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Body Shape Variation in Atlantic Salmon (*Salmo salar*, L.) Fed Fishmeal and Fish Oil-Free Diets

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Abstract: Post-smolt Atlantic salmon were fed control (C), plant protein- (PP), and animal protein (AP)-based diets over a 90-day period. At trial start, the outline shape variation in the salmon body was recorded using two-dimensional Cartesian coordinates of a combination of 12 landmarks (LM) and three semi-landmarks from each of the 48 fish. The identical landmarks were then assessed at trial end for the differing dietary treatments. These datasets were used to determine whether diet exerted a measurable effect on body shape to enable authentication of fishmeal/fish oil-free status. Most differences in shape at trial end were visualized at the base of the dorsal and pelvic fins and caudal peduncle. The greatest shape variation between PP and AP groups was found at the base of the pectoral and pelvic fins. While PP and AP groups were more similar in shape than control fish, the recorded differences were not significant enough to verify dietary origins. The number of animals employed and the length of the trial period were likely insufficient to distinguish alterations in body shape with any certainty. Future trials should employ larger numbers of animals and be of longer length to verify whether PP-based feeds cause changes in body shape.

Keywords: alternative proteins; consumer; growth; morphometrics; quality; sustainability

Key Contribution: This manuscript provides a model to study body shape variation in related fish groups and verifies that in Atlantic salmon, full replacement of fishmeal with alternative proteins in aquafeeds does not impact shape over the short term.

Academic Editor: Marina Paolucci

Received: 31 December 2024
Revised: 28 January 2025
Accepted: 31 January 2025
Published: 2 February 2025

Citation: Chollet-Villalpando, J.G.; Barrows, F.T.; McLean, E. Body Shape Variation in Atlantic Salmon (*Salmo salar*, L.) Fed Fishmeal and Fish Oil-Free Diets. *Fishes* **2025**, *10*, 62. https://doi.org/10.3390/fishes10020062

1. Introduction

The consumer's willingness to pay for a specific seafood product may be influenced by a variety of demographic, cultural, psychological and biological landscapes [1,2]. However, appearance is the first visual cue that stimulates a buyer's interest in, or wariness of purchasing a product. This is especially true for farmed fishes sold whole or gutted, where body shape is a key driver in a customer's decision-making process [3]. Consumers purchase fish whose external form resembles their preconceived image of how its wild counterpart should look [4]. Because this morphological trait is economically important, influencing, for example, the market price of various species [5–7], it is used in sorting fish during harvesting and has been incorporated into numerous genetic selection programs [6,8–13]. Throughout the Atlantic salmon lifecycle, body shape is naturally plastic, changing during prominent events such as smoltification and reproduction [14]. Moreover, body shape in salmonids is influenced by genetic factors [15–18] and conditions of rearing [19,20].

Shape represents a particularly important production parameter in salmonids since the visual presentation of Atlantic salmon, for example, affects its aesthetic appeal to consumers. Shape can influence fillet texture and flavor profile and hence mouthfeel and gastronomic delight of the product. Shape also influences carcass and fillet yields in Atlantic salmon [21] and has been linked with fat content and hence nutritional value. For some buyers, shape is considered as a quality indicator, with well-formed fish suggesting good healthy and sustainable farming practices and ethical sourcing. The significance of body form is demonstrated by inclusion in quality schemes. In Norway, for example, farmed Atlantic salmon are graded into four classes *viz.* superior, ordinary, production and reject [22–25]. The superior salmon must exhibit a "natural streamlined shape" (although a definition of this is conveniently absent). Diet can also have an impact upon fish morphology, and this may be influenced by feed preparation. Over the last few decades, salmonid feeds have experienced notable modifications in formulation with the use of fishmeal (FM) and fish oil (FO) declining substantively [26]. Indeed, in 2020, Norwegian formulations comprised 18.5% and 43% of 1990 levels, respectively [27]. Today, specialty salmon feeds, utterly void of marine resources, are commercially available. These product lines rely on mixtures of single-celled, insect, plant and animal derivatives to satisfy Atlantic salmon's nutritional requirements. However, relatively few studies have assessed the effect of marine resource-free feeds on quality attributes of Atlantic salmon. Because refined consumers shy away from substandard foodstuffs, there is a need to determine whether concurrent FM/FO replacement has a negative impact on the most important and fundamental discernible cue. Accordingly, we examined the effect of feeding post-smolt Atlantic salmon with animal and plant-based diets over a 90-day period and assessed whether these feeds influenced the fish's body shape.

2. Materials and Methods

2.1. Raw Material

The fish employed in the present study were derived from a 90-day growth trial undertaken to assess the response of Atlantic salmon morphology to dietary krill meal (KM) inclusion. The results of these experiments, which evaluated seven diets, have been presented previously [26], and this study is a further examination of changes in the overall shape of the fish that were not addressed initially. Two fish were randomly taken from four replicated tanks for each of the seven diets (Table 1; n = 8 fish per diet, −1 for P2 start), which comprised a control FM/FO-based feed (C1), plant-based feeds incorporating 0% (P1), 2.5% (P2), and 5% (P3) KM, and animal-based formulas that incorporated 0% (A1), 2.5% (A2), and 5% (A3) KM. The main protein source in the animal-based feeds was poultry meal while that of the plant-based feed was soy protein concentrate. Both animal and plant-based feeds incorporated *Schizochytrium* sp. and canola oils while the control feed contained FO only. Since each tank accommodated 45 individuals (180 fish per treatment), the sample size represented ~4.5% of the original trial's total population.

Table 1. Ingredients of control (C), plant protein (P) and animal protein (A)-based experimental diets.

.	Control	Plant Protein			Animal Protein		
Ingredient	**C1**	**P1**	**P2**	**P3**	**A1**	**A2**	**A3**
%							
Fishmeal [a]	25.27	0	0	0	0	0	0
Poultry meal [b]	0	0	0	0	26.27	26.27	26.27
Krill meal [c]	0	0	2.5	5	0	2.5	5
Menon Pro50FF [d]	13	13	13	13	13	13	13
SPC Selecta 60 [e]	11.88	27.1	27.1	27.1	10	7.76	5.42
CPC E75 [f]	1.87	11.9	10.1	7.7	0.96	0.96	0.6
Blood meal [g]	6	6	6	6	6	6	6
Wheat gluten meal	2.15	2.15	2.15	2.15	2.15	2.15	2.15
Wheat flour [h]	15.944	10.004	10.004	11.134	17.834	17.844	18.644
Fish oil [i]	19.79	0	0	0	0	0	0
Canola oil [j]	0	17.7	17.4	16.95	14.07	13.80	13.30
Algae oil [k]	0	4.5	4.5	4.5	4.5	4.5	4.5
Monoammonium phos	1.85	4.3	3.98	3.25	1.7	1.7	1.6
Vitamin mineral premix [l]	0.7	0.7	0.7	0.7	0.7	0.7	0.7
Lysine HCL	0.65	1.45	1.3	1.2	1.45	1.4	1.4
Taurine	0.5	0.5	0.5	0.5	0.5	0.5	0.5
DL-methionine	0.39	0.6	0.6	0.65	0.6	0.65	0.65
Threonine	0	0.09	0.16	0.16	0.26	0.26	0.26
Asta, pink [l]	0.006	0.006	0.006	0.006	0.006	0.006	0.006
Total	100	100	100	100	100	100	100
Proximate composition [26]							
Moisture	4.9	6.1	4.4	3.3	4.8	4.9	5.2
Lipid	22.9	21.7	24.1	23.1	24	24	23.9
Protein	46	46.4	46.3	46	44.1	44.5	43.8
Ash	7.7	6.1	6.7	6.2	6.7	6.3	6.5
Biometric details *							
Start weight	149.0	148.7	148.7	148.1	147.6	148.6	147.9
End weight	542.1	496.8	527.7	549.6	520.5	531.2	543.3

[a] Orion SA, 670 g/kg protein; [b] Seara Alimentos LTDA, Brazil, 650 g/kg protein; [c] Pesca Chile SA, Santiago, Chile; [d] hydrolyzed soy (50% protein), Menon Renewable Products Inc., San Diego, CA, USA; [e] soy protein concentrate (60% protein) Kabsa, Brazil; [f] corn protein concentrate (75% protein) Cargill Andina Chile Limitada, Santiago, Chile; [g] Sonac Bad Bramstedt GmBH, Bramstedt, Germany; [h] Molini San Pablo, Los Lagos, Chile; [i] Orizon SA, Santiago, Chile; [j] Agrotop, Temuco, Chile; [k] Veramaris, Blair, NE, USA; [l] DSM Nutritional Products Chile SA, Puerto Varas, Chile. * For full details, see [26].

2.2. Image Acquisition and Shape Analyses

Fish used for final image acquisition were sacrificed using an overdose of benzocaine (100 mg L^{-1}) and pinned to a polystyrene board that incorporated a metric scale, tank, and specimen number. Animals were photographed from the left side using a Canon EOS T7i + 18–55 mm lens mounted on a stand at a 90° angle, and all images were acquired under fluorescent light. Since there were no differences in fish shape across all tanks at trial start, these were used as the control start shape in statistical analyses. A metric scale was added to all digitized specimens that were used to obtain geometric shape data for the seven treatments. The outline shape variation in the body was recorded using two-dimensional Cartesian coordinates of a combination of 12 landmarks (LM) and three semi-landmarks (SLM) (15 points in total; Figure 1) using the tpsDig 2.32 software [28]. We also used two points that registered the scale coordinates in each image (1 cm). Landmarking represents a critical factor during morphometric evaluation of digitized images, and because inter-observer differences in point selection can significantly impact analyses [29], all landmark datasets were assigned using one individual only. The positions of the landmarks employed are depicted in Figure 1. One open curve was used to capture the shape of the dorsal cephalic contour. We used the tool "draw background curves" to resample the curve using the length criterion in tpsDig 2.32 software [28]. In this curve (the dorsal cephalic contour), we placed three semi-landmarks between points 1 and 5 (Figure 1). Finally, the curve was converted to points using the "append tps curve to landmarks" function included in tpsUtil version 1.76 [30]. The resulting points were reordered so that the last two points registered the scale, as Zelditch et al. [31] suggested.

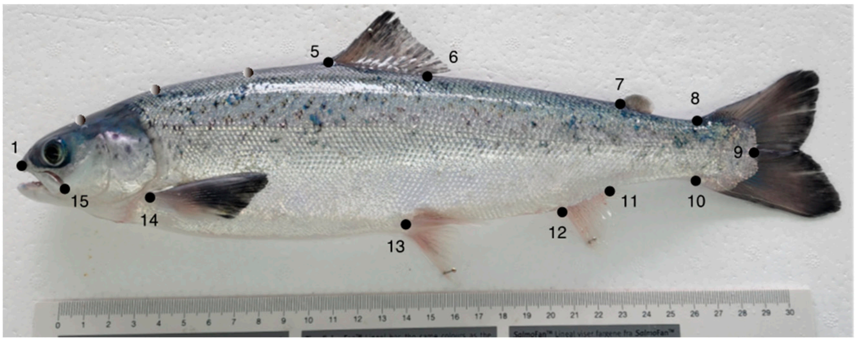

Figure 1. Biological position of landmarks (black dots) and semi-landmarks (grey dots) of post-smolt Atlantic salmon taken from an image of a specimen derived from the P1 plant-based diet. The landmarks identified were: 1. tip of the snout, 5. anterior-most spine of the dorsal fin, 6. posterior-most radius of the dorsal fin, 7. origin of the adipose fin, 8. the dorsal start of the caudal fin, 9. the intersection between the lateral line and the caudal radius, 10. the ventral start of the caudal fin, 11. the last radius of the anal fin, 12. the first spine of the anal fin, 13. the first spine of the pelvic fin, 14. the first radius of the pectoral fin and 15. the base of the maxillary. One open curve was used to capture the shape of the dorsal cephalic contour.

2.3. Superimposition and Alignment

Two superimpositions were performed with the set of shape coordinates. First, we superimposed the 48 specimens belonging to the controlled-start feeding treatment based exclusively on the FM/FO diet (Control S), the control end treatment (Control E-C1), and alternative diets exclusively of plant end (Plant E-P1) and animal end (Animal E-A1) treatments. Second, the 111 specimens of the controlled-start feeding treatment solely based on the FM/FO diet (Control S), the control end treatment (Control E-C1), and the alternative diets of plant end (Plant E-P1, P2, and P3) and animal end (Animal E-A1, A2, and A3) treatments, or common diets were superimposed concurrently. We superimposed the 15 points of the body shape contour using the gpagen function in the geomorph package 4.0.5 [32] in R 4.2.1 version. The Generalized Procrustes Analysis (GPA) superimposed all the configurations into a common coordinate system using the mean shape of all specimens as a reference, removing the differences produced by the scale, position, and orientation. Also, we aligned the semi-landmark points along the dorsal cephalic contour by sliding along their tangent vectors until their positions minimized the shape difference among specimens based on Procrustes distance [33,34].

2.4. Body Shape Variation

Before conducting the statistical analyses of shape variation according to diet, we explored whether geometric shape deviations in the seven sampled treatments depended on size (i.e., the allometric component). We used the set of shape variables obtained from the aligned GPA coordinates to examine allometry at the intraspecific level. Regression analysis was performed to determine if fish size was a linear predictor of body shape variation. We used the procD.lm function [32,35] from the geomorph package (version 4.0.5) to calculate regression statistics, using body shape as the dependent variable (Y) and the log-transformed Centroid Size (CS) as the independent variable (X). CS is a measure of the geometric size of each fish [36]. The null hypothesis tested that size and shape are unrelated. Bootstrap permutations (2500 replicates) were used to estimate the significance of the regression parameters. If size accounts for very little variation in shape, it suggests that size provides weak insight into fish body shape variation.

Body shape variation was analyzed using the Partial Warp Scores produced from the GPA superimposed and aligned coordinates for each set separately. We performed two Canonical Variate Analyses (CVA) using the package Morpho 2.9 [37] in R 4.2.1 version. First, we carried out a CVA analysis comparing a controlled-start feeding treatment based exclusively on the FM/FO diet (Control S) with the control end treatment (Control E-C1) and alternative diets exclusively of plant (Plant E-P1) and animal (Animal E-A1) end treatments to explore their shape variation. In a second analysis, we compared the controlled-start feeding treatment solely based on the FM/FO diet (Control_S) with the control end treatment (Control E-C1) and the alternative diets of plant (Plant E-P1, P2 and P3) and animal (Animal E-A1, A2 and A3) end treatments, or common diets. CVA analyses were conducted using 50,000 rounds. Shape changes explained by the first two Canonical Variates (CV) were visualized in scatterplots using vectors on landmarks for CV1 and CV2. We also depicted the shape affinities among the *a priori* four groups, using UPGMA dendrograms based on Mahalanobis distances.

3. Results

Regression analyses for exclusive (C1, P1 and A1) and common (P2, P3 and A2, A3) diets revealed no dependence of shape variation on fish size, i.e., there was no allometry in the set. Only 4.80% ($p < 0.05$) of shape variations were explained by variation in size (CS-log).

3.1. Exclusive Diets (C1, P1 and A1)

The shape variation in the body for the exclusive diet treatments (C1, P1, A1) showed a dispersion pattern that added up to 98.60% of the variance with the first two eigenvalues (2 CV axes) from CVA. The first CV explained 95.50% of the total variance, and 3.10% was related to the second CV. Differences between the controlled-start feeding treatment and all the end treatment groups were detected. However, no significant differences were detected among the end treatments in the exclusive diet groups (i.e., Control E-C1, Plant E-P1 and Animal E-A1). A substantial percentage of the specimens were correctly assigned to their *a priori*-determined group based on Mahalanobis distances. The *a posteriori* classification from the CVA scores was 97.91% correct and significant, and only one specimen (12.5%) of the Plant E group was assigned incorrectly and significantly within the Control E group from all specimens analyzed. Body shape variation showed a spatial dispersion with the shape scores for Control S ubicated in the positive extreme of the CV1. In contrast, the shapes of Control E, Plant E and Animal E were located in the opposing extreme. Finally, the shape of Animal E was in the positive extreme of the CV2 (Figure 2). Most differences among these shape types along the CV1 were in the dorsal cephalic profile (i.e., the base of the dorsal fin), the ventral portion of the abdominal region, and the intersection between the lateral line and the caudal radius, as shown by the vector deformations (Figure 3a). We also depicted the shape differences between the mean shapes of the *a priori* groups Animal E and Control E (i.e., the most distinct shapes, see Figures 2 and 4). The greatest shape variation between these two diet groups was in the base of the pectoral fin and the peduncle caudal base, with a tendency for a more elongated caudal fin in the Animal E diet group (Figure 3b).

Visualization of the degree of morphological distinction for the body shape among the exclusive diets (C1, P1, and A1) revealed two main groups as having the most distinctive shapes. One group was that of the Control S diet. The second group was observed in the end diet treatments Control E, Animal E, and Plant E, with the shape of diet treatments Control E and Plant E being the most similar (Figure 4).

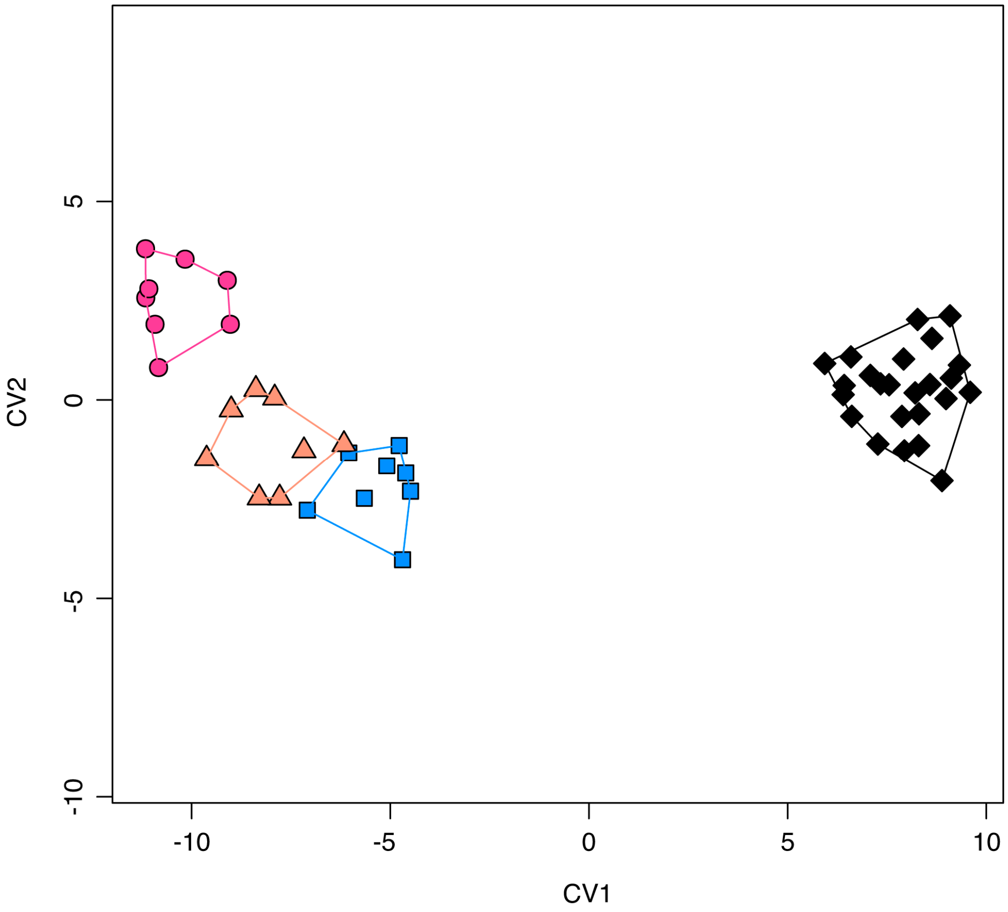

Figure 2. Scatterplot of the body shape variation in Atlantic salmon for control S, control E (C1), Plant E (P1) and Animal E (A1) using the scores from CV1 vs. CV2. Symbols are as follows: black rhombus, Control S; blue squares, Control E; orange tringles, Plant E; pink circles, Animal E.

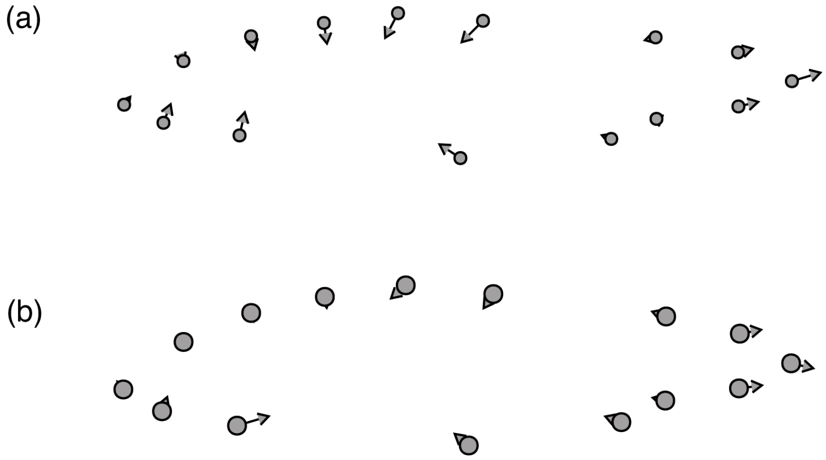

Figure 3. Body shape variation among C1, P1 and A1. (**a**) Body shape variation along the CV1. (**b**) shape variation between the mean shape of the a priori groups Plant E (P1) and Animal E (A1).

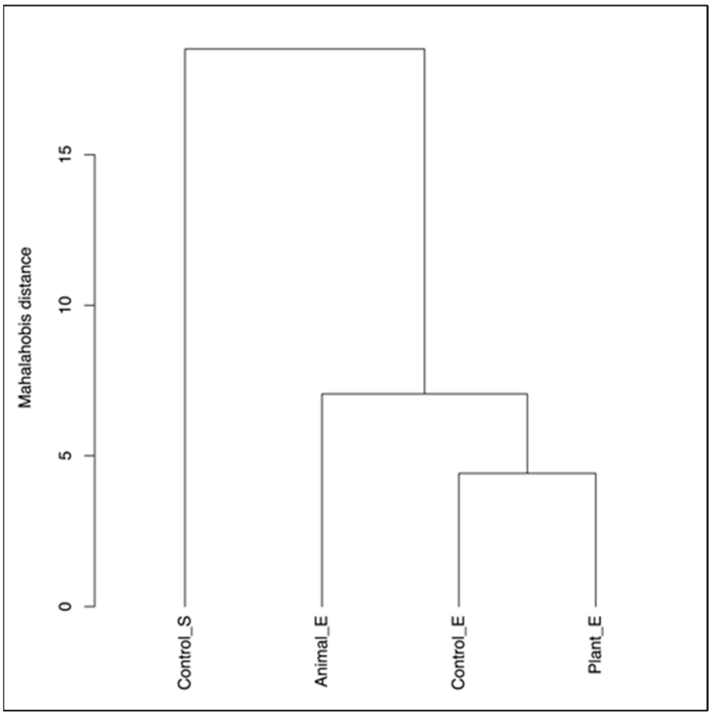

Figure 4. Dissimilitude dendrogram of the overall multivariate pattern of shape similarity among Control S, Control E (C1) Plant E (P1) and Animal E (A1) based on Mahalanobis distances computed from the CVA scores.

3.2. Common Diets (C1, P1-3, A1-3)

Body shape variation in the common diet treatments (C1, P1-P3 and A1-A3) showed a dispersion pattern that added up to 97.73% of the variance with the first two eigenvalues (2 CV axes) from CVA. The first CV explained 94.34% of the total variance, and 3.38% was related to the second CV. As in the exclusive diets, differences among the controlled-start feeding treatment and all the end treatments as *a priori* groups were detected. However, no significant differences were detected among the end treatments designed as exclusive diets (i.e., Control E C1, Plant E P1, P2, P3, and Animal E A1, A2, A3). Once again, the percentage of correctly and significantly assigned specimens based on Mahalanobis distances from the CVA scores was high, with 93.69%. Seven specimens were assigned incorrectly from all samples analyzed. Two specimens of the Animal E diet were assigned for both Control

E and Plant E diets (8.33%). In addition, two specimens of the Plant E diet were assigned within Control E (8.33%) and only one within the Animal E diet (4.16%).

Shape variation in the body showed a spatial dispersion with the shape scores for the Control S ubicated in the negative extreme of the CV1. In contrast, the shapes of Control E, Animal E, and Plant E diets were positioned in the opposing extreme. Finally, the Control E diet shape was in the most positive extreme along the CV2 (Figure 5). The majority of differences among these groups of shapes along the CV1 were in the dorsal and ventral cephalic profile (i.e., the base of the dorsal fin), the base of the pelvic fin, and at the base of the caudal peduncle (Figure 6a). We also depicted the shape differences between the mean shapes of the *a priori* groups Animal E and Control E. The greatest shape variation between these two diet groups was in the base of the pectoral and pelvic fins (Figure 6b).

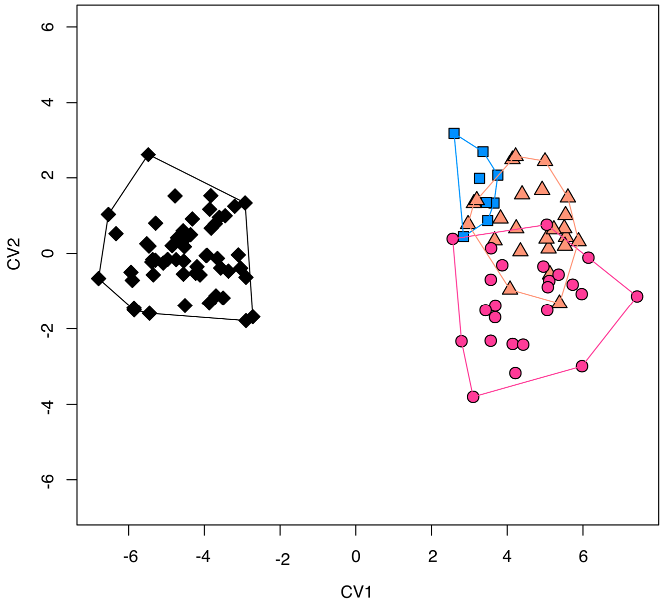

Figure 5. Scatterplot of the body shape variation for the common diets Control S, Control E (C1), Plant E (P1, P2 and P3) and Animal E (A1, A2 and A3) using the scores from CV1 vs. CV2. Symbols are as follows: black rhombus, Control S; blue squares, Control E; orange tringles, Plant E; pink circles, Animal E.

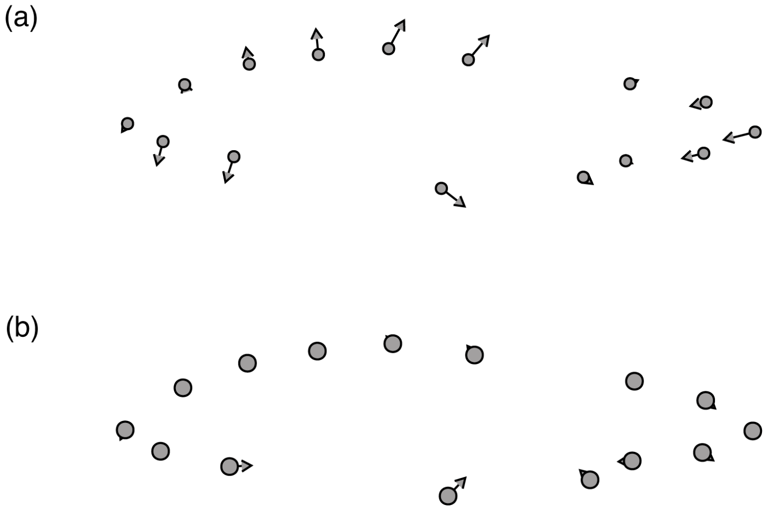

Figure 6. Body shape variation among all groups. (**a**) body shape variation along the CV1 and (**b**) shape variation between the mean shape of the a priori groups Plant E (P1, P2 and P3) and Animal E (A1, A2 and A3).

Visualization of the degree of morphological distinction for body shape among the common diets revealed two main groups exhibiting the greatest shape differences. Once again, the Control S diet formed a separate group. A second group was observed in the end diet treatments Control E, Animal E, and Plant E, with the shape of the diet treatments Animal E and Plant E being the most similar (Figure 7).

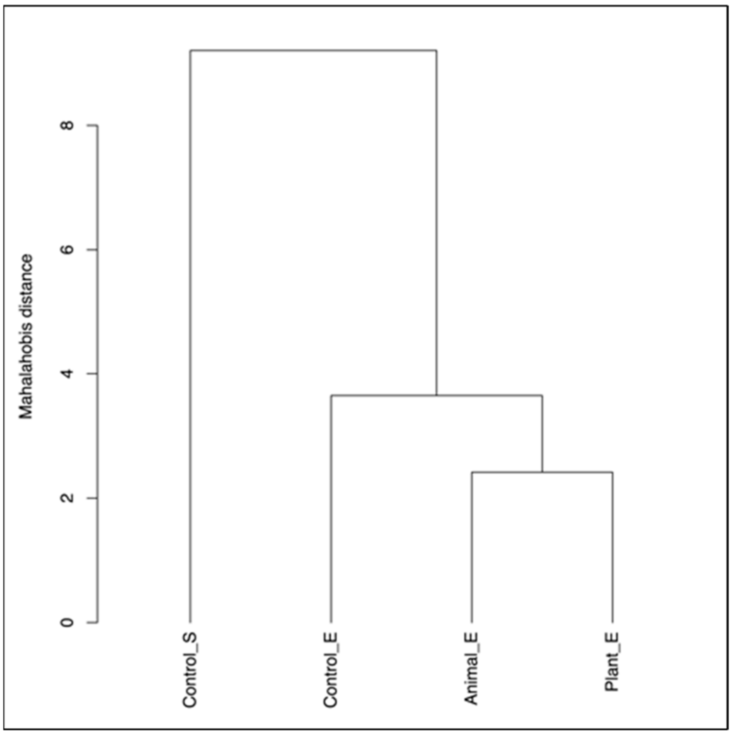

Figure 7. Dissimilitude dendrogram of the overall multivariate pattern of shape similarity for the common diets Control S, Control E (C1), Plant E (P1, P2 and P3) and Animal E (A1, A2 and A3) based on Mahalanobis distances computed from the CVA scores.

4. Discussion

The fish examined in the present study were derived from a feeding trial undertaken to compare the response of Atlantic salmon to animal- and plant-based feeds, with or without krill meal, versus a traditional FM formulation. This study was executed using a recirculating system in which all fish were subjected to identical water quality parameters, and no between-group differences in size, length or condition factor were measured at the trial start [26]. The only difference in animal husbandry between groups was feed. Most studies with Atlantic salmon that have evaluated dietary FM substitution with plant proteins report reduced weight and length growth over time [38–41]. In contrast, replacement of FM by animal proteins results in equivalent weight gain, while length growth may be lower. Both circumstances result in an augmented condition factor or *K*, which is frequently associated with a more streamlined fish. These scenarios were played out in the feeding study noted above and represented the impetus for resolving whether differences in feeds modified salmon body shape.

It is generally recognized that feed-induced morphological changes occur in a diverse range of teleosts at various points throughout their life cycles, as exemplified by Floridian largemouth bass [42], spotted guapote [43], redhump eartheater [44], orange-spotted sunfish [45], chinook salmon [46], and perjerry [47]. In Atlantic salmon, fasting, starvation, compensatory growth and the quality and quantity of feeds also influence body form [46,48–53] and it is well-established that as Atlantic salmon grow, they change body shape [54]. The present study ratified this, with fish from the starting group (Control S) differing in shape to those evaluated at trial termination (Control E, Plant E and Animal E). By the trial's end, discernable between-group differences in body shape were detected with those fed the FM-based diet separate from those receiving the alternative protein formulations. However, these body shape variations were not statistically significant. It is noteworthy that, like the present study, previous research with salmonids has likewise detected changes in head and fin dimensions over time, with diet, and variations in water flow [17,46,55,56]. It is conceivable that diet-induced morphometric changes may be augmented over the length of a production cycle and that shape differences may offer the potential to discriminate between salmon fed marine resource-free and FM/FO-based diets, a possibility deserving of further examination. The prospect of a sex-associated morphometric difference was not considered in the present study since this does not diverge in immature Atlantic salmon [57].

Because affluent consumers demand high levels of perfection with their food purchases [58–61], and are willing to pay higher prices for well-proportioned and shaped whole/gutted salmonids, body shape is of increasing interest to producers, processors, wholesalers, and the retail sectors [5,10,62]. In some instances, bulk fish purchasers may visit production facilities to check external appearance [5,63]. It is probably not too surprising to find, therefore, that at least three European Atlantic salmon breeding programs are known to have specifically incorporated body shape as a desired trait for selection [64]. However, selection programs have generally focused on growth and feed conversion, which may negatively impact selection for other traits such as shape. For example, fish selected for rapid growth may result in the production of more rotund and less desirable individuals due to the existence of a positive genetic correlation of body mass with body shape and K [1,5,11].

5. Conclusions

The ability to discriminate fish fed plant protein-based diets from those fed FM/FO-based feeds has become more important from a sustainability perspective. Contemporary consumers are now more aware of topics relating to overfishing, environmental degradation and associated issues, and increasingly base purchasing decisions on these concerns. At present, identification of salmonids fed FM/FO-free diets relies on destructive biochemical tests (e.g., C:N ratios) and alternative, non-destructive methods of verification are needed. The findings of the current trial indicate that Atlantic salmon shape is relatively unyielding to changes in feed type over the short term. However, the results adduced also allude to the possibility that over a longer timeframe, it may be possible to differentiate fish fed FM/FO-free diets based on their shape. But the number of animals employed herein was likely insufficient to distinguish alterations in body form following only 90-day feeding, and future trials should employ larger numbers of animals over a longer interval to increase the fidelity of results.

Author Contributions: Conceptualization, F.T.B.; draft manuscript preparation, E.M.; resources, J.G.C.-V., F.T.B., and E.M.; writing—review and editing, F.T.B. and J.G.C.-V.; data analysis, J.G.C.-V. All authors have read and agreed to the published version of this manuscript.

Funding: This research received funding through the Anthropocene Institute, 855 El Camino Real, Ste 13A N399, Palo Alto, CA 94301, USA.

Institutional Review Board Statement: This study was executed at the Centro Experimental Acuícola, Vitapro Chile, Carretera Austral km 23.8, Quillaipe, Puerto Montt, Chile. The described research complied with all relevant internal (code: CEA-1-C-0522) and international animal welfare laws, guidelines, and policies.

Data Availability Statement: All author-owned experimental data are available on request.

Acknowledgments: The authors express gratitude to the staff of the Centro Experimental Acuícola, Chile for assistance in executing the trial, and the Anthropocene Institute for its unwavering support throughout. J.G.C.-V. is grateful to Secretaría de ciencia, Humanidades, Tecnología e Innovación (SECIHTI) for the postdoctoral fellowship granted under the program "Estancias Posdoctorales por México 2022–3" (grant number 349241).

Conflicts of Interest: Frederick T. Barrows was employed by the company Aquatic Feed Technologies LLC. Ewen McLean was employed by the company Aqua Cognoscenti LLC. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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