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ORIGINAL ARTICLE

Feeding green: Spirulina (*Arthrospira platensis*) induced changes in production performance and quality of salmonid species

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Abstract

Spirulina is an interesting candidate for fish nutrition. This study aims to investigate the effect of the complete replacement of fishmeal with spirulina (*Arthrospira platensis*) in the diets of brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta fario*), in relation to growth and product quality. Two isoenergetic and isonitrogenous experimental diets containing either fishmeal or spirulina as a main source of protein were used for a 10-week feeding trial. Differences in the spirulina acceptance and conversion between species were observed. The experimental diets were well accepted except for brown trout. A species–diet interaction was observed, which led to a reduction in final body weight due to the spirulina supplementation for brook and rainbow trout ($p < 0.05$). Parallel, the feed conversion ratio increased to the same extent in the spirulina-fed fish ($p < 0.05$), fostering the assumption, that both species did not differ in converting the spirulina diet. Spirulina led to a significant increase ($p < 0.05$) in yellow and red coloration in both raw and cooked fillets. The diet had a significant effect on the fatty acid profile, resulting in an increase in SFA and MUFA, while PUFA levels decreased significantly in spirulina-fed fish ($p < 0.05$). Overall, total replacement of fishmeal with Spirulina goes along with a reduced production performance and effects on major product quality traits such as fillet colour and fatty acid pattern. In particular, consumer acceptance of the yellow fillet colour should be further investigated.

KEYWORDS
cyanobacteria, fishmeal replacement, growth performance, microalgae, pigmentation

1 | INTRODUCTION

The current trend in aquaculture is moving towards the more intensive production of carnivorous fish (Bostock et al., 2010), whose main protein source is fishmeal (Teles et al., 2019). Carnivorous fish have a dietary protein demand between 40% and 55%, higher than that of the herbivorous or omnivorous fish species with 25%–35%, (National Research Council, 2011). Considering this trend, and the predicted further increase in global aquaculture production (World Bank, 2013), an even higher demand on fishmeal for aquafeed can be expected. Despite the strict reduction of fishmeal in aquafeed over the past years, the change to full supplementation with alternative protein sources has shown to lead to reduced growth performance and health issues in fish (Teles et al., 2019).

Algae recently gained attention as potential supplements for fishmeal (Rosas et al., 2019). Microalgae/cyanobacteria such as

Arthrospira platensis and *A. maxima*, which are known collectively as *Spirulina*, have both a high protein content and represent an important source of vitamin B12 (Estrada, 2001). In nature, algae also contribute to the food chain as a primary source of polyunsaturated fatty acids (PUFA) (Legeżyńska et al., 2014). In Europe, about half of the algae produced is exclusively spirulina (Araújo et al., 2021). These algae species are of interest as a substitution for fishmeal, as they contain high amounts of essential amino acids and essential fatty acids (Becker, 2007, 2013).

Dietary ingredients can have an impact on the product quality of fish (Larsson et al., 2014; Webster et al., 2004), and in salmonid fish, spirulina can improve nutritional value by increasing the content of PUFA (Roohani et al., 2019; Teimouri et al., 2016). Consumer demands and their requirements on fish product quality vary geographically (Rasmussen, 2001). In Europe, for example, the flesh colour of trout is described as white or red/pink when carotenoids are added to the diet. It has been known for some time that organisms like plants and protists are able to synthesize carotenoids and thus are the source for the pigmentation of fish flesh (Isler et al., 1971; Steven, 1948). These carotenoids are incorporated directly into the fish muscle without further conversion (Hata & Hata, 1974). This pigmentation of the fish fillets can affect consumer acceptance: For example, in salmon, this leads to a higher willingness to pay for fillets with increased redness (Alfnes et al., 2006). However, algae-like spirulina were shown to cause a yellow coloration of the fillet colour in trout (Roohani et al., 2019; Teimouri et al., 2013). In Italian trout farms, an unusual yellow flesh coloration occurs during spring and summer times, induced by algae (*Cladophora glomerata*) resulting in high economic losses due to the reduced acceptability to consumers (Welker et al., 2001).

This study utilized three different salmonid species which were fed for 10 weeks with two experimental isoenergetic and isonitrogenous diets, containing either fishmeal or spirulina (*Arthrospira platensis*) as the main protein source. Therefore, rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta fario*), which are the three most important salmonid species for German aquaculture production (Brämick, 2019), were used. We hypothesized that the conversion of spirulina differs between species, regarding growth performance and product quality.

2 | MATERIALS AND METHODS

2.1 | Rearing of experimental fish

Fish eggs of rainbow, brook and brown trout were collected and fertilized in the experimental farm of the University of Goettingen in Relliehausen (Dassel, Germany) and transferred in plastic bags in a Styrofoam box to the Department of Animal Science in Göttingen (distance 44 km). Hatching took place in vertical incubators comprised with 10°C water. Larvae (full siblings) were reared in a recirculated aquaculture system and fed with commercial trout starter and fattening feed (BIOMAR, Denmark) until they reached the required body weight for the experimental trial. All three species were transferred into experimental tanks (250 L) one week before the experiment started to acclimate. Afterwards, the fish were divided into two experimental groups with $n = 60$ fish per treatment in three tanks (replicates) with $n = 20$ fish. All fish were fed, for 10 weeks, with two isoenergetic and isonitrogenous diets, based on the recommendation for rainbow trout from the National Research Council (2011), consisting of 20% fishmeal (FM100), whereas in the experimental group, the fishmeal was completely replaced by spirulina (SP100) (Table 1). Diet quantity was adjusted to 1% of the fish biomass (based on a previous study by Dietz et al., 2020) and fed once a day per hand (about 50% of the feed ration), and the rest was applied by an automatic feeder (FIAP GmbH, Germany). The rainbow trout were stocked first, followed two days later by the brook trout, and the brown trout seven weeks later, due to slower growth. The initial average body weight ± standard deviation of brook trout was 111.80 ± 8.92 g, rainbow trout was 100.8 ± 5.96 g and for brown trout 98.25 ± 9.76 g. All experimental fish were exposed to 14 h of light and 10 h of darkness. In order to keep the stocking density constant, dead fish were replaced with full siblings of a comparable body weight (±10 g) and tagged with a passive integrated transponder.

TABLE 1 Feed ingredients and approximate composition of FM100 and SP100 diets

Ingredient (% dry matter)	FM100	SP100
Fishmeal[a]	20.00	0.00
Spirulina[b]	0.00	20.00
Fish oil	10.70	10.70
Wheat meal	14.00	12.50
Wheat gluten	20.00	21.50
Soy protein concentrate[c]	20.00	20.00
Rapeseed oil	10.70	10.70
Vit./Min. Premix	1.00	1.00
$CaHPO_4$	1.00	1.00
Carboxymethyl Cellulose (Binder)	1.29	1.08
TiO_2 (Marker)	0.50	0.50
Fe_3O_4—black (Dye)	0.07	0.07
L-Lysin (HCl-Lys, 78% Lys)	0.70	0.90
D,L-Methionine	0.01	0.04
L-Tryptophan	0.03	0.01
Approximate composition (%)		
Dry matter	94.6	94.0
Crude protein (N × 6.25)	45.4	45.7
Crude lipids	24.6	23.9
N-free Extracts	17.5	19.0
Crude ash	7.1	5.4
Gross Energy [MJ/kg]	23.4	23.5
Digestible Energy [MJ/kg]	20.0	20.0

[a]Crude protein: 62% as is.
[b]Crude protein: 63% as is.
[c]Crude protein: 67% as is.

These fish were still used for growth parameters, but excluded from other analyses, since they were fed with a commercial trout fattening diet (BIOMAR, Denmark) in advance. Every two weeks, fish weight was recorded and rations were adjusted on the basis of biomass and feed conversion ratio (FCR). Water temperature and oxygen contents were recorded daily in the tanks with a handheld sensor (OxyGuard, Denmark). A colour scale for indicator solution UNISOL 410 (MACHEREY-NAGEL, Germany) was used weekly to measure the pH value. Ammonium and nitrite concentrations were measured photometrically by a NANOCOLOR 300 D (MACHEREY-NAGEL, Germany). The mean water temperature was 16.82 ± 0.69°C with a mean oxygen saturation of 92.21 ± 0.03% and a mean oxygen content of 8.75 ± 0.30 mg/L. The mean pH value was 7.42 ± 0.36 as well as low amounts of ammonium and nitrate with 0.06 ± 0.03 and 0.09 ± 0.08 respectively.

2.2 | Sampling of experimental fish

120 fish per species were anaesthetized with a sharp blow to the head and killed by exsanguination at the end of the 10-week feeding experiment. Body weight and length (fork length) were recorded for all experimental fish. Due to the large number of fish, sampling took place on two consecutive days. For product quality measurements, all fish were filleted and the right side of the fillet was frozen at −20°C and the left side at −80°C until further processing.

2.3 | Colour measurements

In order to maintain consistency and remove any storage effects the colour was measured immediately after slaughtering the fish, skin and fillet colour parameters were measured on a white filleting board with a CM-600d spectrophotometer (KONICA MINOLTA, Japan) with following settings: illuminant D65, two degrees observer and a measuring unit of 10 mm in diameter. Skin colour was measured on three points on each side of the fish: between the head and dorsal fin, below the dorsal fin and below the adipose fin (Figure 1). For the fillet colour, skinless fillets were cleaned with tap water and measured on three points on the internal surface of the dorsal fish muscle: between the head and dorsal fin, below the dorsal fin and below the adipose fin (Figure 2). Colour values based on the CIELAB system (CIE, 1977) and displayed as lightness (L^*), red/green (a^*) and blue/yellow (b^*). Chroma (C^*) describes the colour saturation and was calculated as follows:

$$C^* = \sqrt{a^{*2} + b^{*2}};$$

$h°$ describes the colour appearance and was calculated as follows:

$$h^\circ = \arctan\left(\frac{b^*}{a^*}\right).$$

2.4 | Colour stability and cooking loss

120 fillets (right side) were thawed for 24 h at 4°C, then brought to room temperature. Before the cooking process, fillets were weighed and put in plastic bags and then boiled in a water bath at 78°C until the core temperature reached 70°C. Released fluids were removed using paper tissues and the fillet weight was once again determined when the cooked fillets had reached room temperature. Cooking loss was calculated as follows:

$$\text{Cooking loss [\%]} = \frac{(\text{initial weight [g]} - \text{cooked weight [g]})}{\text{initial weight [g]}} * 100$$

Afterwards, fillet colour was measured again as described previously for skinless fillet.

2.5 | Shear force

Cooked fillets were cut with a template into rectangular probes matching the blade holder frame, and the weight of each probe was determined. The myomeres of the sample were placed parallel to the shear blades. A 5-blade Allo-Kramer shear cell (Stable Micro Systems Ltd., Surrey, UK), which was mounted to a TA.XT Plus Texture Analyser (Stable Micro System Ltd., Surrey, UK) with a 50-kg load cell, was used with following settings: pre-test speed of 5 mm/s, test speed of 2 mm/s, post-test speed of 10 mm/s (Aussanasuwannakul et al., 2010) and triggering force of 1000 g.

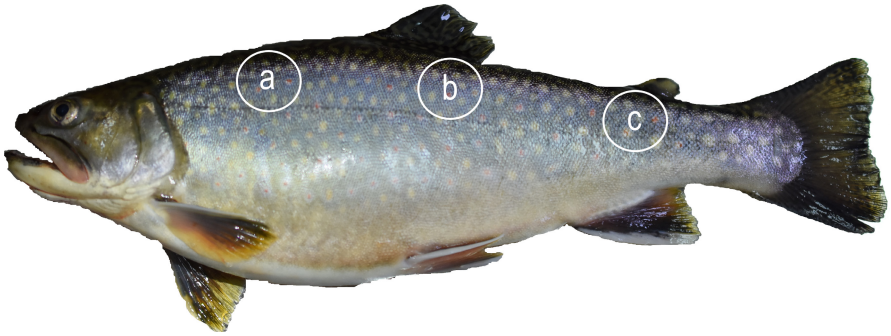

FIGURE 1 Fish skin colour measurement locations. (a) Between the head and dorsal fin, (b) below the dorsal fin and (c) below the adipose fin.

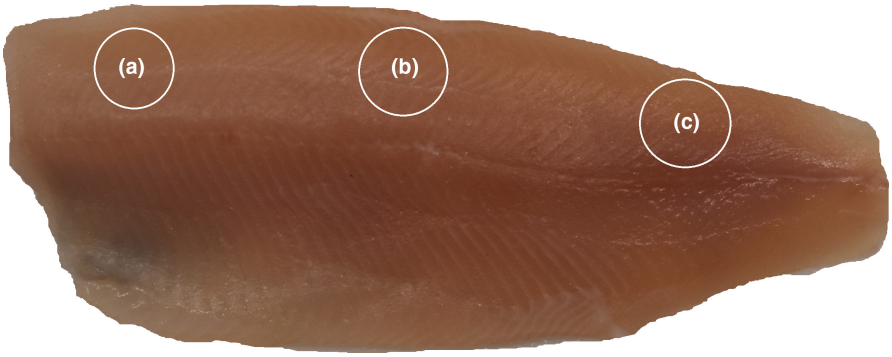

FIGURE 2 Fillet colour measurement locations. (a) Between the head and dorsal fin, (b) below the dorsal fin and (c) below the adipose fin.

2.6 | Fatty acids

40 fish per species (20 per treatment) were used for fatty acid analyses. Fish fillets and feed samples were freeze-dried overnight. Fillets were weighed before and after dry-freezing to calculate the water content. Then, freeze-dried fillets and feed were minced with an EGK 200 spice and coffee grinder. The samples were stored in hermetically sealed boxes in the refrigerator until further processing the next day. Gas chromatography Flame Ionization Detector (GC-FID) analysis of fatty acid methyl esters (FAMEs) for fish and feed samples was conducted as described by Rosenau et al. (2021).

2.7 | Statistical analysis

R was used for statistical analysis (R Core Team, 2020). The visualization of the data was performed with ggplot2 (Wickham, 2016) and factoextra (Kassambara & Mundt, 2020) package. A principal component analysis (PCA) was computed on standardized data (i.e., to mean = 0 and standard deviation = 1) such as the PCA is merely based on correlations of the studied variables. Normality was checked visually with quantile–quantile plot (Aldor-Noiman et al., 2013). Fixed effects of species, diet and their interaction on performance and product quality traits were analysed by two-way ANOVA with subsequent Tukey's honestly significant difference test for mean differences when appropriate (Barros, 2013). A multiple linear regression model was calculated (Stats and R, 2021) to observe interactions between final weight, species, diet and initial fish weight with the following equation:

$$y_{ikl} = \mu + S_i + S_i(T_k) + S_i(W_l) + e_{ikl};$$

with y_{ikl} being the final body weight in gram, S_i the fixed effect of species (rainbow trout and brook trout), T_k fixed effect of the type of diet (FM100 and SP100), and W_l as the regression of the initial tank weight mean, both nested within species and e_{ikl} the residual error per individual.

3 | RESULTS

3.1 | Performance

The brown trout had accepted the fishmeal diet but not the spirulina diet, causing a weight loss in the spirulina groups after two weeks. We aborted the trial for this species due to animal welfare concerns. However, the experimental diets were well received by the brook and rainbow trout. Results are presented in Figure 3 and Table S1. The initial body weight of brook and rainbow trout groups differed significantly between species ($p < 0.05$). A higher final body weight was observed in FM100 brook trout group (298.03 ± 3.61 g) than in SP100 brook trout group (250.12 ± 4.73 g) and rainbow trout FM100 (226.47 ± 2.29 g) and SP100 (201.70 ± 0.44 g) groups respectively. Final weight and weight gain showed a significant species–diet interaction ($p < 0.05$). Length, specific growth rate (SGR) and FCR showed a statistically significant difference between species and diets respectively ($p < 0.05$). The overall FCR was low (=efficient) across all groups. We were able to find lower FCR values for FM100 than for SP100 groups ($p < 0.05$), but no significant interaction of species and diet was observed ($p > 0.05$).

A multiple linear regression was calculated to predict the final body weight based on species, diet and initial fish weight (Figure S1). A significant regression equation was observed ($F[5, 234] = 42.99$, $p < 0.05$) with an R^2 of 0.479. Predicted final weight for brook trout and rainbow trout is equal to 412.59–148.31 (species rainbow trout)—45.15 (brook trout SP100)—24.36 (rainbow trout SP100)—1.04 (brook trout tank weight)—0.38 (rainbow trout tank weight), where final weight is measured in gram. The dietary treatment for brook trout and rainbow trout were significant predictors of final weight ($p < 0.05$).

3.2 | Colour parameters

Species–diet interactions were observed for a^*, b^* and C^* values in all treatment groups ($p < 0.05$). A more intense yellow/orange fillet colour was observed visually in spirulina-fed fish (Figure 4). The photometric data (Table 2) show that redness and yellowness increased

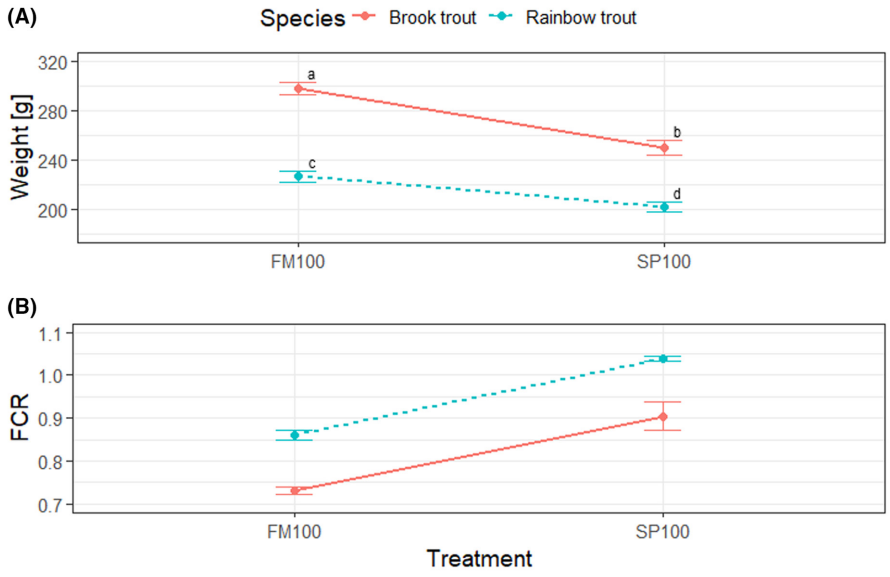

FIGURE 3 Line chart of estimated mean with standard error of performance parameters for brook trout and rainbow trout groups fed ten weeks FM100 and SP100 diets. Body weight (A) is calculated from every fish ($n = 120$ per species) and feed conversion ratio (B) are means of triplicate groups. Different letters in the same plot are significantly different at a level of $p < 0.05$ (Tukey's test).

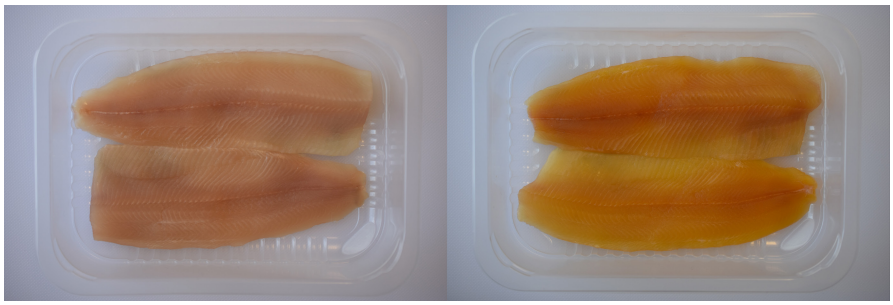

FIGURE 4 Rainbow trout fillets fed for ten weeks with FM100 (left) and SP100 (right).

the skin of brook trout for SP100 diet ($p < 0.05$), whereas the diet had no significant influence on all skin colour parameters in rainbow trout ($p > 0.05$). The fillet redness, yellowness and chroma increased due to the spirulina supplementation in both species ($p < 0.05$). Yellow and red coloration was higher in brook trout fed with SP100 than in rainbow trout fed with SP100 diet ($p < 0.05$). Yellow coloration increased after the cooking process of the fillet for all groups, whereas redness slightly decreased in SP100 groups. However, most of the significant differences between the two diets in brook and rainbow trout are also displayed in the cooked fillets. In cooked fillets, no significant difference was observed between species fed with FM100 diet ($p > 0.05$).

3.3 | Water content and cooking loss

The water content was similar between species and diets (Table 3), and no significant effects were observed ($p > 0.05$). Mean cooking loss was higher in brook trout than in rainbow trout ($p < 0.05$). Statistical differences were observed between species and diet, resulting in higher cooking loss for SP100 fed fish ($p < 0.05$).

3.4 | Shear force

Results show that the fillet of brook trout ($n = 116$) is more tender than rainbow trout fillet ($n = 120$) ($p < 0.05$). Also the species–diet interaction had an impact on the tenderness of the fillet ($p < 0.05$). In brook trout, the spirulina-fed fillets were less tender with $0.79 \pm 0.11\,kg^{*}g^{-1}$ than control group with $0.71 \pm 0.17\,kg^{*}g^{-1}$ ($p < 0.05$). The opposite effect was observed in rainbow trout with more tender fillets in the SP100 group ($0.96 \pm 0.14\,kg^{*}g^{-1}$) than in FM100 group ($1.04 \pm 0.21$) ($p < 0.05$).

3.5 | Fatty acids

The most abundant fatty acids in the fish muscle were docosahexaenoic (C22:6n3; DHA), oleic (C18:1), palmitic (C16:0), eicosapentaenoic (C20:5n3; EPA) and linoleic acid (C18:2n6c) (Figure 5 and Table S2). Species showed significant differences for C16:0, DHA and EPA ($p < 0.05$), while diet, that is replacement of fishmeal with spirulina affected all of the most abundant fatty acids ($p < 0.05$). DHA and C16:0 content decreased significantly due to the spirulina feeding ($p < 0.05$). In general, SP100 diet lowers the EPA content in

TABLE 2 Colour parameter of skin, fillet and cooked fillet of FM100 and SP100 diet in brook trout ($n = 116$) and rainbow trout ($n = 120$)

	Brook trout		Rainbow trout		*p*-values		
	FM100	SP100	FM100	SP100	Species	Diet	Species × diet
Skin colour							
L^*	60.23 ± 4.43	58.81 ± 4.18	58.96 ± 5.89	58.6 ± 5.37	ns	ns	ns
a^*	0.88 ± 0.63^{c}	1.88 ± 0.57^{a}	1.48 ± 0.94^{b}	1.63 ± 0.97^{ab}	ns	***	***
b^*	0.07 ± 1.53^{c}	2.64 ± 1.62^{b}	4.08 ± 1.27^{a}	4.34 ± 1.74^{a}	***	***	***
C^*	2.93 ± 0.72^{c}	4.18 ± 1.08^{b}	5.07 ± 0.90^{a}	5.43 ± 1.35^{a}	***	***	***
$h°$	192.87 ± 57.04^{a}	114.22 ± 51.49^{b}	87.21 ± 31.65^{c}	80.5 ± 21.01^{c}	***	***	***
Raw fillet							
L^*	48.87 ± 1.76	46.8 ± 1.84	47.86 ± 1.48	46.5 ± 2.27	*	***	ns
a^*	0.77 ± 1.18^{c}	7.19 ± 1.87^{a}	0.33 ± 0.68^{c}	4.29 ± 1.46^{b}	***	***	***
b^*	11.78 ± 1.25^{c}	23.6 ± 3.39^{a}	9.45 ± 1.01^{d}	17.3 ± 2.73^{b}	***	***	***
C^*	11.90 ± 1.34^{c}	24.7 ± 3.72^{a}	9.60 ± 1.00^{d}	17.9 ± 2.92^{b}	***	***	***
$h°$	87.12 ± 5.08	73.5 ± 2.74	89.26 ± 3.96	77.4 ± 3.66	***	***	ns
Cooked fillet							
L^*	82.03 ± 1.58	80.8 ± 2.83	81.43 ± 1.45	80.8 ± 1.25	ns	***	ns
a^*	1.16 ± 0.92^{c}	4.63 ± 1.79^{a}	0.68 ± 0.62^{c}	2.17 ± 1.00^{b}	***	***	***
b^*	17.11 ± 1.15^{c}	29.6 ± 5.55^{a}	16.12 ± 1.10^{c}	23.0 ± 2.87^{b}	***	***	***
C^*	17.18 ± 1.21^{c}	30.0 ± 5.64^{a}	16.16 ± 1.11^{c}	23.2 ± 2.93^{b}	***	***	***
$h°$	86.30 ± 2.76	83.0 ± 12.55	87.76 ± 2.13	85.0 ± 2.04	*	***	ns

Note: L^* (lightness), a^* (red/green), b^* (yellow/blue), C^* (chroma) and $h°$ (hue angle). Values are means ± SD, followed by different letters in the same row are significantly different at a level of $p < 0.05$ (Tukey's test).
***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

TABLE 3 Water content ($n = 80$) and cooking loss ($n = 236$) of FM100 and SP100 diet in brook trout and rainbow trout

	Brook trout		Rainbow trout		*p*-values		
Parameter	FM100	SP100	FM100	SP100	Species	Diet	Species × diet
Water content [%]	74.05 ± 0.64	75.16 ± 1.52	73.90 ± 1.35	74.13 ± 2.06	ns	ns	ns
Cooking loss [%]	11.67 ± 1.66	13.78 ± 1.92	8.89 ± 1.48	10.24 ± 2.51	***	***	ns

Note: Values are means ± SD.
Abbreviation: ns, not significant.
***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

the fish muscle for brook and rainbow trout ($p < 0.05$). C18:2n6c was higher in SP100 group than in FM100 ($p < 0.05$), and C18:1 did not show any statistical differences between species ($p > 0.05$), but between experimental diets ($p > 0.05$). Saturated fatty acid (SFA) were significantly influenced by species and diet ($p > 0.05$), while monounsaturated fatty acids (MUFA) and PUFA were affected only by diet. SFA and MUFA content showed a significant increase and PUFA levels were reduced in SP100 group ($p > 0.05$). Both species responded similarly to the diets in terms of the omega-6 fatty acid (n6), omega-3 fatty acid (n3) content and n6/n3 ratio, leading to statistical differences between experimental diets ($p < 0.05$).

The fatty acid content in the experimental diets was characterized by higher values of SFA in SP100 with 29.47 ± 0.44% than in FM100 with 22.86 ± 0.01% (Table 4). In SP100, MUFA accounted for half (50.69 ± 0.38%) of the fatty acids, while in FM100, the amount of MUFA was lower (43.79 ± 0.26%). Overall, the proportion of PUFA was higher in the FM100 diet (33.23 ± 0.27%) than in SP100 (19.77 ± 0.06%). Also noticeable was a reduced DHA and EPA content in SP100 diet.

3.6 | Principal component analysis

PCA plot (Figure 6) implies that colour parameters of the raw and cooked fillet had a stronger influence on the descriptive characteristics than the skin colour. Also, fatty acid profile contributes to the distinction between the diets. Performance parameters indicated only a low explanatory contribution. Product quality traits,

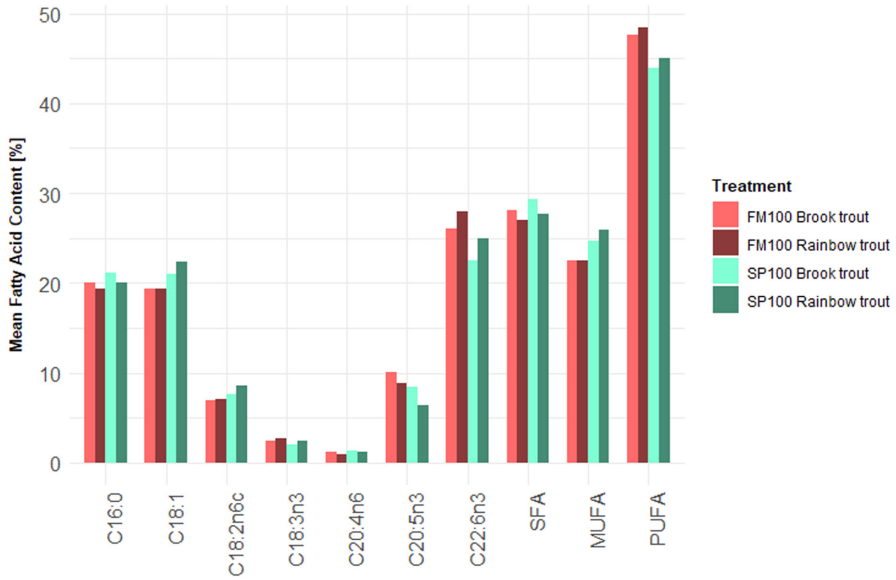

FIGURE 5 Most abundant fatty acids (%) in fish muscle of brook trout ($n = 40$) and rainbow trout ($n = 40$) fed with FM100 and SP100 diet; SFA: saturated fatty acids, MUFA: monounsaturated fatty acids, PUFA: polyunsaturated fatty acids, n6: mega-6 fatty acids, n3: omega-3 fatty acids.

especially colour and fatty acids, are main factors distinguishing between FM100 and SP100 groups. The SP100 groups are associated with increased fillet colour values for red (a^*) and yellow (b^*), whereas the FM100 groups are associated with higher PUFA and n3 levels. It is also notable that the variability in the SP100 groups is higher than in FM100 groups as to be seen from the size of the confidence ellipses.

4 | DISCUSSION

While brook and rainbow trout accepted the experimental spirulina diet, it led to uneaten food particles and a decline in mean body weight of the brown trout. Since the FM100 diet had been eaten by the brown trout, we considered that brown trout may have an aversion to the flavour of the diet. The trial was aborted for brown trout due to animal welfare concerns. Brook and rainbow trout showed overall reduced growth performance in response to the spirulina supplementation. In a multiple linear regression model, we observed that the significant predictor for final weight was the dietary treatment and the slight differences in the initial body weight did not affect the final weight. In that way, we were able to show that brook trout had a higher growth rate and were stronger influenced by the spirulina diet. The feed conversion was efficient in all groups in accordance with previously observed data from studies examined by Teles et al. (2019) for brook and rainbow trout. Brook and rainbow trout fed with FM100 diet showed to the same extent a significantly lower FCR than the SP100 group. This observation could be explained by the fact that part of the chemical composition of microalgae is indigestible by non-ruminants. It is estimated that 10% of the microalgae consist of cell walls, which are not degradable by the fish gastrointestinal tract (Becker, 2007; Coelho et al., 2020). Current technological approaches to destroy cell walls in order to increase the digestibility of the material have so far only been used for human consumption (Makkar et al., 2016). Further studies would be necessary to see whether such technologies could also be used in the aquaculture sector.

Moreover, it was noticed that especially in spirulina-fed brook trout, the variance was high in final growth, indicating that some fish are either quite effective in converting the spirulina proteins into biomass or some fish had a higher acceptance for the diet, resulting in a significantly higher feed intake. Even though we worked with full siblings, genetic effects of the implementation of the spirulina cannot be excluded for both species. Selective breeding programs could be the key for an improved implementation of alternative protein sources (Le Boucher et al., 2012; Verdal et al., 2018), since some fish seem to use the spirulina protein more effectively.

As expected, colour parameters changed to more yellow and red pigments, induced by the Spirulina carotenoids. About 10% of the total carotenoids of young trout are stored in the skin (No & Storebakken, 1991). We were able to observe a shift towards more red and yellow coloration in the skin of brook trout, but we were not able to find any statistical differences in rainbow trouts' skin. Other parameter like luminosity were also unaffected by species or diet. Differences in chroma und hue were only observed in brook trout. This is contrary to previous reports on trout (Roohani et al., 2019; Teimouri et al., 2013), where a low-level spirulina supplementation led to a significant increase in red and yellow skin colour. Since the pigments are mainly found along the lateral line of trout (Storebakken & No, 1992), it is possible that our measurement of the skin was not performed at the location with the most carotenoids. Another reason for this effect could be due to a different carotenoid metabolism or differences in the amount of lipids in the skin, since carotenoids tend to be linked to a higher lipid content in salmonid fish (Bjerkeng et al., 1997; Einen & Roem, 1997; Jensen et al., 1998). The pigment deposition, due to carotenoid in the feed, depends also on genetic factors (Blanc & Choubert, 1985; Torrissen & Naevdal, 1984). With all variables considered, we are not able to

TABLE 4 Fatty acid content (%) in FM100 and SP100 diet

Fatty acid	FM100	SP100
C6:0	0.00 ±0.00	0.29 ±0.07
C8:0	0.02 ±0.00	0.07 ±0.01
C10:0	0.01 ±0.00	0.01 ±0.00
C11:0	0.00 ±0.00	0.02 ±0.00
C12:0	0.08 ±0.01	0.09 ±0.01
C13:0	0.02 ±0.00	0.02 ±0.00
C14:0	4.15 ±0.14	5.25 ±0.27
C14:1	0.02 ±0.00	0.01 ±0.00
C15:0	0.25 ±0.01	0.29 ±0.01
C15:1	0.00 ±0.00	0.00 ±0.00
C16:0	13.56 ±0.05	18.78 ±0.23
C16:1	4.30 ±0.09	5.42 ±0.16
C17:0	0.19 ±0.00	0.25 ±0.02
C17:1	0.78 ±0.04	0.38 ±0.01
C18:0	2.88 ±0.07	3.41 ±0.10
C18:1	36.96 ±0.34	43.00 ±0.48
C18:2n6c	15.47 ±0.11	13.02 ±0.14
C18:3n6	0.14 ±0.02	1.41 ±0.08
C18:3n3	4.74 ±0.05	2.11 ±0.04
C20:0	0.34 ±0.01	0.42 ±0.02
C20:1n9	1.67 ±0.00	1.76 ±0.04
C20:2	0.11 ±0.01	0.07 ±0.00
C20:3n6	0.06 ±0.00	0.09 ±0.01
C20:4n6	0.50 ±0.01	0.19 ±0.02
C20:3n3	0.05 ±0.00	0.02 ±0.00
C20:5n3	7.79 ±0.11	1.80 ±0.14
C22:0	0.20 ±0.01	0.18 ±0.01
C22:1	0.07 ±0.0.00	0.12 ±0.01
C22:2	0.00 ±0.00	0.03 ±0.01
C23:0	0.31 ±0.00	0.10 ±0.01
C24:0	0.85 ±0.02	0.27 ±0.01
C22:6n3	4.48 ±0.07	1.10 ±0.06
C24:1n9	0.00 ±0.00	0.00 ±0.00
SFA	22.86 ±0.01	29.47 ±0.44
MUFA	43.79 ±0.26	50.69 ±0.38
PUFA	33.23 ±0.27	19.77 ±0.06
n6	16.16 ±0.12	14.71 ±0.20
n3	17.07 ±0.16	5.03 ±0.25
n6/n3	0.95 ±0.00	2.92 ±0.18

Note: Values are means of three replicates ± SD.

Abbreviations: MUFA, monounsaturated acids; n6/n3, omega-6, omega-3 fatty acid ratio; PUFA, polyunsaturated fatty acids; SFA, saturated fatty acids.

make an accurate statement about the different colouring effect of yellow and red pigments in the skin of the experimental fish. In order to further elucidate the colouring effect, further investigations of the carotenoid content in the skin would be necessary.

The fillet colour is an important product quality criterion for salmonid fish (Christiansen et al., 1995). In European countries, trout fillet is preferred as white or red/pink. In the present study, however, the spirulina-fed fish increased significantly in yellow fillet coloration. Our investigation confirms previous results for trout (Roohani et al., 2019; Teimouri et al., 2013). Fish fed the fishmeal diet were not distinguishable by coloration of the cooked fillet, but the yellow coloration was also displayed in both species. During the cooking process, yellow colour values increased due to the cooking process. It is suspected that carotenoids from spirulina are heat stable up to 70°C as previously described for catfish (Rosenau et al., 2021). To what extent consumers may reject the product due to the yellow fillet coloration is largely unknown. A recent study from Altmann et al. (2022) on chicken breasts, produced using spirulina as feed, showed that mainstream consumers rejected the product, due to the altered colour. However, they were able to reduce this effect by providing information. Therefore, it should be noted that this unusual colour could also be used as a sustainability quality mark. Still, it remains questionable, whether consumers have enough knowledge about fish nutrition to understand the complexities of sustainable aquaculture. In this context, a consumer-specific marketing would be necessary.

Cooking loss and firmness are important characteristics of product quality (Brinker & Reiter, 2011). Fifty-two to 82% of the fish muscle consist of water (Petricorena, 2015). During the cooking process, liquid components leak out of the fillet. Low levels of fluid loss through cooking can lead to a higher solubilization of intramuscular collagen-based tissue, and consequently to a more tender fillet (Pathare & Roskilly, 2016). Herein, cooking loss in rainbow trout was in accordance with the literature (Secci et al., 2019), while there are no data currently available for brook trout. We were able to find a dietary effect on the cooking loss in both species, resulting in significantly higher water loss in spirulina-fed fish in both species. The investigation of Dallaire et al. (2007) demonstrates that algae-fed trout fry have an increased water content in the carcass. The authors explain this observation with a lower protein and lipid content in the diet, leading to reduced lipid content in the muscle. Lower lipid content was observed for several other species fed with spirulina diets (Mustafa et al., 1994; Nandeesha et al., 1998; Teimouri et al., 2016). Accordingly, this lower lipid content is associated with a higher water content in the fish muscle (Guillaume & Watson, 2001).

Shear force is an important tool to estimate the tenderness of a product. Brook trouts were generally more tender than rainbow trouts. However, we found an opposite effect of spirulina supplementation on the tenderness of fillets. While brook trout fed with SP100 were more tender, rainbow trout fed with SP100 were less tender in comparison with the FM100 diet. One influence on this aspect could be the previously described water content of the fish muscle, which tends to increase in spirulina-fed fish, but values were neither significantly different in brook trout nor in rainbow trout.

Fish is the major source for essential fatty acids in human nutrition and provide high amounts of EPA and DHA (Taşbozan & Gökçe, 2017). Omega-3 fatty acids are known to reduce myocardial

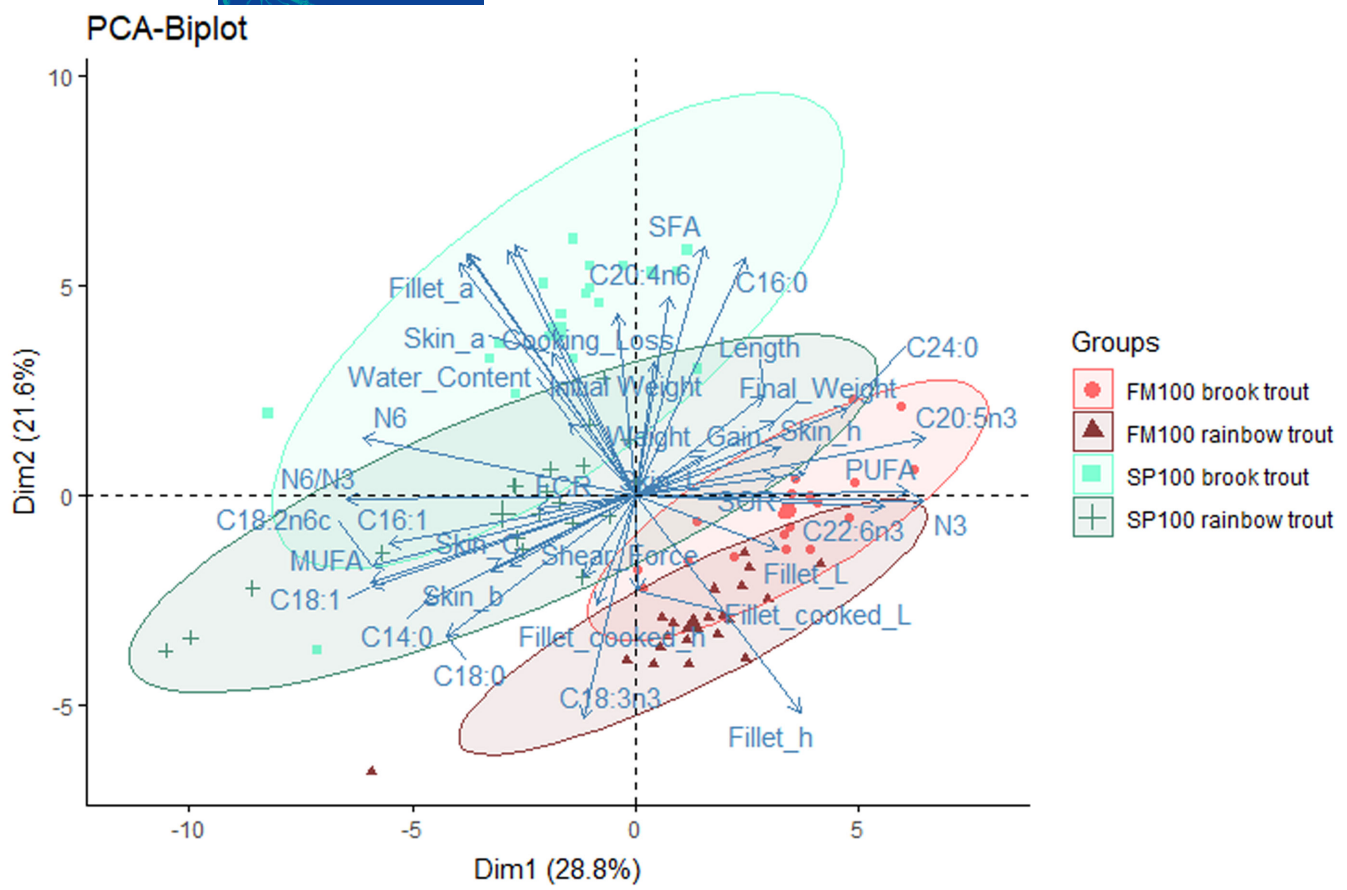

FIGURE 6 PCA biplot of performance parameters, colour parameters, cooking loss, water content, shear force and most frequent fatty acids for rainbow trout and brook trout fed with FM100 and SP100 diet.

infarction and coronary heart disease and therefore they are of great importance for human health (Zheng et al., 2012). However, the fatty acid profile of fish is highly species specific (Passi et al., 2002) and that is why we expected changes in the fatty acid profile between species, and it also varies due to diet. Results show slight differences between species and strong differences between diets. Due to the spirulina supplementation, important fatty acids like EPA decreased in both species, but DHA decreased only in brook trout. Overall, SFA was increased and PUFA decreased significantly in SP100 fed brook trout, while MUFA was not affected at all. Even though the fatty acid composition tended to react similarly to the spirulina diet than the brook trout; we were unable to find statistically significant differences in SFA and MUFA for rainbow trout, but we observed a significant reduction in PUFA. This might be an indicator that because of the lower final body weight of the rainbow trout, the differences were not represented clearly enough in the fatty acid pattern.

The fatty acid pattern of the flesh reflected the fatty acid pattern of the diet. Even though DHA and EPA levels are very low in the SP100 feed, this difference was not observed in the muscle. Also, PUFA levels were quiet low in the feed, but still high after 10 weeks of feeding. Previous studies showed that rainbow trout are able to synthesize long-chain PUFAs up to a certain amount by regulating hepatic expression fatty acyl desaturase (Gregory et al., 2016; Hixson et al., 2014). Furthermore, n6/n3 ratio was still below the recommended level of five in the fish muscle (Elvevoll & James, 2000). In previous studies with trout, the amount of beneficial PUFA with low-level spirulina supplementation increased (Roohani et al., 2019; Teimouri et al., 2016). With increasing exchange rates of fishmeal with spirulina, this effect was reversed (Jafari et al., 2014), indicating that spirulina supplementation could be limited to a certain extent to avoid unwanted reduction of desirable PUFA. It remains unknown, whether long time feeding with high exchange rates might lead to an even stronger reduction of PUFA.

Overall, the main performance and product quality characteristics were influenced by the diet. Especially colour parameters and fatty acid content differed significantly between treatments. It must be emphasized that the variability in these variables was higher in the spirulina-fed fish than in the control fish. It is possible that the experimental fish were genetically adapted to the fishmeal diet due to selection in the aquaculture facility, as the conventional diets contain high proportions of fishmeal. Both tested species reacted in a similar way to the spirulina supplementation. Finally, sole use of spirulina as the main protein source still leads to acceptable growth performance, but product quality traits were strongly affected too. In the end, possible ways to compensate the losses in production could be achieved by a marketing scheme that addresses sustainability of fish production, but it remains unclear, if the consumer would accept the alteration in fillet colour.

5 | CONCLUSION

For a sustainability transition of aquaculture production, replacing traditional protein sources like fishmeal is paramount. Our study shows that the conversion of spirulina differs in some growth and production traits between species. A total replacement of fish meal with spirulina was accepted by brook trout and rainbow trout, but not by brown trout; we hypothesize that the brown trout had an aversion to the flavour of the spirulina diet. A complete replacement of fishmeal with spirulina comes along with reduced growth performance and feed efficiency. Yet, growth performance observed in brook trout and rainbow trout is considered acceptable. A species–diet interaction was found for final weight and weight gain, but not for the feed conversion. Total replacement of fishmeal reduced PUFA and n-3 fatty acid levels, which is regarded a disadvantage from a human health perspective. The spirulina-induced change in fillet coloration towards a strong yellow may have an impact on the consumer acceptance, but might also be a chance for marketing. Based on the presented investigation, we plan to conduct a consumer study, to get more insights on the consumer preferences.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTIONS

Simon Rosenau: Conceptualization; Methodology; Visualization; Formal Analysis; Investigation; Writing – Original Draft. **Marco Ciulu:** Methodology; Writing – Review & Editing. **Christian Reimer:** Formal Analysis; Validation, Writing – Review & Editing. **Alexander Charles Mott:** Writing – Review & Editing. **Jens Tetens:** Resources; Writing – Review & Editing; Project administration. **Daniel Mörlein:** Resources; Writing – Review & Editing; Supervision; Project administration.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS CLEARANCE

All animal work followed relevant national guidelines. Good veterinary practice was applied to all procedures. The study is in accordance with the German legal and ethical requirements of appropriate animal procedures. The experiment was approved by the Institutional Animal Welfare Body (no. T2-2019, 27.06.2019).

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