1.44	1.35		
Pellet size 9 mm	*(n = 71)*	*(n = 10)*	*(n = 20)*	*(n = 10)*	*(n = 2)*	*(n = 2)*
Dry matter, %	93.7 ± 0.2	94.1 ± 0.1	94.0 ± 0.2	94.2 ± 0.1	94.1 ± 1.0	94.3 ± 0.5
Crude protein, %	42.0 ± 0.2	35.4 ± 0.1	40.2 ± 0.3	34.5 ± 0.2	42.7 ± 0.1	35.4 ± 0.4
Lipid, %	32.6 ± 0.2	35.9 ± 0.1	34.4 ± 0.2	35.8 ± 0.2	32.1 ± 0.7	36.0 ± 0.6
Ash, %	8.1 ± 0.1	6.4 ± 0.1	8.0 ± 0.1	6.7 ± 0.1	7.9 ± 0.2	7.1 ± 0.2
Starch, %*	8.4 ± 0.2	9.6 ± 0.1	9.1 ± 0.1	9.8 ± 0.8	8.5 ± 0.2	11.0 ± 0.4
DP. %**	36.1 ± 0.1	30.4 ± 0.1	34.6 ± 0.3	29.6 ± 0.2	36.7 ± 0.1	30.4 ± 0.3
DE, MJ/kg**	21.6 ± 0.1	22.0 ± 0.0	21.9 ± 0.1	21.8 ± 0.1	21.6 ± 0.3	21.9 ± 0.3
DP:DE, g/MJ**	16.7 ± 0.1	13.9 ± 0.1	15.8 ± 0.1	13.6 ± 0.1	17.0 ± 0.2	13.9 ± 0.0
Protein-to-lipid ratio	1.29	0.99	1.17	0.96	1.33	0.98

* Starch content was not analysed in all feed batches. The stated value is the average of the analysed batches.

**Digestible protein and digestible energy were calculated, based on the measured proximate feed composition, assuming 23.7, 39.5 and 17.2 MJ per kg of protein, lipids and nitrogen-free extractives (NFE), respectively. The apparent digestibility coefficients used for protein, lipid and NFE in Atlantic salmon, were 0.86 (Einen & Roem 1997), 0.94 (Einen & Roem 1997) and 0.50 (Arnesen & Krogdahl 1993).

Table 2 Overview of the feeding period for each pellet size within both dietary treatments in the large-scale trials. The pellet sizes are fed in relation to the preferred fish weight intervalls which is also given.

Large-scale S1	Pellet size used	Preferred fish weight, g	First feed delivery	Feeding period
HP	3 mm	~ 100 - 150	07.04.2009	9 weeks (week 15 - week 24)
	4 mm	~ 150 - 300	16.06.2009	11 weeks (week 24 - week 35)
	6 mm	~ 300 - 800	28.08.2009	6 weeks (week 35 - week 41)
	9 mm	~ 800+	08.10.2009	44 weeks (week 41 - week 33)
LP	3 mm	~ 100 - 150	27.03.2009	10 weeks (week 13 - week 23)
	4 mm	~ 150 - 300	04.06.2009	11 weeks (week 23 - week 34)
	6 mm	~ 300 - 800	18.08.2009	7 weeks (week 34 - week 41)
	9 mm	~ 800+	19.10.2009	49 weeks (week 41 - week 38)
Large-scale S0				
HP	6 mm	~ 300 - 800	18.03.2009	16 weeks (week 12 - week 28)
	9 mm	~ 800+	09.07.2009	35 weeks (week 28 - week 21)
LP	6 mm	~ 300 - 800	04.03.2009	20 weeks (week 10 - week 30)
	9 mm	~ 800+	26.06.2009	39 weeks (week 26 - week 23)

Table 3 Differences in specific feeding rate (SFR), feed conversion (FCR) and growth rate (TGC) based on live body weight (BW) and carcass weight (CW) in S1 and S0 Atlantic salmon in the large-scale experiments. Significant differences between dietary treatments (D) and smolt group (SG) and the interaction (D x SG) in the two-way ANOVA are given whilst the values in brackets depict statistical trends, and non-significant differences are highlighted as ns. Dietary statistics within smolt group is visualized by P.

Smolt group	S1			S0			Two-way ANOVA			
Dietary group	HP (n = 3)	LP (n =2)	*P*	HP (n = 2)	LP (n =2)	*P*	D	SG	D x SG	R^2
SFR	0.55 ± 0.01	0.56 ± 0.02	ns	0.51 ± 0.02	0.52 ± 0.02	ns	ns	0.03	ns	0.50
FCR_{BW}	1.29 ± 0.03	1.36 ± 0.03	ns	1.21 ± 0.03	1.25 ± 0.02	ns	(0.06)	0.01	ns	0.73
FCR_{CW}	1.47 ± 0.04	1.57 ± 0.01	ns	1.40 ± 0.02	1.47 ± 0.03	ns	0.03	0.04	ns	0.67
TGC_{BW}	3.18 ± 0.04	2.98 ± 0.07	(0.06)	3.16 ± 0.03	3.09 ± 0.09	ns	0.04	ns	ns	0.46
TGC_{CW}	3.05 ± 0.03	2.84 ± 0.07	(0.06)	2.99 ± 0.03	2.91 ± 0.09	ns	0.02	ns	ns	0.59

Table 4 Seasonal differences in specific feeding rate (SFR), feed conversion (FCR) and growth rate (TGC) based on live body weight (BW) and carcass weight (CW), relative nutrient retention (RnR: % of ingested) and absolute nutrient retention (AnR: g 100^{-1} feed for protein and fat, and MJ kg^{-1} feed for energy) of protein (P), lipid (L) and energy (E), respectively, in S1 Atlantic salmon from September to June in small-scale experiment (mean ± SEM, n = 3). Significant differences between dietary treatments within season are denoted with small letters. Significant P-values in the two-way ANOVA and non-significant differences are highlighted as ns.

Period	SEP - DEC		DEC - APR		APR - JUN		Two-way ANOVA				Overall weighted mean	
Dietary group	HP	LP	HP	LP	HP	LP	D	S	D x S	R^2	HP	LP
SFR	0.87 ± 0.01^b	0.93 ± 0.01^a	0.31 ± 0.01	0.33 ± 0.01	0.43 ± 0.01	0.44 ± 0.00	< 0.001	< 0.001	< 0.01	0.99	0.55 ± 0.01^b	0.58 ± 0.00^a
FCR_{BW}	0.94 ± 0.01^b	1.05 ± 0.01^a	1.04 ± 0.03	1.09 ± 0.01	1.13 ± 0.02^b	1.22 ± 0.02^a	< 0.001	< 0.001	ns	0.89	1.03 ± 0.00^b	1.12 ± 0.00^a
FCR_{CW}	1.07 ± 0.01^b	1.21 ± 0.02^a	1.19 ± 0.04	1.26 ± 0.02	1.30 ± 0.05^b	1.46 ± 0.02^a	< 0.001	< 0.001	ns	0.87	1.18 ± 0.02^b	1.30 ± 0.00^a
TGC_{BW}	3.71 ± 0.06^a	3.52 ± 0.02^b	3.18 ± 0.09	3.18 ± 0.05	2.53 ± 0.06	2.41 ± 0.03	0.05	< 0.001	ns	0.97	3.19 ± 0.00^a	3.08 ± 0.02^b
TGC_{CW}	3.55 ± 0.05^a	3.36 ± 0.02^b	3.03 ± 0.08	3.02 ± 0.02	2.41 ± 0.09	2.23 ± 0.03	0.02	< 0.001	ns	0.96	3.04 ± 0.02^a	2.92 ± 0.02^b
RnR_P	38.9 ± 2.9	38.8 ± 3.8	40.4 ± 4.1	50.9 ± 3.5	32.4 ± 4.8	43.5 ± 1.4	0.05	ns	ns	0.22	37.7 ± 0.9^b	44.7 ± 0.2^a
RnR_L	77.7 ± 1.4	68.0 ± 4.7	61.0 ± 5.5	64.4 ± 6.2	53.8 ± 4.7	40.3 ± 8.6	ns	0.002	ns	0.57	65.0 ± 0.9	58.9 ± 2.3
RnR_E	57.0 ± 0.9^a	53.0 ± 1.4^b	46.5 ± 3.0	51.1 ± 1.5	45.0 ± 3.3^a	40.1 ± 2.9^b	ns	0.001	ns	0.61	49.9 ± 0.9	48.8 ± 1.7
AnR_P	16.6 ± 1.2	13.7 ± 1.4	17.3 ± 1.8	18.0 ± 1.2	13.8 ± 2.0	15.4 ± 0.5	ns	ns	ns	-	16.1 ± 0.4	15.7 ± 0.1
AnR_L	25.0 ± 0.3	24.5 ± 1.0	19.6 ± 1.8^b	23.2 ± 2.2^a	17.3 ± 1.5	14.5 ± 3.1	ns	0.001	ns	0.59	20.9 ± 0.3	21.2 ± 0.8
AnR_E	12.3 ± 0.1	11.6 ± 0.2	10.0 ± 0.7	11.3 ± 0.3	9.7 ± 0.7^a	8.8 ± 0.6^b	ns	0.001	ns	0.63	10.8 ± 0.2	10.7 ± 0.4

References

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. *Aquaculture Research,* **42**, 248-259.

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.

Azevedo P.A., Leeson S., Cho C.Y. & Bureau D.P. (2004) Growth and feed utilization of large size rainbow trout (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*) reared in freshwater: diet and species effects, and responses over time. *Aquaculture Nutrition,* **10**, 401-411.

Bendiksen E.Å., Berg O.K., Jobling M., Arnesen A.M. & Måsøval 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**, 283-299.

Brett J.R. (1979) Environmental factors and growth. In: *Fish Physiology* (ed. by W.S. Hoar, D.J. Randall & J.R. Brett.), pp. 599-214. Academic Press, New York.

Bureau D.P., Kaushik S.J. & Cho C.Y. (2002) Bioenergetics. In: *Fish Nutrition* (ed. by J.E. Halver & R.W. Hardy), pp. 1-59. Academic Press, Sand Diego.

Dessen J.-E., Weihe R., Hatlen B., Thomassen M.S. & Rørvik K.-A. (2017) Differenth 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*, 345-354.

Einen O., Holmefjord I., Åsgård T. & Talbot C. (1995) Auditing nutrient discharges from fish farms: theoretical and practical considerations. *Aquaculture Research,* **26**, 701-713.

Einen O., Waagan, 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**, 84-105.

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.

Einen O. & Roem A.J. (1997) Dietary protein/energy ratios for Atlantic salmon in relation to fish size: growth, feed utilization and slaughter quality. *Aquaculture Nutrition,* **3**, 115-126.

Einen O., Waagan 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.

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.

Hemre G.I. & Sandnes K. (2008) Seasonal adjusted diets to Atlantic salmon (*Salmo salar*): Evaluations of a novel feed based on heat-coagulated fish mince, fed throughout 1 year in sea: Feed utilisation, retention of nutrients and health parameters. *Aquaculture,* **274**, 166-174.

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.

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. *Aquaculture Nutrition,* **4**, 89-97.

Jobling M. (1997) Temperature and growth: modulation of growth rate via temperature change. In: *Implications for freshwater and marine fish* (ed. by C.M. Wood & D.G. McDonald), pp. 225-253. Chapman & Hall, London.

Jobling M. (1998) Influence of dietary fat level and increased adiposity on growth and fat deposition in rainbow trout, *Oncorhyncus mykiss* (Walbaum). *Aquaculture Research,* **29**, 601-607.

Jobling M. (2001) Nutrient partitioning and the influence of feed composition on body composition. In: *Food intake in fish* (ed. by D. Houlihan, T. Boujard & M. Jobling), pp. 354-375. Blackwell Science, Oxford.

Jobling M., Larsen A.V., Andreassen B. & Olsen R.L. (2002) Adiposity and growth of post-smolt Atlantic salmon *Salmo salar* L. *Aquaculture Research,* **33**, 533-541.

Johansen S.J.S., Ekli M. & Jobling M. (2002) Is there lipostatic regulation of feed intake in Atlantic salmon *Salmo salar* L. *Aquaculture Research,* **33**, 515-524.

Johansen S.J.S., Sveier H. & Jobling M. (2003) Lipostatic regulation of feed intake in Atlantic salmon *Salmo salar* L. defending adiposity at the expence of growth. *Aquaculture Research,* **34**, 317-331.

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. *Aquaculture Nutrition,* **13**, 256-265.

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.

Kestemont P. & Baras E. (2001) Environmental factors and feed intake: Mechanisms and interactions. In: *Food intake in fish* (ed. by D. Houlihan, T. Boujard & M. Jobling), pp. 131-156. Blackwell Science, Oxford.

Kiessling A., Ruohonen K. & Bjørnevik M. (2006) Muscle fibre growth and quality in fish. *Archiv Tierzucht Dummerstorf,* **49**, 137-146.

Lysfjord G., Jobling M. & Solberg C. (2004) Atlantic salmon, *Salmo salar* L., smolt production strategy affects body composition and early seawater growth. *Aquaculture,* **237**, 191-205.

Måsøval K.A., Åsgård T., Wathne E., Shearer K.D., Staurnes M. & Sigholt T. (1994) Survival, growth and osmoregulation of Atlantic smolts transferred to seawater during smoltification and desmoltification. In: *Proceedings of an International Fish Physiology Symposium held at the University of British Columbia*, Vancouver, Canada*,* pp. 16-21.

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 + smolt or 1 + smolts. *Aquaculture,* **199**, 145-157.

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.

National Research Council (1993) *Nutrient requirements of Fish,* National Academy Press, Washington DC.

National Research Council (2011) *Nutrient requirements of Fish and Shrimp,* National Academy Press, Washington DC.

Nystøyl R. (2017) Trender - Produksjon & marked - Atlantisk laks 2017. In: *Aliráðstevnan 2017*, Hotel Føroyar, Tórshavn, Faroe Islands*,* pp. 44.

Oehme M., Grammes F., Takle H., Zambonino-Infante J.-L., Refstie S., Thomassen M.S., Rørvik K.-A. & Terjesen B.F. (2010) Dietary supplementation of glutamate and arginine to Atlantic salmon (*Salmo salar L.*) increases growth during the first autumn in sea. *Aquaculture,* **310**, 156-163.

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 products at medium or high lipid level. *Aquaculture,* **193**, 91-106.

Silverstein J.T., Shearer KD, Dickhoff W.W. & Plisetskaya EM (1999) Regulation of nutrient intake and energy balance in salmon. *Aquaculture,* **177**, 161-169.

Tacon A.G.J. & Metian M. (2009). Fishing for aqualculture: Non-food use of small pelagic forage fish - a global perspecitve. *Reviews in Fisheries Science,* **17**, 305-317.

Torrisen O., Olsen R.E., Toresen R., Hemre G.I., Tacon A.G.J., Asche F., Hardy R.W. & Lall S. (2011) Atlantic salmon (*Salmo salar*): The "super-chicken" of the sea? *Reviews in Fisheries Science,* **19**, 257-278.

Waagbø R., Berntssen M.H.G., Danielsen T., Helberg H., Kleppa A.L., Berg Lea T., Rosenlund G., Tvenning L., Susort S., Vikeså V. & Breck O. (2013) Feeding Atlantic salmon diets with plant ingredients during the seawater phase - a full-scale net production of marine protein with focus on biological performance, welfare, product quality and safety. *Aquaculture Nutrition,* **19**, 598-618.

Wathne E. (1995) Strategies for directing slaughter quality of farmed Atlantic salmon (Salmo salar) with emphasis on diet composition and fat deposition. In: *Department of Animal Science*. Agricultural University of Norway, Ås.

Wilson R.P. (2002) Amino acids and proteins. In: *Fish Nutrition* (ed. by J.E. Halver & R.W. Hardy), pp. 143-179. Academic Press, San Diego.

Ytrestøyl T., Aas T.S. & Åsgård T. (2015) Utilisation of feed resources in production of Atlantic salmon (*Salmo salar*) in Norway. *Aquaculture,* **448**, 365-374.