

1 **Title:**

2 A systematic review and analysis of long-term growth trials on the effect of diet on omega-3 fatty acid
3 levels in the fillet tissue of post-smolt Atlantic salmon

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Abstract

Elucidating the specific effects of diet on the fatty acid composition in Atlantic salmon (*Salmo salar*), particularly health beneficial omega-3 long-chain polyunsaturated fatty acids (n-3 LC PUFA), remains an area of intense commercial interest given the increasing market restrictions placed on the supply of fishmeal and fish oil. The present study conducted a systematic review and subsequent analysis of published nutritional data from long-term growth trials using post-smolt Atlantic salmon to provide a summary of currently available information and to identify the most significant drivers of omega-3 levels on Atlantic salmon fillet tissue. Overall, there were relatively few studies which met the selection criteria and this had implications for further explanation of some results. Statistically significant regression models were generated for fillet DHA and fillet n-3 LC PUFA. Fish weight was a significant predictor in both models, and dietary 22:6n-3 (DHA) was an intuitive predictor of fillet DHA. Furthermore, dietary EPA and dietary 22:1 isomers were significant predictors of fillet n-3 LC PUFA.

Keywords:

Atlantic salmon, omega-3, modelling, systematic review, nutrition

1. Introduction

The Atlantic salmon (*Salmo salar*) aquaculture industry is constantly balancing the expectation of producing fish with high levels of health promoting omega-3 long-chain polyunsaturated fatty acids (n-3 LC PUFA) whilst relying on dietary ingredients which are subject to intense market volatility (Oglend 2013; Sprague et al. 2016; Troell et al. 2014; Turchini et al. 2009). Therefore, the continuous evolution of dietary lipid and fatty acid compositions in aquafeed formulations is often influenced by the need of balancing both the fish's and consumer's nutritional requirements, coupled the fluctuations in cost and availability of dietary oil sources (Bendiksen et al. 2011; Hardy 2010; Sprague et al. 2016; Tacon & Metian 2015). A major trend in recent years has been the increasing level of substitution of marine derived oil sources, such as fish oil, with more readily available oils of terrestrial origin (Bendiksen et al. 2011; Sprague et al. 2016; Tacon & Metian 2015; Turchini et al. 2010). Whilst this has enabled the continual growth of the Atlantic salmon industry, it has resulted in compromises in product quality, and specifically in the reduction in the level of n-3 LC PUFA deposited in the fillet (Henriques et al. 2014; Nichols et al. 2014; Sprague et al. 2016). In order to further develop nutritional solutions to enhance the viability of Atlantic salmon aquaculture both industry and academia routinely engage in experimental dietary growth trials. Within industry, these trials are essential to the uptake of more cost-effective and sustainable aquafeed formulations, yet much of the quantitative data remains in-house and rarely makes its way to peer-reviewed academic journals (Henriksson et al. 2012). On the other hand, despite significant research interest in Atlantic salmon, university and research and development provider-based experiments are often subject to financial and logistical limitations, including facility availability and the high cost of lengthy trials. However, from a biological perspective, confidence in recorded nutritional data is reliant on the assimilation of dietary fatty acids into fillet tissues, which are both time and growth dependent (Jobling 2003; Jobling 2004). In response, Rosenlund et al. (2016) advocated for a greater representation of long-term growth trials in the published literature to better elucidate n-3 LC PUFA utilisation in Atlantic salmon. Complicating this

endeavour, methods in data reporting often vary between research groups leading to inconsistencies when attempting to evaluate relevant quantitative data (Sales & Glencross 2011). The outcome is few attempts to collate and quantify published nutritional information on Atlantic salmon (Collins et al. 2013; Sales & Glencross 2011).

A potential strategy to quantify the dietary effects on fillet n-3 LC PUFA in Atlantic salmon reported in published literature is via meta-analytic methods. Such methods are used to combine information from multiple studies to more accurately, and at the same time more broadly, evaluate or estimate an overall effect (Tweedie 2001). Analyses of this kind have traditionally been popular in the sociological and medical sciences and they are more recently being utilised as an effective quantitative tool to measure outcomes in numerous disciplines, including fish nutrition (Collins et al. 2013; Sales & Glencross 2011; Tweedie 2001). Specifically, Sales and Glencross (2011) quantified the effects of fish oil substitution on growth performance and fatty acid composition in Atlantic salmon. However, despite elucidating relationships between vegetable oils and fish performance, further extrapolation of results was hindered by a lack of uniformity and replication in the collected numerical data (Sales & Glencross 2011). Therefore, additional effort is required to identify the major drivers of fillet n-3 LC PUFA in post-smolt Atlantic salmon and also to assess whether a lack of published information is prohibitive to a robust discussion and interpretation of these drivers.

The objective of the present study was to utilise existing published data from long-term growth trials to i) summarise the extent of published information regarding long-term nutritional growth trials conducted on Atlantic salmon in seawater, and where possible, ii) describe the most significant drivers of fillet n-3 LC PUFA in seawater-reared Atlantic salmon. This was achieved by means of a systematic review and the subsequent analyses of the extracted data via meta-regression techniques.

2. Material and Methods

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80 2.1 Systematic review

81 A systematic review of the literature was conducted to identify published studies that reported viable
82 data for inclusion in the meta-analysis. The majority of literature was identified by entering two search
83 terms 1) “Atlantic salmon fatty acid growth” and 2) “Salmo salar fatty acid growth” into the database
84 ‘Web of Science’ with a time constraint of studies published post 1950. Manual searching techniques
85 such as scanning of reference lists and broad searches using Google Scholar® supplemented database
86 searching were used to retrieve more studies. Articles obtained from database searching ($n = 1133$)
87 were added to articles obtained from manual searching techniques ($n = 50$) (Figure 1). Initial screening
88 of titles and abstracts removed duplicates and studies not using the target species. The remaining
89 articles ($n = 254$) were subject to full text assessments against the pre-determined eligibility criteria
90 listed below.

- 91 a) Lipid proximate composition of feed must be reported
- 92 b) Lipid proximate composition of fillet must be reported
- 93 c) Fish must be post-smolt and reared in saltwater (not juvenile)
- 94 d) Fish must have had an increased weight of a minimum of 300%

95

96 The selection criteria above were agreed upon by a panel comprised of all co-authors and additional
97 staff at Deakin University, and aimed at identifying only studies that would provide reliable, relevant
98 data for the meta-analysis. Following methods described in Sales & Glencross (2011), only peer-
99 reviewed works published in English were considered. Data was extracted from studies meeting the
100 pre-determined selection criteria and included: i) growth, feed efficiency and biometric data, ii) dietary
101 and fillet proximate composition iii) dietary and fillet fatty acid composition and iv) physio-chemical
102 parameters. Where the same growth trial data was presented in multiple studies, the study best
103 meeting the selection criteria or with the most complete dataset was included. Within studies,
104 individual treatment groups that did not meet all requirements of the selection criteria were omitted

from inclusion in the database. To accommodate for changes to dietary proximate composition concomitant with increasing fish size within treatments, where necessary, the dietary proximate composition was reported as the average fed to experimental fish based on the percentage of total fish growth at each dietary proximate composition level.

2.2 Unit conversion

All fatty acid data used in the present study was converted to mg g^{-1} of diet and $\text{mg } 100\text{g}^{-1}$ fillet for diet and fillet fatty acid data, respectively. Due to a large number of studies reporting fatty acid data as a percentage of total fatty acids, two separate conversion factors were applied to the data. Based on studies by Emery et al. (2014) and Norambuena et al. (2015) a conversion factor of 0.76678 was applied to dietary fatty acid data reported in percentage of fatty acids to convert to mg g^{-1} lipid. Similarly, based on studies by Emery et al. (2014) and Wilke et al. (2015) a conversion factor of 0.78831 was used to convert fillet fatty acid data reported in % of fatty acids to mg g^{-1} lipid. Finally, diet and fillet proximate data was used to make the final conversion in order to report all fatty acid data as mg g^{-1} diet and $\text{mg } 100\text{g}^{-1}$ fillet.

2.3 Data analysis

Although the present study has combined multiple studies and analysed the resultant data, it is not, strictly, a meta-analysis as it did not measure outcome variables in response to a common control. Whereas dietary fish oil percentage has been used as a control in a meta-analysis by Sales & Glencross (2011), the present study focussed on the entire suite of dietary variables collected as predictors.

2.3.4 Identification of collinearity

Initially, 63 variables, each with up to 85 data points, were sorted into independent (36) and dependent (27) sets, then de-identified to avoid any bias in the analysis. Variables with fewer than 40 data points were removed from the analysis; these were regarded as not having enough data to

contribute to analyses involving four or more variables. Collinearity amongst independent variables was checked by an exploration of a correlation matrix (Figure 2). Subsequently, a directed graph of variables with common $R^2 \geq 0.9$ was obtained and collapsed according to principles of least missing data and fewest remaining nodes, resulting in twenty-six independent variables. Three pairs had fewer than 40 shared data points, resulting in 23 dependent variables. Histograms of each variable were checked for normality by fitting with both normal and lognormal curves.

2.3.5 Principal component analysis

Initially, an attempt to reduce the multidimensional space of the independent variables was made by standardising each variable and using principal component analysis (PCA), imputing missing data via the alternating least squares (ALS) algorithm. Histograms of the original and consequent datasets sometimes showed spurious imputation at either negative or large values. In most cases, but not all with respect to larger values, log-normal transformation of data eliminated negative values. Probabilistic PCA (PPCA) was trialled, but exhibited similar issues. Attempts to not impute data were confounded by a large number and distribution of missing data, resulting in fewer than 40 data points covering all variables, which, did not meet the threshold for reasonable multidimensional modelling. Similar issues occurred when repeating the processes over the dependent variable set. Hence, a reduction in dimensionalities via PCA was abandoned as an initial step.

2.3.6 Multiple step-wise regression analysis

Stepwise linear regression was then separately applied to the independent variables for two dependent variables of particular interest: fillet 22:6n-3 (DHA, docosahexaenoic acid) and n-3 LC PUFA. However, this process included variables of little practical significance including variables which violated distribution assumptions.

Therefore, the eight methodological and categorical variables were removed, leaving 18 purely experimental variables. Stepwise regression was again performed for fillet DHA and n-3 LC PUFA. Statistically significant models with three and five independent variables were created for fillet DHA and fillet n-3 LC PUFA, respectively. PCA with ALS over these identified variables again gave spurious values for imputed data, so basic PCA was carried out over the points with data for all variables (Figure 3).

In both cases, the three variables with the largest contributions to explaining the overall dataset variance were identified, and multiple regressions for each dependent variable of interest were performed (Figures 4 and 5). These figures show multiple perspectives on the three-dimensional spaces mapped by the remaining independent variables. Colour is used to indicate both the target dependent variable values and their estimation by the regression models.

3. Results

The systematic review resulted in the full text assessment of 254 peer reviewed articles, of which 15 passed the pre-determined selection criteria (Figure 1). The studies included consisted of a variety of farm and laboratory-based studies. A brief summary of the relevant data extracted from the selected studies is presented below.

3.1 Water temperature, feed intake and biometry

A summary of experimental water temperature, feed intake and biometry measures are presented in Table 1. The studies consisted of a variety of on-farm and laboratory-based trials and where reported, water temperature was given as temperature range or average or both (Table 1). The average water temperature combining studies was 10.9 °C. Final weights of fish ranged from 342 g to 3833 g, in

studies by Bell et al. (2001) and Rosenlund et al. (2016) respectively, and the average combining studies was 2001 g. The average food conversion ratio combining studies was 1.1.

3.2 Diet fish oil percentage, proximate composition and fatty acid composition

A summary of fish oil percentage, proximate composition and protein: energy ratios is presented in Table 2. Fish oil (expressed as percentage of added oil) varied from 0 to 100 % and averaged 37.6 %. Dietary protein and lipid (expressed as mg g⁻¹ diet) averaged 438.3 and 303.2, respectively. Dietary fatty acid composition of the 85 dietary treatments was expectedly varied (Table 3). Saturated fatty acid (SFA) content ranged from 20.9 to 101.8 mg g⁻¹ diet, presented in Torstensen et al. (2004) and Bell et al. (2002), respectively, and averaged 46.3 mg g⁻¹ diet across all dietary treatments. The level of dietary n-3 PUFA also varied amongst studies, concomitant with individual experimental aims. Dietary 18:3n-3 (ALA, α -linolenic acid) levels ranged from negligible amounts to in excess of 100 mg g⁻¹, yet the average across all treatments was 23.9 mg g⁻¹ diets. Levels of both 20:5n-3 (EPA, eicosapentaenoic acid) and DHA varied, consistent with fish oil inclusion level, and averaged 10.1 and 10.8 mg g diet⁻¹ respectively. The sum of n-3 LC PUFA ranged from 3.8 to 59.1 mg g⁻¹ diet in dietary treatments presented in Torstensen et al. (2005) and Friesen et al. (2015), respectively. The mean dietary n-3 LC PUFA level was 21.9 mg g⁻¹ diet.

3.3 Fillet proximate and fatty acid composition

In line with the selection criteria, all studies included reported the lipid proximate composition of the fillet and ranged from 37.7 to 165 mg g⁻¹ fillet tissue across the 85 treatments (Table 4). As expected, fillet fatty acid composition varied considerably among the 85 dietary treatments. Average fillet SFA content was 1443.8 mg 100g⁻¹ fillet and ranged from 595.1 to 2540 mg 100g⁻¹ fillet tissue in treatments presented in Bell et al. (2001) and Rosenlund et al. (2001), respectively. Reporting of individual monounsaturated fatty acids (MUFA) was often incomplete and, as such, the sum of MUFA was not included in the dataset. The predominant fatty acid 18:1n-9 was generally reported and ranged from

650.8 to 3804.5 mg 100g⁻¹ fillet tissue. Fillet levels of 22:1 (isomers not differentiated) were also consistently reported, averaging 318.0 mg 100g⁻¹ fillet tissue and showed large variation between treatments, ranging from 18.9 to 1488.2 mg 100g⁻¹ fillet tissue in treatment groups reported in Friesen et al. (2015) and Torstensen et al. (2001), respectively. Consistent with their relative importance in nutritional growth trials, n-3 PUFA was consistently reported and varied in accordance with dietary inclusion levels. Fillet levels of DHA (in terms of mg 100g⁻¹ fillet tissue) ranged from 198.0 to 1332.1 in Bell et al. (2004) and Bell et al. (2010), respectively, and averaged 514.0 across all 85 dietary treatments. The sum of n-3 LC PUFA was not always reported and, where necessary, was taken as the sum of EPA + DPA + DHA (where DPA is 22:5n-3, docosapentaenoic acid). Fillet levels averaged 850.2 and ranged from 303.2 and 2216.7 mg 100g⁻¹ fillet tissue in treatments presented in Bell et al. (2002) and Bell et al. (2010), respectively.

3.4 Modelling of fillet DHA and n-3 LC PUFA

Step-wise multiple regression analysis was used to model both DHA and n-3 LC PUFA. Statistically significant models for both fillet DHA and fillet n-3 LC PUFA were created using the three independent variables with the largest contributions to explaining the overall dataset variance. For both fillet DHA and fillet n-3 LC PUFA, final weight as an independent variable explained a large amount of the total variance (Figure 3). The independent variables used to predict fillet DHA were: i) final weight, ii) diet ALA and iii) diet DHA (Figure 4). The independent variables used to predict fillet n-3 LC PUFA were: i) final weight, ii) diet 22:1, and iii) diet EPA (Figure 5). The resulting models were as follows:

$$1) \text{ Fillet DHA} = (5.48) + (-0.001053 \times \text{final weight}) + (-0.016158 \times \text{diet ALA}) + (0.39596 \times \text{diet DHA});$$

$$R^2 = 0.96854; F = 646.6061; p = 3.0028 \times 10^{-47}$$

$$2) \text{ Fillet n-3 LC PUFA} = (-90.3347) + (0.14154 \times \text{final weight}) + (9.615 \times \text{diet 22:1}) + (47.752 \times \text{diet EPA})$$

$$R^2 = 0.85066; F = 119.6209; p = 5.7426 \times 10^{-26}$$

The three-dimensional models used highlight the variability in relationships between the independent and the dependent variables. Although for both models, particularly fillet DHA, the coefficient of determination (R^2) values indicated the data fitted well with the regression field.

4. Discussion

The first and most salient finding of the present study is that there is a paucity of industry-derived, peer-reviewed, published data from long-term growth trials conducted in seawater. This is despite the recognition of the continued resource volatility affecting dietary formulations in Atlantic salmon aquafeed, and the considerable amount of research effort that has been focussing on elucidating the impacts on fillet nutritional quality, especially levels of n-3 LC PUFA. The authors assert this is a current limitation to the uptake of more efficient aquafeed formulations necessary to ensure the long-term viability of the aquaculture sector.

It has been demonstrated that long-term growth trials are needed to ensure the effects of dietary lipid manipulation are accurately reflected in the fillet tissue of post-smolt Atlantic salmon (Rosenlund et al. 2016; Sissener et al. 2016b). With respect to the present study, an extensive search of peer reviewed literature, including the full-text assessment of 254 published articles, uncovered only 15 studies with recorded nutritional data in post-smolt Atlantic salmon experiencing > 300 % growth on a single experimental diet during the growth trial period. Shorter trials may risk type II error, via an incomplete 'dilution' of the pre-trial fatty acid composition, hence, partially obscuring the actual influence of the administered dietary treatment (Jobling 2003). Additionally, ontogenetic change concurrent with a seawater life stage in Atlantic salmon affects fatty acid uptake and metabolism (Tocher 2010). Therefore, an enhanced focus on post-smolt Atlantic salmon subject to relatively long growth periods is warranted in order to maximise the commercial relevance of available nutritional

data. It is recognised that long-term growth trials in seawater are logistically constrictive to research groups due to high costs and scarcity of suitable trial facility infrastructure. However, these limitations can be, at least partially ameliorated with, or overcome by, successful industry collaboration allowing access to on-farm facilities that complement the necessary analytical capabilities typically available in research institutions (Hardy 1999; Perkmann & Walsh 2007). Hence, the present study advocates the continued progression of strong industry-academia partnerships within the aquaculture sector.

Despite a limited dataset, a robust statistical approach was implemented in order to minimise multicollinearity within the resultant models. Consequently, statistical integrity was prioritised in order to confidently discuss the biological relevance of the resultant models. Final weight was a significant predictor for both fillet DHA and fillet n-3 LC PUFA. Although counterintuitive as a 'predictor', the final weight of a fish is often pre-determined in both a commercial and laboratory setting (Dunham 2011; Glencross et al. 2014). As such, final weight should be considered a controllable input variable for the purpose of the present discussion. Given the highly variable final weights in the dataset, final weight was responsible for a large amount of the variance within the dataset and therefore, unsurprisingly, was identified by PCA. From a biological perspective, relationships between fish size and fillet proximate composition, including, lipid level are known to exist in many species, including Atlantic salmon (Einen & Roem 1997; Kaufman et al. 2007; Salam & Davies 1994; Shearer et al. 1994; Shearer 1994). Specifically, fish size is often positively correlated with fillet lipid composition (Shearer et al. 1994). Given fillet fatty acid composition in the present study is reported in mg 100g⁻¹ fillet – the ultimate goal from a consumer nutritional information viewpoint – dietary lipid level and by extension final weight would be expected to have a positive relationship with fillet DHA and n-3 LC PUFA. Furthermore, dietary n-3 LC PUFA has been reported as essential to optimal growth in seawater reared Atlantic salmon (Hixson et al. 2017; Rosenlund et al. 2016). Despite this, final weight was both negatively and positively correlated with fillet DHA and fillet n-3 LC PUFA, respectively. The dataset was limited with respect to the reporting of final weight and often only a single figure was reported

as an experiment mean across dietary treatments. Therefore, despite a change in other independent variables, such as fillet proximate and fatty acid compositions within a study, final weight was sometimes clustered at a single value. Consequently, further extrapolation of the biological relationship between final weight and fillet DHA and n-3 LC PUFA composition is required.

Dietary DHA was positively correlated with fillet DHA as is intuitive, given the well reported 'mirroring' effect between dietary and fillet fatty acids, and in particular even more so for DHA itself (Bendiksen et al. 2011; Sales & Glencross 2011; Tocher 2015; Turchini et al. 2009). Dietary DHA is, indeed, generally unaffected by factors which can obscure or further modulate this mirroring effect, such as preferential β -oxidation and is, therefore well conserved (Bell et al. 2003; Bransden et al. 2003; Francis & Turchini 2017; Mourente et al. 2005; Pratoomyot et al. 2010). Finally, with respect to the fillet DHA model, dietary ALA was negatively correlated with fillet DHA, and this was somewhat unexpected and counterintuitive. In contrast to dietary DHA, dietary ALA is readily β -oxidised by salmonids (Bell et al. 2001; Mourente et al. 2005; Stubhaug et al. 2007; Tocher et al. 2002; Turchini & Francis 2009) and under certain dietary and environmental conditions, such as the absence of dietary DHA, can be converted to longer and more unsaturated fatty acid homologues (Bell et al. 2001; Ruyter & Thomassen 1999; Sissener et al. 2016a; Tocher 2003; Turchini et al. 2013). Owing to these properties, dietary lipid sources with relatively high concentrations of ALA, such as rapeseed/canola oil, linseed/flaxseed oil and camelina oil have been routinely used to substitute dietary fish oil both commercially and experimentally (Bell et al. 2003; Collins et al. 2013; Higgs et al. 2006; Hixson et al. 2017; Turchini et al. 2010). Despite the recorded potential of endogenous production of DHA from dietary ALA in salmonids, it is not expected to fully compensate for an absence of dietary added DHA sources, such as fish oil. In the present study, 11 out of the 15 studies in the analysis (Bell et al. (2001), Bell et al. (2003), Bell et al. (2004), Bell et al. (2010), Friesen et al. (2015), Liland et al. (2013), Rosenlund et al. (2001), Rosenlund et al. (2016), Sissener et al. (2016a), Torstensen et al. (2004) and Torstensen et al. (2005)) substituted dietary fish oil with lipid sources containing high concentration of ALA.

Consequently, this may explain the negative correlation between dietary ALA and DHA in the present study.

Understandably, n-3 LC PUFA are the subject of high scientific interest in fish nutrition studies owing to their extensively reported health benefits for consumers (Kris-Etherton et al. 2002; Nestel et al. 2015; Ruxton et al. 2004; Simopoulos 2008). However, fillet concentrations of MUFA, in particular, 22:1n-9 and 22:1n-11 receive considerably less attention. Despite this, the sum of 22:1 isomers often contributes substantially to the overall fatty acid composition of the fillet tissue in Atlantic salmon (Bell et al. 2010; Bell et al. 2003; Rosenlund et al. 2001; Torstensen et al. 2005; Torstensen et al. 2001) and was identified as a significant predictor of fillet n-3 LC PUFA in the present study. The activity of the Δ -9 desaturase enzyme, responsible for catalysing the synthesis of monounsaturated fatty acids, has been well described in marine invertebrates (Monroig et al. 2013) and is considered important for cold water adaption in warm water fish such as grass carp (*Ctenopharyngodon idella*) and Nile tilapia (*Oreochromis niloticus*) (Tiku et al. 1996; Zerai et al. 2010). Despite the potential for Δ -9 desaturation of saturated fatty acids to biosynthesise 22:1 isomers, the vast majority of these fatty acids in Atlantic salmon is believed to be of marine dietary origin – specifically due to an abundance of these fatty acids present in capelin and herring oil originating in the Northern Hemisphere (Ackman et al. 1988; Bell et al. 2003; Halver & Hardy 2002). Therefore, the positive relationship between dietary 22:1 and fillet n-3 LC PUFA is likely an effect of treatment diets containing fish oil sourced from the Northern Hemisphere, that are concomitantly high in 22:1 and n-3 LC PUFA. However, also it should be noted that 22:1 has been reported as a preferential substrate for catabolic processes (fatty acid β -oxidation) in salmonids and thus a larger dietary availability might directly contribute to increased n-3 LC PUFA retention by sparing them from catabolism (Henderson & Sargent 1985; Henderson et al. 1982; Stubhaug et al. 2007).

The final significant predictor included in the fillet n-3 LC PUFA model was dietary EPA which had an expectedly positive relationship with fillet n-3 LC PUFA. Although physiologically essential, dietary EPA is often not as well conserved as DHA in Atlantic salmon (Codabaccus et al. 2011; Stubhaug et al. 2007; Tocher 2010). Nevertheless, its overall contribution to fillet n-3 LC PUFA and importance in predicting final fillet levels of n-3 LC PUFA is hereby recognised by the model.

5. Conclusion

In conducting the systematic review and analysis of long-term nutritional growth trials focusing on seawater reared Atlantic salmon, the present study has provided a summary of the current body of research and has identified the major dietary drivers of fillet DHA and n-3 LC PUFA. Both models revealed several biologically intuitive variables as having a significant effect on the dependent variables, namely, fillet DHA and n-3 LC PUFA. It is clear, however, and in agreement with Sales and Glencross (2011), that the conclusiveness of these findings is limited by a relatively small dataset and incomplete or inconsistent data reporting in some studies. It is envisaged that continued cooperation between industry and academia will serve to increase the transparency of available nutritional data. Furthermore, this cooperation may enable the development of more sophisticated mechanistic modelling techniques that rely on a suite of environmental and nutritional information to quantitatively predict fillet n-3 LC PUFA in Atlantic salmon. Nevertheless, the present study provides a snapshot of the current state of published information that identifies the major drivers of fillet n-3 LC PUFA in post-smolt Atlantic salmon – an important task, given the increasing value of these fatty acids in aquaculture.

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Figure 1 caption:

Schematic of systematic review procedure showing number of articles at each stage; i) identification of articles matching search terms and identified via ad-hoc searching techniques, ii) screening to remove duplicate articles and articles not on the study species, iii) articles subject to full text assessment against the pre-determined eligibility criteria and, iv) articles included in the data analysis.

Figure 2 caption:

Correlation matrix across all (de-identified) variables.

Figure 3 caption:

(Color online) Principal components analyses on stepwise regression outputs for fillet DHA (left) and fillet PUFA (right) across all non-methodological independent variables. Upper plots are biplots showing the relative contributions of each variable to each principal component; lower plots show the proportion of total variance explained by each principal component.

Figure 4 caption:

(Color online) Multiple regression of fillet DHA on the three strongest predictors from Fig. 3 (left). Upper left is a perspective view of the 3D regression; dot colours show the actual data values of fillet DHA whilst rings show the regression model's predictions. The other three subfigures show perspectives along each axis. The regression model and various statistics are shown.

Figure 5 caption:

(Color online) Multiple regression of fillet PUFA on the three strongest predictors from Fig. 3 (left). Upper left is a perspective view of the 3D regression; dot colours show the actual data values of fillet PUFA whilst rings show the regression model's predictions. The other three subfigures show perspectives along each axis. The regression model and various statistics are shown.

Table 1

Experimental temperature, feed intake and biometry of Atlantic salmon fed 85 different diets from 15 studies.

Study/year	Temperature range (°C)	Temperature average	Initial weight (g)	Final Weight (g)	Weight gain (g)	Feed intake (g)	FCR	Final length (cm)	Fillet yield (%)	Condition factor (K)
(Bell et al. 2001)	7.9-14.2	11.7	83	342	259	339	1.3	30.2	–	1.2
(Bell et al. 2001)	7.9-14.2	11.7	83	342	259	339	1.3	30.2	–	1.2
(Bell et al. 2001)	7.9-14.2	11.7	83	342	259	339	1.3	30.2	–	1.2
(Bell et al. 2001)	7.9-14.2	11.7	83	342	259	339	1.3	30.2	–	1.2
(Bell et al. 2001)	7.9-14.2	11.7	83	342	259	339	1.3	30.2	–	1.2
(Bell et al. 2002)	5.9-14.7	11.0	55	410	354	549	1.6	33.3	–	1.1
(Bell et al. 2002)	5.9-14.7	11.0	53	417	364	535	1.5	33.7	–	1.1
(Bell et al. 2002)	5.9-14.7	11.0	57	394	337	509	1.5	33.1	–	1.1
(Bell et al. 2002)	5.9-14.7	11.0	56	419	363	544	1.5	33.2	–	1.1
(Bell et al. 2003)	5.5-19.6	10.8	120	2100	1980	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	2300	2180	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	2300	2180	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	2100	1980	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	2000	1880	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	2400	2280	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	2600	2480	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	2400	2280	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	2300	2180	–	–	–	–	–
(Bell et al. 2003)	5.5-19.6	10.8	120	1900	1780	–	–	–	–	–
(Bell et al. 2004)	5.0-16.8	10.8	127	1790	1663	2245	1.4	–	–	–
(Bell et al. 2004)	5.0-16.8	10.8	127	1890	1763	2274	1.3	–	–	–
(Bell et al. 2004)	5.0-16.8	10.8	127	1900	1773	2500	1.4	–	–	–
(Bell et al. 2004)	5.0-16.8	10.8	127	1870	1743	2248	1.3	–	–	–
(Bell et al. 2004)	5.0-16.8	10.8	127	1870	1743	2353	1.4	–	–	–
(Bell et al. 2010)	5.5-17.0	11.5	81	3120	3039	3738	1.2	65.3	–	1.1
(Bell et al. 2010)	5.5-17.0	11.5	90	3030	2941	4087	1.4	63.7	–	1.2
(Bell et al. 2010)	5.5-17.0	11.5	92	3180	3088	3335	1.1	63.9	–	1.2
(Bell et al. 2010)	5.5-17.0	11.5	84	2840	2756	3279	1.2	62.5	–	1.2
(Bell et al. 2010)	5.5-17.0	11.5	53	2750	2697	2913	1.1	63.1	–	1.1
(Bell et al. 2010)	5.5-17.0	11.5	52	2890	2838	3009	1.1	62.8	–	1.2
(Friesen et al. 2015)	7.9-13.2	–	83	558	475	380	0.8	36.1	–	1.2
(Friesen et al. 2015)	7.9-13.2	–	84	578	494	395	0.8	36.2	–	1.2

(Friesen et al. 2015)	7.9-13.2	–	86	595	510	414	0.8	36.6	–	1.2
(Friesen et al. 2015)	7.9-13.2	–	84	611	527	415	0.8	36.9	–	1.2
(Friesen et al. 2015)	7.9-13.2	–	98	637	539	418	0.8	37.1	–	1.3
(Friesen et al. 2015)	7.9-13.2	–	84	534	450	381	0.8	35.0	–	1.3
(Friesen et al. 2015)	7.9-13.2	–	84	545	460	393	0.9	35.5	–	1.2
(Larsson et al. 2014)	3.0-16.0	8.7	105	3100	2995	2980	1.0	59.6	72.7	1.5
(Larsson et al. 2014)	3.0-16.0	8.7	105	3100	2995	2980	1.0	60.0	72.4	1.5
(Liland et al. 2013)	9.9	9.9	840	3398	2558	2982	1.2	60.2	–	1.6
(Liland et al. 2013)	9.9	9.9	804	3459	2655	2748	1.0	59.3	–	1.6
(Liland et al. 2013)	9.9	9.9	792	3475	2683	2759	1.0	59.5	–	1.7
(Liland et al. 2013)	9.9	9.9	825	3267	2442	2573	1.1	58.3	–	1.6
(Rosenlund et al. 2001)	5-15	–	120	2700	2580	–	–	–	–	–
(Rosenlund et al. 2001)	5-15	–	120	2700	2580	–	–	–	–	–
(Rosenlund et al. 2001)	5-15	–	120	2700	2580	–	–	–	–	–
(Rosenlund et al. 2001)	5-15	–	120	2700	2580	–	–	–	–	–
(Rosenlund et al. 2001)	5-15	–	120	2700	2580	–	–	–	–	–
(Rosenlund et al. 2001)	5-15	–	120	2700	2580	–	–	–	–	–
(Rosenlund et al. 2016)	12.0	12.0	161	2780	2619	2671	1.0	–	–	1.6
(Rosenlund et al. 2016)	12.0	12.0	163	3085	2922	2864	1.0	–	–	1.5
(Rosenlund et al. 2016)	12.0	12.0	161	3056	2895	3011	1.0	–	–	1.6
(Rosenlund et al. 2016)	12.0	12.0	163	3057	2894	2952	1.0	–	–	1.6
(Rosenlund et al. 2016)	12.0	12.0	163	3074	2911	2707	0.9	–	–	1.6
(Rosenlund et al. 2016)	12-6	9.1	161	3249	3088	3242	1.1	–	–	1.8
(Rosenlund et al. 2016)	12-6	9.1	163	3764	3601	3457	1.0	–	–	1.7
(Rosenlund et al. 2016)	12-6	9.1	161	3833	3672	3599	1.0	–	–	1.8
(Rosenlund et al. 2016)	12-6	9.1	163	3639	3476	3406	1.0	–	–	1.7
(Rosenlund et al. 2016)	12-6	9.1	163	3556	3393	3088	0.9	–	–	1.7
(Sissener et al. 2016a)	12.0	12.0	190	764	574	443	0.8	36.8	–	1.5
(Sissener et al. 2016a)	12.0	12.0	192	780	588	444	0.8	36.7	–	1.6
(Sissener et al. 2016a)	12.0	12.0	189	760	571	448	0.8	36.8	–	1.5
(Sissener et al. 2016a)	12.0	12.0	189	765	576	443	0.8	36.3	–	1.5
(Sissener et al. 2016a)	12.0	12.0	190	767	577	436	0.8	36.9	–	1.5
(Sissener et al. 2016a)	12.0	12.0	189	777	588	464	0.8	37.1	–	1.6
(Torstensen et al. 2001)		8.2	148	697	549	494	0.9	–	–	–

(Torstensen et al. 2004)	3.9-15.3	–	143	1463	1320	1406	1.1	–	–	–
(Torstensen et al. 2004)	3.9-15.3	–	143	1463	1320	1406	1.1	–	–	–
(Torstensen et al. 2004)	3.9-15.3	–	143	1463	1320	1406	1.1	–	–	–
(Torstensen et al. 2004)	3.9-15.3	–	143	1463	1320	1406	1.1	–	–	–
(Torstensen et al. 2004)	3.9-15.3	–	143	1463	1320	1406	1.1	–	–	–
(Torstensen et al. 2004)	3.9-15.3	–	143	1463	1320	1406	1.1	–	–	–
(Torstensen et al. 2005)	–	–	50	2515	2465	2514	1.0	–	–	–
(Torstensen et al. 2005)	–	–	120	2380	2260	3028	1.3	–	–	–
(Torstensen et al. 2005)	–	–	50	2420	2370	2323	1.0	–	–	–
(Torstensen et al. 2005)	–	–	120	2698	2578	3145	1.2	–	–	–
(Young et al. 2006)	–	–	52	2075	2023	–	–	–	–	–
(Young et al. 2006)	–	–	52	1975	1923	–	–	–	–	–
(Young et al. 2006)	–	–	52	2562	2510	–	–	–	–	–
(Young et al. 2006)	–	–	52	2168	2116	–	–	–	–	–
(Young et al. 2006)	–	–	52	1936	1884	–	–	–	–	–
(Young et al. 2006)	–	–	52	2458	2406	–	–	–	–	–
(Young et al. 2006)	–	–	52	2113	2061	–	–	–	–	–
(Young et al. 2006)	–	–	52	2193	2141	–	–	–	–	–
(Young et al. 2006)	–	–	52	2512	2460	–	–	–	–	–

Fish oil (%), proximate composition (mg g ⁻¹ diet), and protein: energy ratio of 85 diets from 15 studies fed to Atlantic salmon during experimental trials									
Study/year	Fish oil (% of total added lipid)	Protein	Moisture	Lipid	Ash	Dry matter	NFE	Diet energy (kJ g ⁻¹ diet)	Protein / energy ratio
(Bell et al. 2001)	100	467.0	78.0	277.0	98.0	922.0	80.0	23.3	2.0
(Bell et al. 2001)	90	463.0	81.0	264.0	96.0	919.0	96.0	23.0	2.0
(Bell et al. 2001)	75	448.0	82.0	263.0	96.0	918.0	111.0	22.9	2.0
(Bell et al. 2001)	50	456.0	75.0	257.0	97.0	925.0	115.0	22.9	2.0
(Bell et al. 2001)	0	469.0	68.0	256.0	97.0	932.0	110.0	23.1	2.0
(Bell et al. 2002)	100	464.0	55.0	288.0	84.0	945.0	109.0	24.2	1.9
(Bell et al. 2002)	75	455.0	63.0	279.0	81.0	937.0	122.0	23.9	1.9
(Bell et al. 2002)	50	465.0	49.0	287.0	82.0	951.0	117.0	24.3	1.9
(Bell et al. 2002)	0	466.0	45.0	282.0	83.0	955.0	124.0	24.3	1.9
(Bell et al. 2003)	100	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	66	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	33	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	0	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	66	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	33	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	0	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	0	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	0	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2003)	33	444.0	72.0	273.0	79.9	928.0	131.1	23.5	1.9
(Bell et al. 2004)	100	441.0	59.0	294.0	71.0	941.0	135.0	24.3	1.8
(Bell et al. 2004)	75	441.0	59.0	294.0	71.0	941.0	135.0	24.3	1.8
(Bell et al. 2004)	50	441.0	59.0	294.0	71.0	941.0	135.0	24.3	1.8
(Bell et al. 2004)	25	441.0	59.0	294.0	71.0	941.0	135.0	24.3	1.8
(Bell et al. 2004)	0	441.0	59.0	294.0	71.0	941.0	135.0	24.3	1.8
(Bell et al. 2010)	100	410.0	46.0	349.0	60.0	954.0	135.0	25.8	1.6
(Bell et al. 2010)	0	405.0	51.0	335.0	60.0	949.0	149.0	25.4	1.6
(Bell et al. 2010)	100	410.0	46.0	349.0	60.0	954.0	135.0	25.8	1.6
(Bell et al. 2010)	0	405.0	51.0	335.0	60.0	949.0	149.0	25.4	1.6
(Bell et al. 2010)	100	410.0	46.0	349.0	60.0	954.0	135.0	25.8	1.6
(Bell et al. 2010)	0	405.0	51.0	335.0	60.0	949.0	149.0	25.4	1.6
(Friesen et al. 2015)	100	453.0	43.0	265.0	90.0	957.0	149.0	23.7	1.9
(Friesen et al. 2015)	50	465.0	45.0	264.0	85.0	955.0	141.0	24.2	1.9
(Friesen et al. 2015)	25	452.0	45.0	260.0	87.0	955.0	156.0	23.9	1.9
(Friesen et al. 2015)	25	453.0	50.0	260.0	88.0	950.0	149.0	24.0	1.9
(Friesen et al. 2015)	25	454.0	42.0	264.0	88.0	958.0	152.0	24.1	1.9
(Friesen et al. 2015)	25	450.0	43.0	255.0	91.0	957.0	161.0	23.4	1.9
(Friesen et al. 2015)	25	449.0	50.0	261.0	86.0	950.0	154.0	24.1	1.9
(Larsson et al. 2014)	73	353.0	73.0	351.0	54.0	927.0	169.0	25.1	1.4
(Larsson et al. 2014)	73	353.0	73.0	351.0	54.0	927.0	169.0	25.1	1.4
(Liland et al. 2013)	100	411.0	70.0	341.0	53.0	930.0	125.0	25.3	1.6
(Liland et al. 2013)	20	408.0	60.0	336.0	52.0	940.0	144.0	25.4	1.6
(Liland et al. 2013)	20	413.0	70.0	345.0	52.0	930.0	120.0	25.4	1.6
(Liland et al. 2013)	20	406.0	70.0	332.0	52.0	930.0	140.0	25.1	1.6
(Rosenlund et al. 2001)	40-50	426.0	34.8	338.0	54.3	965.3	147.0	25.9	1.6
(Rosenlund et al. 2001)	40-50	426.0	34.8	338.0	54.3	965.3	147.0	25.9	1.6
(Rosenlund et al. 2001)	40-50	426.0	34.8	338.0	54.3	965.3	147.0	25.9	1.6
(Rosenlund et al. 2001)	40-50	426.0	34.8	338.0	54.3	965.3	147.0	25.9	1.6
(Rosenlund et al. 2001)	40-50	426.0	34.8	338.0	54.3	965.3	147.0	25.9	1.6

(Rosenlund et al. 2001)	40-50	426.0	34.8	338.0	54.3	965.3	147.0	25.9	1.6
(Rosenlund et al. 2016)	0	436.4	58.8	365.1	79.9	941.2	59.9	25.7	1.7
(Rosenlund et al. 2016)	2	431.1	58.0	363.8	79.9	942.0	67.3	25.7	1.7
(Rosenlund et al. 2016)	4	431.6	60.2	363.8	79.9	939.8	64.6	25.7	1.7
(Rosenlund et al. 2016)	6	429.7	62.3	361.5	79.9	937.7	66.6	25.6	1.7
(Rosenlund et al. 2016)	8	431.0	65.5	366.2	79.9	934.5	57.5	25.6	1.7
(Rosenlund et al. 2016)	0	436.4	58.8	365.1	79.9	941.2	59.9	25.7	1.7
(Rosenlund et al. 2016)	2	431.1	58.0	363.8	79.9	942.0	67.3	25.7	1.7
(Rosenlund et al. 2016)	4	431.6	60.2	363.8	79.9	939.8	64.6	25.7	1.7
(Rosenlund et al. 2016)	6	429.7	62.3	361.5	79.9	937.7	66.6	25.6	1.7
(Rosenlund et al. 2016)	8	431.0	65.5	366.2	79.9	934.5	57.5	25.6	1.7
(Sissener et al. 2016a)	20	489.1	39.0	275.8	79.9	961.0	116.3	24.4	2.0
(Sissener et al. 2016a)	20	500.5	41.0	280.5	79.9	959.0	98.1	24.6	2.0
(Sissener et al. 2016a)	20	502.1	44.0	288.7	79.9	956.0	85.3	24.7	2.0
(Sissener et al. 2016a)	20	502.6	45.0	277.5	79.9	955.0	95.0	24.5	2.1
(Sissener et al. 2016a)	20	520.3	39.0	278.9	79.9	961.0	81.9	24.7	2.1
(Sissener et al. 2016a)	20	522.5	43.0	294.7	79.9	957.0	60.0	25.0	2.1
(Torstensen et al. 2001)	100	450.0	50.0	323.8	65.0	950.0	111.2	25.3	1.8
(Torstensen et al. 2004)	75	450.0	60.0	300.0	70.0	940.0	120.0	24.5	1.8
(Torstensen et al. 2004)	50	450.0	60.0	300.0	70.0	940.0	120.0	24.5	1.8
(Torstensen et al. 2004)	25	450.0	60.0	300.0	70.0	940.0	120.0	24.5	1.8
(Torstensen et al. 2004)	0	450.0	60.0	300.0	70.0	940.0	120.0	24.5	1.8
(Torstensen et al. 2004)	50	450.0	60.0	300.0	70.0	940.0	120.0	24.5	1.8
(Torstensen et al. 2004)	100	450.0	60.0	300.0	70.0	940.0	120.0	24.5	1.8
(Torstensen et al. 2005)	100	421.0	70.0	314.0	70.0	930.0	125.0	24.5	1.7
(Torstensen et al. 2005)	100	421.0	70.0	314.0	70.0	930.0	125.0	24.5	1.7
(Torstensen et al. 2005)	25	412.0	64.0	328.0	71.0	936.0	125.0	24.8	1.7
(Torstensen et al. 2005)	0	429.0	65.0	313.0	66.0	935.0	127.0	24.7	1.7
(Young et al. 2006)	13.7	427.1	80.5	211.3	89.7	919.5	191.5	21.7	2.0
(Young et al. 2006)	13.8	423.3	81.6	208.5	84.5	918.4	202.1	21.7	2.0
(Young et al. 2006)	14.3	418.2	80.3	205.7	86.3	919.7	209.6	21.6	1.9
(Young et al. 2006)	19.9	406.8	70.8	278.2	84.5	929.3	159.8	23.3	1.7
(Young et al. 2006)	19.9	411.5	71.3	267.4	86.3	928.7	163.5	23.1	1.8
(Young et al. 2006)	20.4	412.5	71.2	269.7	83.4	928.8	163.3	23.2	1.8
(Young et al. 2006)	26.2	413.5	54.4	336.1	86.1	945.6	109.9	24.9	1.7
(Young et al. 2006)	26.4	420.7	55.4	322.7	92.4	944.6	108.8	24.5	1.7
(Young et al. 2006)	26.7	414.6	57.4	325.2	88.0	942.6	114.8	24.6	1.7

Table 3

Fatty acid composition of 85 diets from 15 studies fed to Atlantic salmon during experimental trials (mg g⁻¹ diet)

Study/year	14:0	16:0	18:0	SFA	20:1	22:1	18:1n-9	18:2n-6	20:4n-6	18:3n-3	18:4n-3	20:4n-3	20:5n-3	22:5n-3	22:6n-3	n-3 LC PUFA
(Bell et al. 2001)	–	–	–	50.8	17.2	25.3	26.1	5.1	1.3	3.4	–	–	18.1	–	25.3	43.3
(Bell et al. 2001)	–	–	–	43.3	15.0	20.9	38.1	10.3	0.8	5.9	–	–	13.8	–	20.4	34.2
(Bell et al. 2001)	–	–	–	39.1	12.7	16.5	47.0	14.3	0.8	7.7	–	–	13.1	–	17.5	30.7
(Bell et al. 2001)	–	–	–	34.3	10.8	13.6	58.3	18.5	0.6	9.7	–	–	10.2	–	13.4	23.6
(Bell et al. 2001)	–	–	–	23.4	5.9	4.5	86.2	30.2	0.4	15.9	–	–	5.1	–	5.5	10.6
(Bell et al. 2002)	11.5	38.9	5.3	59.8	9.3	14.1	38.0	7.9	1.3	4.6	7.1	1.5	18.1	2.2	30.0	50.3
(Bell et al. 2002)	9.4	47.7	6.0	66.1	7.7	11.1	45.4	11.3	1.1	3.6	5.6	1.3	14.1	1.9	23.5	39.6
(Bell et al. 2002)	7.7	58.5	6.8	75.5	6.6	9.5	55.7	15.0	0.9	2.9	4.4	0.9	11.4	1.5	19.1	32.1
(Bell et al. 2002)	3.7	88.2	8.4	101.8	3.2	4.3	67.5	20.3	0.2	1.1	1.3	0.2	3.5	0.6	6.1	10.2
(Bell et al. 2003)	11.7	28.5	5.2	50.2	20.1	27.6	31.6	9.4	1.3	3.6	5.9	1.7	15.3	2.5	22.0	41.4
(Bell et al. 2003)	7.5	24.3	6.1	42.3	12.6	17.2	33.7	16.5	0.8	38.9	3.8	1.3	11.1	2.1	17.6	32.0
(Bell et al. 2003)	4.6	20.1	7.1	35.0	7.7	10.0	34.3	23.9	0.6	69.1	2.1	0.6	6.9	1.3	11.1	19.9
(Bell et al. 2003)	2.3	15.9	7.5	27.6	4.0	4.8	34.7	28.5	0.4	95.0	1.0	0.2	3.8	0.6	5.7	10.3
(Bell et al. 2003)	7.7	24.5	4.8	41.7	13.6	17.4	55.9	19.9	1.0	9.8	4.0	1.3	11.9	2.3	18.2	33.7
(Bell et al. 2003)	4.8	19.7	4.2	32.4	9.6	11.3	78.5	29.3	0.6	13.8	2.3	0.8	8.2	1.3	12.4	22.6
(Bell et al. 2003)	2.5	15.1	4.0	23.9	6.3	5.7	101.1	37.5	0.4	18.6	0.8	0.2	4.0	0.6	6.1	10.9
(Bell et al. 2003)	2.5	16.1	6.3	27.2	4.6	5.4	54.2	30.6	0.4	68.9	0.8	0.4	4.6	0.8	7.1	13.0
(Bell et al. 2003)	2.3	15.9	5.0	22.8	5.4	5.7	77.2	34.2	0.4	42.3	0.8	0.2	4.4	0.8	7.3	12.8
(Bell et al. 2003)	4.0	18.4	5.7	31.2	7.3	9.0	60.3	28.7	0.4	46.1	1.9	0.4	6.5	1.0	10.3	18.2
(Bell et al. 2004)	14.2	27.3	2.5	44.9	40.4	34.7	26.8	9.5	0.5	2.0	6.5	0.9	13.3	–	11.3	24.6
(Bell et al. 2004)	10.6	23.9	3.8	38.8	29.5	26.2	30.7	16.7	0.5	31.6	4.7	0.7	10.4	–	9.0	19.4
(Bell et al. 2004)	7.7	21.0	4.7	34.0	20.3	18.3	34.0	22.1	0.2	57.7	3.6	0.5	7.9	–	7.7	15.6
(Bell et al. 2004)	4.5	18.3	6.1	29.3	11.3	10.8	36.1	27.7	0.2	85.2	2.0	0.5	5.0	–	5.4	10.4
(Bell et al. 2004)	0.9	13.8	7.0	23.7	2.5	2.7	38.3	34.0	0.2	113.6	0.5	0.2	2.3	–	3.4	5.6
(Bell et al. 2010)	15.5	40.1	8.0	69.8	22.7	36.7	27.0	9.4	1.1	4.3	9.4	1.6	22.7	2.1	27.0	51.9
(Bell et al. 2010)	2.3	40.8	9.0	55.7	10.3	4.1	96.6	42.4	0.3	25.7	1.0	0.3	3.1	0.3	3.9	7.2
(Bell et al. 2010)	15.5	40.1	8.0	69.8	22.7	36.7	27.0	9.4	1.1	4.3	9.4	1.6	22.7	2.1	27.0	51.9
(Bell et al. 2010)	2.3	40.8	9.0	55.7	10.3	4.1	96.6	42.4	0.3	25.7	1.0	0.3	3.1	0.3	3.9	7.2
(Bell et al. 2010)	15.5	40.1	8.0	69.8	22.7	36.7	27.0	9.4	1.1	4.3	9.4	1.6	22.7	2.1	27.0	51.9
(Bell et al. 2010)	2.3	40.8	9.0	55.7	10.3	4.1	96.6	42.4	0.3	25.7	1.0	0.3	3.1	0.3	3.9	7.2
(Friesen et al. 2015)	15.2	36.2	7.1	60.1	–	2.6	25.2	12.6	3.3	2.0	4.9	1.6	38.2	4.3	16.7	59.1

(Friesen et al. 2015)	8.1	39.9	9.9	58.9	–	1.6	56.1	22.1	2.0	3.4	2.4	0.8	18.4	2.2	8.5	29.1
(Friesen et al. 2015)	6.2	40.5	9.8	57.4	–	1.0	60.6	24.9	1.2	5.8	1.8	0.6	13.2	1.8	7.4	22.3
(Friesen et al. 2015)	5.0	18.7	7.4	31.7	–	0.8	30.5	27.1	1.0	73.0	1.6	0.4	12.4	1.6	6.6	20.5
(Friesen et al. 2015)	5.3	19.2	4.9	29.8	–	0.8	77.3	34.6	1.0	16.2	1.6	0.4	12.6	1.6	6.7	20.9
(Friesen et al. 2015)	5.1	18.0	4.7	28.4	–	1.0	74.3	33.4	1.2	14.9	1.8	0.6	13.1	1.6	5.9	20.5
(Friesen et al. 2015)	5.4	18.6	4.8	29.2	–	1.0	76.0	34.2	1.0	15.4	1.8	0.4	13.2	1.6	6.0	20.8
(Larsson et al. 2014)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(Larsson et al. 2014)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(Liland et al. 2013)	17.8	41.6	7.6	70.1	14.6	26.7	31.1	7.1	1.3	3.7	6.8	1.8	21.2	–	26.1	–
(Liland et al. 2013)	3.9	31.9	8.5	46.4	3.6	5.2	129.6	31.2	0.3	10.6	1.3	0.5	4.9	–	5.9	–
(Liland et al. 2013)	5.3	20.6	6.6	34.9	6.3	7.4	113.0	41.8	0.5	20.6	1.9	0.5	6.6	–	7.9	–
(Liland et al. 2013)	4.3	37.7	9.7	54.0	3.6	5.6	54.7	95.5	0.3	11.2	1.5	0.5	5.1	–	6.1	–
(Rosenlund et al. 2001)	–	30.1	–	–	19.3	22.0	95.0	41.9		34.5	–	–	11.8	–	10.8	22.6
(Rosenlund et al. 2001)	–	51.4	–	–	3.7	2.7	56.8	34.1		76.4	–	–	20.3	–	16.6	36.8
(Rosenlund et al. 2001)	–	45.3	–	–	14.5	15.5	92.6	35.2		10.8	–	–	13.5	–	11.8	25.4
(Rosenlund et al. 2001)	–	54.8	–	–	16.6	21.0	62.9	32.1		57.5	–	–	11.8	–	10.8	22.6
(Rosenlund et al. 2001)	–	42.9	–	–	41.9	51.0	35.5	12.8		3.7	–	–	25.4	–	19.3	44.6
(Rosenlund et al. 2001)	–	49.7	–	–	4.4	3.7	52.1	88.2		10.8	–	–	25.4	–	19.9	45.3
(Rosenlund et al. 2016)	1.8	41.8	6.8	52.2	3.7	2.2	–	46.3	0.0	35.0	0.4	0.0	2.2	0.3	2.1	4.6
(Rosenlund et al. 2016)	3.3	41.6	6.5	53.6	4.6	3.7	–	43.9	0.3	32.0	1.0	0.3	4.0	0.6	3.7	8.3
(Rosenlund et al. 2016)	4.3	41.9	6.3	54.4	5.4	4.7	–	41.6	0.3	30.7	1.2	0.3	5.1	0.6	4.6	10.4
(Rosenlund et al. 2016)	5.1	41.7	6.4	55.4	6.1	5.7	–	40.0	0.3	28.4	1.7	0.3	6.4	0.8	5.7	12.9
(Rosenlund et al. 2016)	6.4	42.1	6.4	56.9	7.0	6.9	–	38.7	0.5	27.4	2.0	0.5	7.9	1.1	7.0	16.0
(Rosenlund et al. 2016)	1.8	41.8	6.8	52.2	3.7	2.2	–	46.3	0.0	35.0	0.4	0.0	2.2	0.3	2.1	4.6
(Rosenlund et al. 2016)	3.3	41.6	6.5	53.6	4.6	3.7	–	43.9	0.3	32.0	1.0	0.3	4.0	0.6	3.7	8.3
(Rosenlund et al. 2016)	4.3	41.9	6.3	54.4	5.4	4.7	–	41.6	0.3	30.7	1.2	0.3	5.1	0.6	4.6	10.4
(Rosenlund et al. 2016)	5.1	41.7	6.4	55.4	6.1	5.7	–	40.0	0.3	28.4	1.7	0.3	6.4	0.8	5.7	12.9
(Rosenlund et al. 2016)	6.4	42.1	6.4	56.9	7.0	6.9	–	38.7	0.5	27.4	2.0	0.5	7.9	1.1	7.0	16.0
(Sissener et al. 2016a)	4.5	15.0	4.1	25.8	7.7	9.1	80.9	29.7	0.2	18.5	1.8	–	4.9	–	5.7	10.6
(Sissener et al. 2016a)	4.7	35.7	6.0	48.3	6.8	8.5	71.2	24.3	0.2	20.4	1.7	–	4.5	–	5.2	9.7
(Sissener et al. 2016a)	3.8	41.9	7.8	55.4	3.6	5.3	52.3	52.1	0.2	22.0	1.3	–	4.0	–	5.3	9.3
(Sissener et al. 2016a)	2.8	23.4	6.5	34.9	3.5	4.7	40.4	77.6	0.2	21.7	1.0	–	3.7	–	4.7	8.5
(Sissener et al. 2016a)	4.1	19.1	5.3	30.2	6.8	8.2	57.5	52.0	0.2	19.9	1.6	–	4.5	–	4.9	9.5
(Sissener et al. 2016a)	3.9	34.4	6.5	46.9	4.5	5.4	64.4	48.2	0.2	21.8	1.3	–	4.3	–	5.6	9.9

[illegible]

Table 4

Proximate composition of fillet tissue of Atlantic salmon fed 85 different diets from 15 studies (mg g⁻¹ of fillet tissue)

Study/year	Protein	Moisture	Lipid	Ash
(Bell et al. 2001)	185	747	54	15
(Bell et al. 2001)	189	751	48	17
(Bell et al. 2001)	191	752	46	14
(Bell et al. 2001)	191	752	45	17
(Bell et al. 2001)	195	742	51	14
(Bell et al. 2002)	203	728	57	15
(Bell et al. 2002)	199	739	47	16
(Bell et al. 2002)	202	742	41	15
(Bell et al. 2002)	205	741	38	17
(Bell et al. 2003)	–	–	86	–
(Bell et al. 2003)	–	–	76	–
(Bell et al. 2003)	–	–	95	–
(Bell et al. 2003)	–	–	75	–
(Bell et al. 2003)	–	–	81	–
(Bell et al. 2003)	–	–	78	–
(Bell et al. 2003)	–	–	70	–
(Bell et al. 2003)	–	–	70	–
(Bell et al. 2003)	–	–	75	–
(Bell et al. 2003)	–	–	69	–
(Bell et al. 2004)	–	–	81	–
(Bell et al. 2004)	–	–	81	–
(Bell et al. 2004)	–	–	81	–
(Bell et al. 2004)	–	–	81	–
(Bell et al. 2004)	–	–	81	–
(Bell et al. 2010)	194	–	116	–
(Bell et al. 2010)	199	–	128	–
(Bell et al. 2010)	191	–	132	–
(Bell et al. 2010)	192	–	129	–
(Bell et al. 2010)	193	–	123	–
(Bell et al. 2010)	195	–	113	–
(Friesen et al. 2015)	–	–	65	–
(Friesen et al. 2015)	–	–	70	–
(Friesen et al. 2015)	–	–	68	–
(Friesen et al. 2015)	–	–	60	–
(Friesen et al. 2015)	–	–	66	–
(Friesen et al. 2015)	–	–	64	–
(Friesen et al. 2015)	–	–	73	–
(Larsson et al. 2014)	234	–	143	–
(Larsson et al. 2014)	236	–	143	–
(Liland et al. 2013)	–	–	131	–
(Liland et al. 2013)	–	–	150	–
(Liland et al. 2013)	–	–	142	–
(Liland et al. 2013)	–	–	134	–
(Rosenlund et al. 2001)	203	680	106	14
(Rosenlund et al. 2001)	204	688	97	13
(Rosenlund et al. 2001)	205	682	103	14
(Rosenlund et al. 2001)	200	676	113	14
(Rosenlund et al. 2001)	204	669	117	13

(Rosenlund et al. 2001)	200	662	127	13
(Rosenlund et al. 2016)	–	–	165	–
(Rosenlund et al. 2016)	–	–	152	–
(Rosenlund et al. 2016)	–	–	159	–
(Rosenlund et al. 2016)	–	–	142	–
(Rosenlund et al. 2016)	–	–	150	–
(Rosenlund et al. 2016)	–	–	137	–
(Rosenlund et al. 2016)	–	–	143	–
(Rosenlund et al. 2016)	–	–	130	–
(Rosenlund et al. 2016)	–	–	138	–
(Rosenlund et al. 2016)	–	–	133	–
(Sissener et al. 2016a)	210	669	124	–
(Sissener et al. 2016a)	213	674	117	–
(Sissener et al. 2016a)	210	673	121	–
(Sissener et al. 2016a)	213	672	112	–
(Sissener et al. 2016a)	210	673	118	–
(Sissener et al. 2016a)	210	671	115	–
(Torstensen et al. 2001)	–	–	130	–
(Torstensen et al. 2004)	207	–	66	–
(Torstensen et al. 2004)	207	–	71	–
(Torstensen et al. 2004)	207	–	81	–
(Torstensen et al. 2004)	212	–	70	–
(Torstensen et al. 2004)	204	–	64	–
(Torstensen et al. 2004)	209	–	66	–
(Torstensen et al. 2005)	–	–	126	–
(Torstensen et al. 2005)	–	–	87	–
(Torstensen et al. 2005)	–	–	116	–
(Torstensen et al. 2005)	–	–	98	–
(Young et al. 2006)	–	–	95	–
(Young et al. 2006)	–	–	113	–
(Young et al. 2006)	–	–	151	–
(Young et al. 2006)	–	–	92	–
(Young et al. 2006)	–	–	102	–
(Young et al. 2006)	–	–	131	–
(Young et al. 2006)	–	–	93	–
(Young et al. 2006)	–	–	105	–
(Young et al. 2006)	–	–	145	–

Study/year	14:0	16:0	18:0	SFA	20:1	22:1	18:1n-9	18:2n-6	20:4n-6	18:3n-3	18:4n-3	20:4n-3	20:5n-3	22:5n-3	22:6n-3	n-3 LC PUFA
(Bell et al. 2001)	165.1	732.4	114.3	1037.3	321.8	376.8	724.0	105.8	21.2	59.3	84.7	63.5	245.6	88.9	626.6	961.1
(Bell et al. 2001)	149.8	685.3	101.1	962.5	235.9	250.9	876.3	179.8	15.0	78.6	56.2	41.2	157.3	52.4	434.4	644.1
(Bell et al. 2001)	124.4	567.0	102.4	815.8	208.5	219.5	951.1	226.8	14.6	106.1	47.6	43.9	168.3	62.2	424.4	654.8
(Bell et al. 2001)	92.2	450.6	99.3	663.4	195.1	198.7	1011.1	287.4	14.2	141.9	42.6	39.0	152.6	60.3	397.4	610.2
(Bell et al. 2001)	56.3	414.2	108.6	595.1	164.9	104.5	1572.2	494.6	16.1	225.2	28.1	28.1	112.6	44.2	289.5	446.3
(Bell et al. 2002)	189.4	802.7	130.8	1168.0	216.5	216.5	825.3	153.3	22.5	81.2	90.2	67.6	257.1	85.7	735.1	1077.8
(Bell et al. 2002)	122.8	744.3	122.8	1019.6	160.0	148.9	822.4	182.3	18.6	55.8	59.5	48.4	182.3	63.3	561.9	807.5
(Bell et al. 2002)	86.4	694.6	108.8	912.3	128.0	112.0	806.6	192.1	12.8	38.4	38.4	35.2	134.4	48.0	467.3	649.8
(Bell et al. 2002)	47.6	701.5	110.0	867.9	101.1	53.5	1105.7	315.1	11.9	14.9	11.9	11.9	56.5	17.8	228.9	303.2
(Bell et al. 2003)	297.4	956.8	181.0	1493.4	523.7	646.5	982.7	284.5	32.3	90.5	109.9	103.4	362.0	161.6	827.5	1454.6
(Bell et al. 2003)	219.8	834.0	213.3	1318.9	375.0	465.5	995.6	459.0	25.9	969.7	77.6	97.0	252.1	116.4	614.2	1079.6
(Bell et al. 2003)	148.7	711.1	219.8	1118.4	239.2	271.5	1047.3	601.2	19.4	1706.7	71.1	97.0	174.6	84.0	439.6	795.2
(Bell et al. 2003)	77.6	588.3	245.7	943.9	129.3	122.8	1079.6	756.4	6.5	2417.9	64.6	103.4	103.4	38.8	271.5	517.2
(Bell et al. 2003)	219.8	808.1	174.6	1254.2	407.3	459.0	1609.8	549.5	25.9	245.7	77.6	84.0	258.6	122.8	646.5	1112.0
(Bell et al. 2003)	155.2	698.2	168.1	1066.7	329.7	278.0	2211.0	769.3	19.4	342.6	45.3	58.2	168.1	77.6	459.0	762.9
(Bell et al. 2003)	84.0	575.4	168.1	879.2	252.1	129.3	2683.0	943.9	12.9	439.6	38.8	45.3	97.0	38.8	323.2	504.3
(Bell et al. 2003)	77.6	575.4	206.9	892.2	161.6	122.8	1648.6	846.9	12.9	1706.7	71.1	84.0	109.9	38.8	297.4	530.1
(Bell et al. 2003)	84.0	588.3	187.5	905.1	213.3	142.2	2139.9	879.2	12.9	1066.7	58.2	77.6	116.4	45.3	303.9	543.1
(Bell et al. 2003)	148.7	711.1	193.9	1099.0	290.9	297.4	1622.7	691.8	19.4	1008.5	58.2	77.6	161.6	71.1	452.5	762.9
(Bell et al. 2004)	274.2	752.6	110.9	1161.0	968.5	577.6	933.5	227.5	17.5	46.7	87.5	70.0	250.9	87.5	472.6	811.0
(Bell et al. 2004)	270.6	811.7	159.6	1255.8	825.6	506.5	1207.2	471.8	13.9	797.9	90.2	97.1	208.1	76.3	423.2	707.7
(Bell et al. 2004)	185.2	683.3	178.8	1053.7	555.6	344.9	1124.0	549.2	12.8	1283.6	83.0	95.8	159.7	63.9	338.5	562.0
(Bell et al. 2004)	51.1	613.1	198.0	938.8	306.5	191.6	1124.0	702.5	6.4	1922.2	76.6	102.2	115.0	38.3	274.6	427.9
(Bell et al. 2004)	44.7	530.0	229.9	811.0	102.2	70.2	1187.8	836.6	6.4	2471.4	76.6	115.0	83.0	25.5	198.0	306.5
(Bell et al. 2010)	411.6	1371.8	237.8	2066.9	695.1	777.4	1618.8	448.1	36.6	164.6	155.5	155.5	530.4	265.2	1198.1	1993.7
(Bell et al. 2010)	141.3	1322.0	292.7	1806.4	524.8	201.8	3804.6	1412.8	20.2	676.1	70.6	90.8	171.6	90.8	403.7	666.0
(Bell et al. 2010)	478.7	1561.1	281.0	2372.8	780.5	874.2	1852.4	509.9	41.6	197.7	187.3	176.9	593.2	291.4	1332.1	2216.7
(Bell et al. 2010)	152.6	1393.4	305.1	1912.1	518.7	223.8	3793.6	1352.7	20.3	640.7	81.4	91.5	193.2	91.5	427.2	711.9
(Bell et al. 2010)	436.4	1493.4	271.5	2240.1	707.9	785.5	1794.0	484.9	38.8	174.6	145.5	155.2	533.4	271.5	1231.6	2036.5
(Bell et al. 2010)	133.6	1229.4	285.1	1683.8	454.4	178.2	3305.3	1184.9	17.8	552.4	62.4	71.3	169.3	80.2	400.9	650.4
(Friesen et al. 2015)	317.7	876.3	184.5	1414.4	–	71.7	650.8	287.0	41.0	51.2	87.1	66.6	738.0	235.7	666.2	1639.9
(Friesen et al. 2015)	193.2	998.9	253.9	1479.1	–	38.6	1528.7	579.5	27.6	82.8	44.2	38.6	358.7	121.4	397.4	877.5

(Friesen et al. 2015)	155.5	981.1	252.0	1404.6	–	21.4	1635.2	611.2	32.2	117.9	32.2	32.2	225.2	91.1	375.3	691.6
(Friesen et al. 2015)	108.8	506.2	184.5	818.4	–	18.9	1036.0	624.4	18.9	1088.0	47.3	52.0	198.7	75.7	302.7	577.1
(Friesen et al. 2015)	119.7	562.0	187.3	884.6	–	20.8	1790.0	759.7	20.8	431.9	41.6	46.8	223.8	83.3	322.6	629.6
(Friesen et al. 2015)	126.1	539.9	151.4	832.6	–	20.2	1781.2	761.9	25.2	328.0	45.4	30.3	227.1	80.7	302.7	610.5
(Friesen et al. 2015)	132.4	604.3	178.4	932.4	–	23.0	2077.7	851.8	28.8	385.6	40.3	40.3	264.7	92.1	351.1	707.9
(Larsson et al. 2014)	–	–	–	1989.9	–	–	–	–	–	–	–	–	–	213.1	–	–
(Larsson et al. 2014)	–	–	–	2127.5	–	–	–	–	–	–	–	–	–	192.8	–	–
(Liland et al. 2013)	–	–	–	–	–	–	–	–	–	–	–	–	745.7	–	1252.8	1998.5
(Liland et al. 2013)	–	–	–	–	–	–	–	–	–	–	–	–	234.2	–	600.8	834.9
(Liland et al. 2013)	–	–	–	–	–	–	–	–	–	–	–	–	257.5	–	585.5	843.0
(Liland et al. 2013)	–	–	–	–	–	–	–	–	–	–	–	–	200.7	–	486.0	686.7
(Rosenlund et al. 2001)	–	996.4	–	1537.0	614.8	455.8	3360.2	1208.4	–	710.2	–	–	307.4	–	551.2	858.6
(Rosenlund et al. 2001)	–	1280.4	–	1930.3	184.3	106.7	1784.8	911.8	–	1736.3	–	–	378.3	–	640.2	1018.5
(Rosenlund et al. 2001)	–	1194.8	–	1874.6	597.4	432.6	3069.4	968.2	–	309.0	–	–	298.7	–	597.4	896.1
(Rosenlund et al. 2001)	–	1627.2	–	2282.6	621.5	531.1	2531.2	1017.0	–	1446.4	–	–	316.4	–	553.7	870.1
(Rosenlund et al. 2001)	–	1439.1	–	2258.1	1415.7	1368.9	1544.4	468.0	–	105.3	–	–	631.8	–	900.9	1532.7
(Rosenlund et al. 2001)	–	1612.9	–	2540.0	215.9	114.3	2095.5	3048.0	–	368.3	–	–	647.7	–	990.6	1638.3
(Rosenlund et al. 2016)	91.1	1626.1	416.3	2224.5	299.2	104.1	–	1678.1	26.0	897.6	234.2	104.1	130.1	52.0	273.2	455.3
(Rosenlund et al. 2016)	131.8	1545.9	371.5	2157.1	323.6	143.8	–	1474.0	24.0	814.9	155.8	95.9	143.8	59.9	299.6	503.3
(Rosenlund et al. 2016)	163.0	1642.2	388.6	2306.6	363.5	188.0	–	1541.9	25.1	877.5	163.0	87.8	163.0	62.7	376.1	601.7
(Rosenlund et al. 2016)	179.1	1444.2	335.9	2060.0	347.1	190.3	–	1332.3	22.4	761.3	134.3	89.6	156.7	67.2	380.6	604.6
(Rosenlund et al. 2016)	224.7	1561.1	354.8	2247.0	390.3	248.3	–	1360.0	23.7	816.0	130.1	94.6	201.0	82.8	461.2	745.0
(Rosenlund et al. 2016)	75.6	1306.9	334.8	1793.0	248.4	75.6	–	1425.8	32.4	723.7	216.0	97.2	118.8	54.0	216.0	388.8
(Rosenlund et al. 2016)	124.0	1386.7	349.5	1927.9	304.4	124.0	–	1465.7	22.5	777.9	169.1	101.5	146.6	67.6	259.3	473.5
(Rosenlund et al. 2016)	143.5	1281.2	317.7	1814.1	307.5	143.5	–	1301.7	20.5	717.5	133.2	92.2	143.5	61.5	276.7	481.7
(Rosenlund et al. 2016)	174.1	1349.1	293.8	1893.1	348.2	174.1	–	1360.0	21.8	772.5	119.7	97.9	185.0	76.2	359.0	620.2
(Rosenlund et al. 2016)	199.2	1310.7	304.1	1897.9	346.0	209.7	–	1258.3	21.0	713.0	115.3	94.4	199.2	83.9	408.9	692.1
(Sissener et al. 2016a)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(Sissener et al. 2016a)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(Sissener et al. 2016a)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(Sissener et al. 2016a)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(Sissener et al. 2016a)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(Sissener et al. 2016a)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(Torstensen et al. 2001)	593.2	1404.9	239.4	2268.7	1207.2	1488.2	1280.1	166.5	52.0	104.1	–	156.1	572.4	208.1	1259.2	2039.8

[illegible]

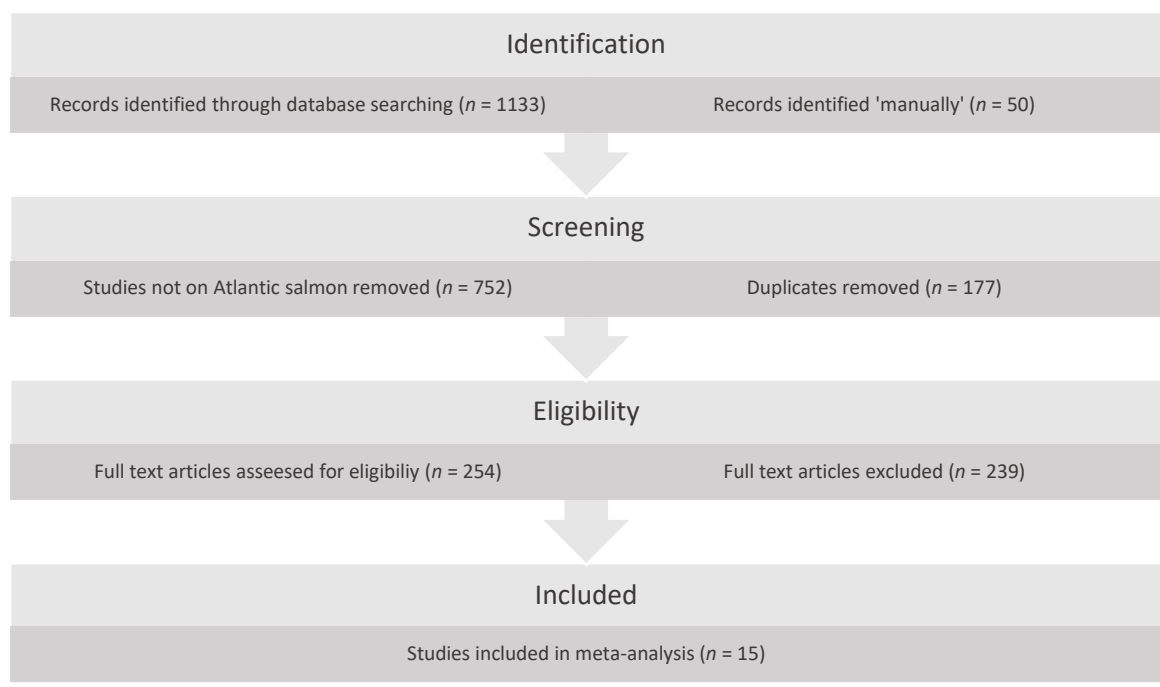


Figure 1

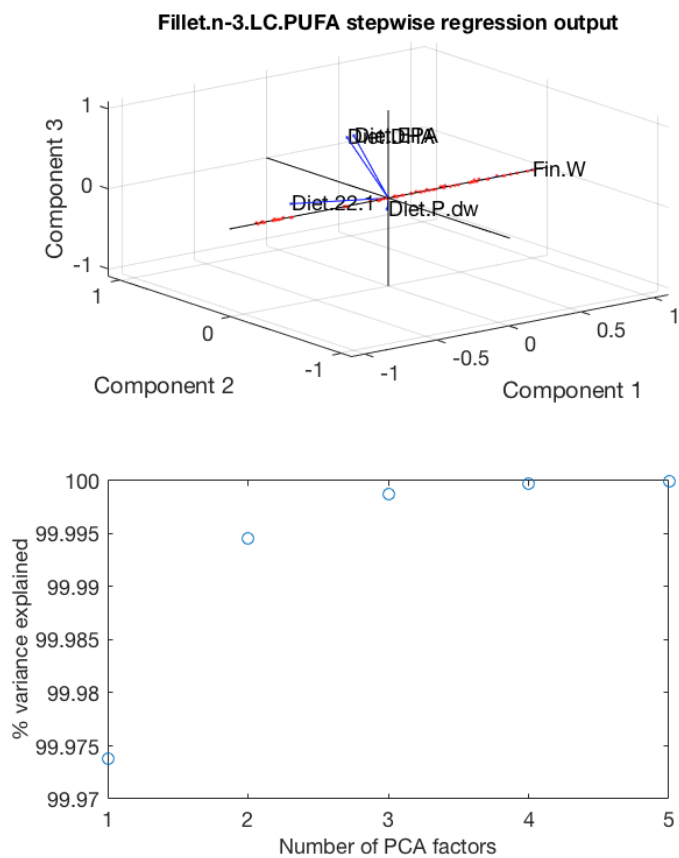
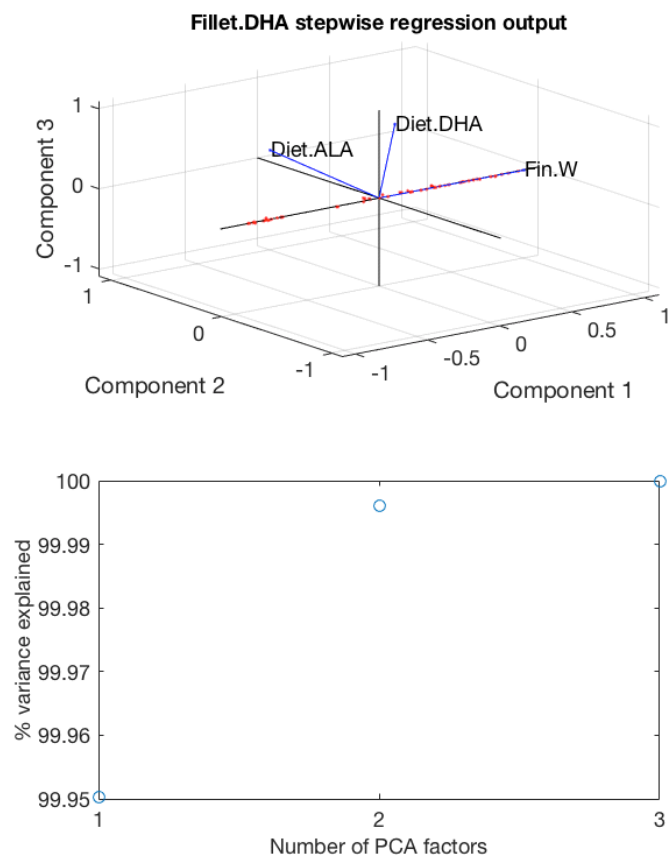


Figure 3

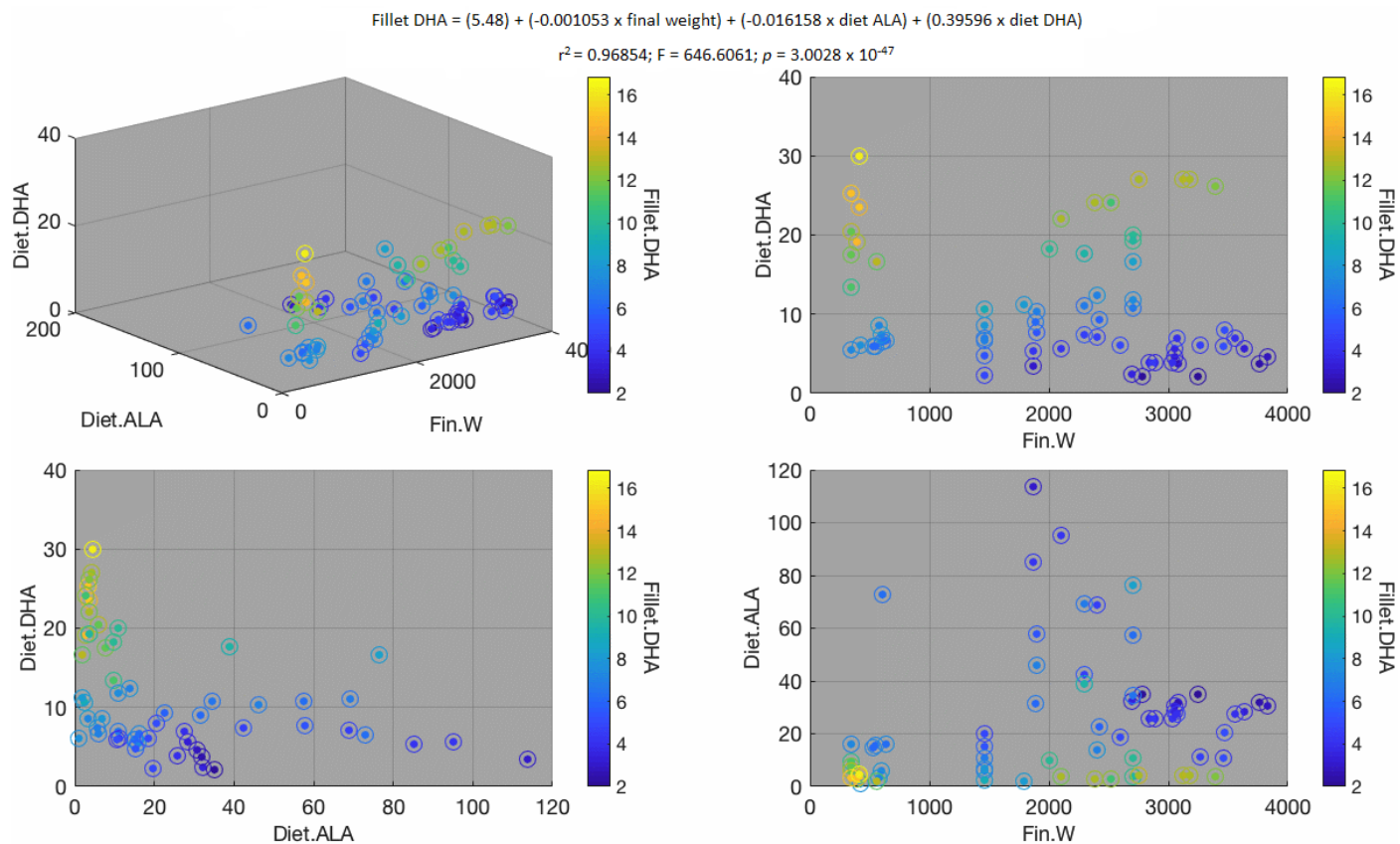


Figure 4

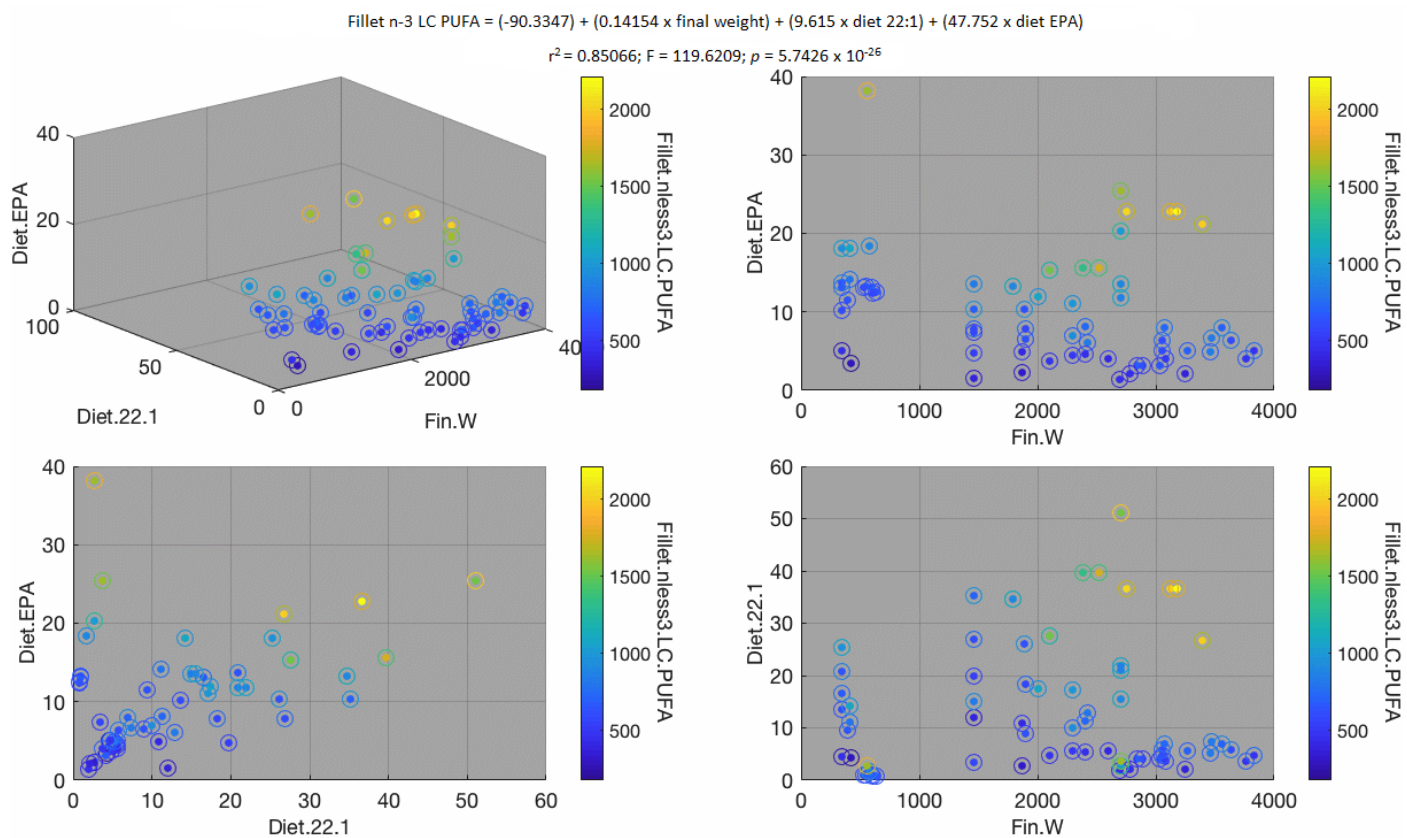


Figure 5