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Realised genetic gains on growth, survival, feed conversion ratio and quality traits after ten generations of multi-trait selection in rainbow trout *Oncorhynchus mykiss*, fed a standard diet or a "future" fish-free and soy-free diet

Marc Vandeputte [a,b,*], Geneviève Corraze [c], Jérôme Doerflinger [d], Florian Enez [e], Frédéric Clota [a,b], Frédéric Terrier [c], Mathilde Horat [d], Laurence Larroquet [c], Vincent Petit [d], Pierrick Haffray [e], Sandrine Skiba-Cassy [c], Mathilde Dupont-Nivet [b]

[a] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, INRAE, Palavas-Les-Flots, France
[b] Université Paris-Saclay, INRAE, AgroParisTech, GABI, Jouy-en-Josas, France
[c] INRAE, Univ. Pau & Pays Adour, E2S UPPA, NUMEA, Saint-Pée-sur-Nivelle, France
[d] Les Sources de l'Avance, Pissos, France
[e] SYSAAF, Station LPGP-INRAE, Rennes, France

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ABSTRACT

There is limited scientific evidence on the real impact of selective breeding in aquaculture on the medium term, while the composition of aquafeeds is rapidly evolving towards plant-based raw materials. We compared a rainbow trout line selected in freshwater for fillet production (improved growth, carcass yield and fillet fat) for ten generations (G10) with an unselected control line from the same base population (G0). We crossed G10 and G0 neomales to the same G10 females, thus creating a Selected and a Control group expected to diverge by half the true difference between G0 and G10. Those were grown to 1.6 kg, and two feeds were compared across the two lines from 264 to 374 days post-hatching. One was a commercial standard, the second was a "future" feed devoid of fishmeal, fish oil and soy-based products, with microalgae as a source of docosahexaenoic acid (DHA). After doubling the difference between the Selected and the Control to estimate the true performance of G0, we saw that G10 was improved relative to G0 for body weight (+61%), feed conversion ratio (−17 to −20%), fillet fat (+28–53%) and carcass yield (+4.2%), but not for fillet yield. Survival was not affected by selection. Both feeds had a similar performance in terms of growth, but the future feed showed a higher FCR, probably due to a feed intake measurement issue. Fish had a good EPA+DHA content (>1.2 g/100 g wet weight) with both feeds, partly linked to endogenous synthesis of these fatty acids. There was little if any genotype by feed interaction. This study shows that selective breeding can produce fast growing, feed efficient and thus provide opportunity for more sustainable fish culture. We showed that highly nutritious fish can be produced with good growth performance without using any fish meal, fish oil or soy-based product.

1. Introduction

Selective breeding, together with nutrition and optimisation of farming practices, can be considered one of the key technologies to improve the profitability and sustainability of aquaculture production. Indeed, in terrestrial livestock production, it has been shown to produce massive long-term performance gains (up to ten times higher body weight and doubling of meat yield at the same age in poultry, see e.g. Havenstein et al., 2003; Nestor et al., 1996), and is likely the main driver of the more than half reduction of the carbon footprint per kg of milk observed in the US dairy sector between 1944 and 2007 (Capper et al., 2009).

In aquaculture, selective breeding is relatively new, as real optimised breeding programmes only date back to the 1970's in salmonids (Gjedrem, 2010; Kincaid et al., 1977), and to the 1990's or later for most other species (Neira, 2010; Rye et al., 2010). While there are a number of

* Corresponding author at: MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, INRAE, Palavas-Les-Flots, France.
E-mail address: Francemarc.vandeputte@inrae.fr (M. Vandeputte).

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reports of selection response for faster growth (higher body weight at a given age) in aquaculture species, with 67 studies reviewed by Gjedrem and Rye (2018), they were generally done on a short time scale (2.8 generation on average). For the other 23 traits mentioned in this review, which include body length, fat content, processing yields, survival, resistance to specific diseases, reproduction traits and colour traits, the number of estimates per trait is much smaller (one to five), with also a limited time scale (one to five generations).

Still, growth rate is not the only trait selected for in fish, and while it is part of the breeding goal in virtually all breeding programmes (Chavanne et al., 2016), it may be more for the ease of its improvement than for real economic gains, as it increases the quantity produced but has no direct effect on production efficiency (Besson et al., 2017, 2014; Gjedrem, 2012). One of the most important traits for aquaculture profitability and sustainability is feed efficiency (i.e. kg of body weight gain per kg of ingested feed), for which no direct selection is applied in practice, due to the inability to precisely record individual feed intake in fish over a long period of time (de Verdal et al., 2018a). While recent developments now make this perspective more realistic (Besson et al., 2019; de Verdal et al., 2018b; Dvergedal et al., 2019), the main way with which fish breeders expect to improve feed efficiency by selective breeding in practice is through selection for growth rate, with the hypothesis that faster growing fish will be more efficient (Besson et al., 2020; Kause et al., 2006; Knap and Kause, 2018). Still, very few selection response studies have investigated the correlated response in feed efficiency to selection for growth. Two of them show positive results, with improved feed conversion ratio (FCR) in fast-growing fish lines (Thodesen et al., 1999; Yamamoto et al., 2015), while the other two show no response in feed efficiency (Ogata et al., 2002; Sanchez et al., 2001). Thus, further investigation of the link between selection for growth and feed efficiency is needed.

Apart from growth and feed efficiency, many other traits are also part of the breeding goals in fish, including morphology, disease resistance, survival, processing yields and product quality, which are present, alone or combined, in more than 30% of the breeding programmes in the EU (Chavanne et al., 2016). Morphology can be important to improve processing yields (Blay et al., 2021a; Haffray et al., 2013; Prchal et al., 2018; Sang et al., 2009; Vandeputte et al., 2019) but also to improve consumer acceptance (Colihueque and Araneda, 2014; Kause et al., 2003). Disease resistance and general survival are also key traits for profitability and sustainability, which can be linked to growth rate, although the sign of their correlation with growth rate can vary a lot (Yáñez et al., 2014). Finally, product quality is also important for consumers, and a key quality parameter is fillet fat percentage, which influences taste, texture and smoking ability of the fish fillet (Mørkøre et al., 2001).

Fish nutrition is also a key driver of production efficiency in aquaculture, for which considerable progress has been achieved over the last decades. However, fish nutrition also has to deal with pressing constraints. While in the 1980's, the raw materials of choice for fish feed were fishmeal and fish oil produced from specialised marine fisheries, the growth of aquaculture, combined with the stagnation of fisheries captures for fishmeal and fish oil production, led to a shortage of these ingredients, which became unsustainable (Naylor et al., 2009). To remain sustainable and maintain acceptable production cost, aquaculture feed production initiated a rapid shift from these fish-based products to various alternative ingredients, such as plant proteins and oils, and processed animal products, as well as more recently to novel ingredients such as single-cell proteins, microalgae and insect meals (Hua et al., 2019). Soybean-derived raw materials are an important contributor to these current diets, but are now being challenged as environmentally unsustainable (Fearnside, 2001). This change in ingredients has consequences on fish growth and health, as well as on their nutrient composition. This is especially true for omega-3 long-chain polyunsaturated fatty acid (LC-PUFA) such as EPA (eicosapentaenoic acid) and DHA (docosahexaenoic acid), which are mostly absent from terrestrial ingredients (Gladyshev et al., 2013; Napier et al., 2020; Tocher, 2015), and for which fish have a relatively low endogenous synthesis capacity from the shorter omega-3 fatty acids present in vegetable oils (Colombo et al., 2018). Thus, it is important to provide adequate omega-3 LC-PUFA levels in fish feeds that are very low in marine ingredients. Diets with low levels of marine ingredients have also been shown to lead to genotype by nutrition interactions, whereby the genotypes that perform the best on a classical marine-based diet are not necessarily the ones that perform the best on plant-based diets (Callet et al., 2017; Le Boucher et al., 2012; Overturf et al., 2013). Therefore, considering the strong trend to move towards plant-based diets, it is important to evaluate selection response both on standard and on "future" diets, which for sure will be more and more devoid of fish meal and fish oil.

Rainbow trout (*Oncorhynchus mykiss*) is one of the main salmonids produced worldwide, and the main fish species farmed in France in fresh water. While initially most of them were sold at portion size (300 g), production has shifted to large trout (1.0–3.5 kg) since the 1990's, in order to produce large fillets, which are consumed fresh or smoked (Haffray, 2018). In this study, we used a selected line of rainbow trout from the Sources de l'Avance breeding company of the Aqualande group (Pissos, France) specifically aimed at producing large trout for fillet production, for which a selective breeding programme was initiated 10 generations ago (more details in Section 2.2). In parallel of the selected line, Aqualande has propagated its unselected base population by random mating, so that it could be used as a control to evaluate the gains produced by the selective breeding programme in the mid- and long-term.

The aim of this study was to evaluate genetic gains produced by ten generations of multi-trait selection on the "large trout" line of Aqualande, and to evaluate the impact of diet on these gains, comparing an industry standard diet with a "future" diet. For this, we produced a Selected cross representative of the 10th generation of selection (G10) from the Aqualande "large trout" selected line, together with a Control group produced with the same females crossed with G0 males from the unselected line. This Control group was expected to have a performance mid-way between that of G0 and G10. The two genotypes were reared in triplicates in commercial conditions in flow-through concrete raceways with non-limiting oxygen capacity. A feeding trial was performed from 264 to 374 days post hatching (dph), comparing both genotypes fed either a Standard commercial diet or a Future diet which was free of marine ingredients and soy, and where DHA was provided by microalgal biomass. A few control fish were reared until 416 dph to reach the same mean weight as 374 dph G10 fish, so that both genotypes could be compared at the same age (374 dph) or at the same weight (≈1650 g). Growth and Feed conversion ratio (FCR) data were collected from 145 to 416 dph. Body composition and nutrient gain were estimated during the feeding trial. At the final sampling, fish were dissected to evaluate processing yields. We estimated the differences between genotypes for all traits measured during the production cycle, and feed effects as well as genotype x feed interactions were estimated during the feeding trial.

2. Material and methods

2.1. Ethics statement

All procedures were conducted following the guidelines for animal experimentation established by the Directive 2010–63-EU of the European Union and the equivalent French legislation. As the experiment only implied normal breeding procedures and terminal sampling, it did not require approval from an Ethics Committee.

2.2. Fish lines used

The breeding programme of Aqualande started in 1998, with an outbred base population originating from different French fish farms

(G0). These fish were selected first for growth rate with PROSPER type individual selection on body length (Chevassus et al., 2004), using microsatellite markers to identify the family origin of all selected broodstock (Estoup et al., 1998) and manage inbreeding ($\Delta F<0.5\%$ per generation), using ≈ 200 broodstock fish (100 neomales, 100 females) at each generation. Additional traits, measured on live breeding candidates, were included in 2001 (3rd generation) to improve fish quality. This included selection for increased fillet lipid with the Distell Fish Fatmeter (https://fishmeatfatmetertester.co.uk/) following Douirin et al. (1998) and Quillet et al. (2007a, 2007b). At the same time, mass-selection for a "salmon-like" more elongated shape with homogeneous muscle repartition along the body, was introduced to improve carcass yield, using ultrasound tomography and 2D external body morphology (Haffray et al., 2013). In 2006 (4th generation), while individual selection for growth was still performed, BLUP selection for carcass yield started to be applied on fish pre-selected for growth, based on breeding values obtained from 1000 to 2000 unselected slaughtered sibs for each cohort, as proposed by Haffray (2018). In total, ten generations of selection were performed since the G0, with an evolving breeding goal, focused on production of large trout for smoking, with fast growth, improved carcass yield and increased fillet lipid. In parallel, the G0 line was propagated by random mating with 50–100 females and 30–50 neomales at each generation, to be used as a control line.

2.3. Comparison of selected and unselected genotypes (phase 1 – until 250 dph)

On December 17, 2018, in the breeding centre of Aqualande (Pissos, France), 30 G10 females were stripped, and their eggs were mixed in equal quantities to create an egg pool, which was divided in two equal parts. The first part of the G10 ovules was separated in 30 aliquots which were individually fertilised with sperm from 30 G10 neomales, to create all-female offspring representative of the G10 line (G10 *G10, Selected genotype). The second part of the G10 ovules was fertilised with sperm from 30 unselected G0 neomales, to produce a G0 *G10 progeny (Control genotype), which is expected to be halfway between the G0 and the G10 lines in terms of genetic level. This was preferred to breeding a pure G0 *G0 line as we wanted 1) to avoid potential maternal non-genetic effects on egg quality, and 2) to ease comparison by avoiding too large a difference in body size between the groups being compared at the same age. The fertilised eggs were placed in incubation trays at 12.2 °C, then transferred to hatching troughs at 7 °C until hatching on January 12, 2019. Exogenous feeding started at 20 days post-hatching (dph).

At 70 dph, fish from the Control and the Selected genotypes were transferred to outside raceways (EOL_0000340) in triplicates (6 raceways of 0.7 m^3, 2850 fish/raceway). The average initial weight was estimated at 83 dph by weighing 100 fish per replicate. Commercial feed (NeoStart, le Gouessant, Lamballe, France) was provided in excess until 145 dph, thus feed efficiency could not be estimated during that period.

At 145 dph, 50 fish per replicate were individually measured for body weight (BW, ATOL_0000351) and fork length (BL, ATOL_0001658). Body shape was assessed by Fulton's $K=BW/BL^3 * 100$, with BW in g and BL in cm. The number of fish was adjusted to 400 in each replicate, and the total biomass was weighed. From that point, fish were fed to near satiation (2 meals per day) with a commercial feed (NeoStart until 162 dph, and then Neo19, Le Gouessant, Lamballe, France) and the amount of feed distributed in each replicate was precisely recorded. Dead fish were collected every day and weighed. Thus, under the hypothesis that almost no feed was wasted, FCR could be estimated over that period at the raceway level, as FCR=Feed intake/Biomass gain (ATOL_0001580). Biomass gain included the biomass of dead fish for the assessment of the biological FCR.

At 192 dph, 50 fish per replicate were individually measured for BW and BL, the total biomass of each raceway was weighed, and the number of fish was adjusted to 160 per replicate. Feeding, collection and weighing of dead fish continued as before.

At 250 dph, the total biomass in each raceway was weighed, and fish were individually tagged, weighed and measured for BL. Muscle fat content (ATOL_0001663) was estimated with one Distell Fish Fatmeter measurement on each side. 100 fish per raceway were individually measured and tagged from each G10 *G10 raceway, vs. 140 from each G0 *G10 raceway. The three replicates from each genotype were mixed, and the two genotypes were kept each in a large raceway, pending transport to the final grow-out site (Belin Béliet, France) at 263 dph.

During this 70–250 dph phase, the average (natural) temperature (EOL_0000247) was 16.4 °C and varied from 11.3° to 21.6°C.

2.4. Comparison of genetic groups with alternative feeds (phase 2, 264–374 dph)

The next experimental sequence consisted in an evaluation of selection response in a feeding trial with a 2 × 2 factorial design, were the two genotypes were fed two alternative diets in order to quantify possible genotype x feed interactions, with each of the four combinations reared in triplicates. The first diet was Aqualande's commercial standard Aqualia, produced by Aqualande's feed mill, with a closed formula, containing among others fish meal, fish oil and soybean (Table 1). This feed will be further referred to as the Standard feed. The second diet was formulated and produced by INRAE, as a potential future sustainable diet in which most ingredients can be produced locally in the EU. It was completely devoid of fishmeal, fish oil and soybean-derived products (Table 1). Microalgal biomass (Microalgal Powder PA116 ≥18% DHA, Greensea, Mèze, France) was added as an alternative source of DHA. In terms of n-3 fatty acids, the Standard feed contained 1.40% ALA, 0.56% EPA and 0.79% DHA, while the Future feed contained 3.15% ALA, 0.03% EPA and 0.95% DHA (see Supplementary Table S1 for the detailed fatty acid composition of the diets). The Future feed was formulated to be isoproteic, isolipidic and isoenergetic compared to the Standard feed.

At 264 dph, the tagged fish were again individually measured for BW

Table 1
Composition and proximal analysis of the two feeds for rainbow trout. "X" indicates that the raw material was used in the formulation but the amount used is not disclosed.

	Standard feed (Aqualia)	Future feed (INRAE)
Ingredients (%)		
Fish meal	X	0
Krill meal	X	0
Crustacean protein hydrolysate	X	0
Dehulled faba beans	X	0
Soybean meal expeller	X	0
Soybean protein concentrate	X	0
Extruded whole wheat	X	16.69
Potato protein concentrate		14.04
Corn gluten	X	13.84
Wheat gluten	X	12.03
Yeast		9.02
Algal biomass		5.01
Alfalfa protein concentrate		2.01
Fish oil	X	0
Rapeseed oil	X	9.58
Linseed oil		5.01
Sunflower oil		3.01
Rapeseed lecithin		2.41
CaHPO4.2H20 (18%P)		2.51
Min. Premix	X	1.50
Vit. Premix	X	1.50
Attractant Mix		1.50
L-lysine		0.30
Astaxanthin		0.03
Dry matter (%)	95.5	94.4
Protein (% DM)	44.8	43.7
Lipids (% DM)	19.4	21.8
Ash (% DM)	7.2	6.0
Energy (kJ/g DM)	24.2	24.5

and BL, and randomly dispatched in 12 cages (3 x 1 m, 0.85 m depth) placed on the bottom of large raceways. Each genotype (Selected, Control) was dispatched in six cages, with 40 fish in Selected cages, and 60 fish in Control cages. This was done to re-equilibrate rearing density owing to the larger size of selected fish, as well as to enable a final growth period for Control fish at the end of the experiment (see below). In each genetic group, three cages were fed the Standard feed and three were fed the Future feed. Fish were fed to near satiation (2 meals per day) and the amount of feed distributed in each replicate was precisely recorded. Dead fish were collected every day and weighed, in order to be able to estimate FCR. An intermediate measurement for individual BW and BL was performed at 311 dph.

At 374 dph, 30 (or less in case some fish died) fish per replicate were euthanized with excess benzocaine (150 mg/l). They were individually measured for BW, BL, muscle fat (Distell FFM-692 Fish Fatmeter), and then dissected in five parts: head, left fillet with skin and ribs, half-carcass (headless carcass with left fillet removed), viscera, liver. All body parts were weighed, and fillet weight was estimated as 2 *left fillet weight, headless carcass weight as half carcass weight + left fillet weight and carcass weight as headless carcass weight + head weight. Yields of body parts (carcass yield - ATOL_0000548, headless carcass yield - ATOL_0002261, fillet yield -ATOL_0002305, head yield - ATOL_0005561, viscero-somatic index- ATOL_0002259, liver yield - ATOL_0001121) were calculated as the ratio of their weight to body weight. A total of 90 Control fish were not euthanized at this stage, and kept for a final growth period on the Standard feed, in two cages, one with fish initially fed the Standard feed and one with fish initially fed the Future feed. They were grown until 416 dph, then slaughtered with the same protocol applied at 374 dph. This was done to be able to compare Control and Selected fish at a similar body weight (Selected: 1688 g at 374 dph, Control: 1631 g at 416 dph).

The average water temperature was 11.0 °C from 264 to 374 dph, a below optimum temperature which enables a good although not maximal growth rate of rainbow trout (Myrick and Cech, 2000). Growth rate between two measurements was estimated by the thermal growth coefficient (ATOL_0001661, Iwama and Tautz, 1981) as: $TGC = 1000(BW_f^{1/3} - BW_i^{1/3})/Tt$, with BW_f and BW_i the final and initial body weight, T the average temperature (°C) and t the length of the period in days.

2.5. Whole body composition and fatty acids

Fish were sampled at different time points to assess whole body composition in the different groups. Two pools of two fish per replicate (thus 4 fish per replicate and 12 per line) were sampled at 145, 192 and 250 dph. In the second phase, two samples of three fish per line at the start (264 dph) and two fish per tank (thus 6 per line x feed combination) were sampled at slaughter, at 374 dph.

Proximate composition of the experimental diet and whole body was determined according to AOAC (2000) as follows: dry matter was analysed by drying the samples to constant weight at 105 °C for 24 h. Crude protein was determined using the Kjeldahl method after acid digestion and estimated by multiplying nitrogen by 6.25. Gross energy content was determined in an adiabatic bomb calorimeter (IKA). Ash content was calculated after combustion in a muffle furnace at 550 °C for 16 h.

Total lipid content of feed and whole fish was quantified gravimetrically after extraction by dichloromethane/methanol (2:1, v/v), containing 0.01% of butylated hydroxytoluene (BHT) as antioxidant, according to Folch et al. (1957). Fatty acid methyl esters were prepared by acid-catalysed transmethylation of the lipid extract, using boron trifluoride according to Shantha and Ackman (1990). Fatty acid methyl esters were then analysed in a Varian 3900 gas chromatograph equipped with a fused silica DB Wax capillary column (30 m x 0.25 mm internal diameter, film thickness 0.25 μm; JW Alltech, France). Injection volume was 1 μL, using helium as carrier gas (1 mL/min). The temperatures of the injector and the flame ionisation detector were 260 °C and 250 °C, respectively. The thermal gradient was as follows: 100–180 °C at 8 °C/min, 180–220 °C at 4 °C/min and a constant temperature of 220 °C for 20 min. Fatty acids were identified with reference to a known standard mixture (Sigma, St Louis, MO, USA) and peaks were integrated using Varian Star Chromatography Software (Star Software, version 5). The results for individual fatty acids were expressed as percentage of total identified fatty acids.

For protein, lipids and selected fatty acids (ALA, EPA, DHA), nutrient gain per kg body weight gain during the feeding trial was calculated as:

$$Nutrient\ gain\ (g/kg\ BWG) = (BW_f\ x\ Nut_f - BW_i\ x\ Nut_i)/(BW_f - BW_i)$$

Where BW_i and BW_f are the initial and final BW and Nut_i and Nut_f are the initial and final content of a specific nutrient content expressed as g/kg wet mass.

2.6. Statistics

In the initial phase, the data point was tank mean for BW, K, survival, FCR and body composition traits. They were analysed with a one-way ANOVA with genetic group as a fixed factor. During the feeding trial, tank mean was the data point for body composition, survival and FCR, and was analysed with a two-way ANOVA (genotype and feed as fixed factors) with interaction. When interaction was not significant, a two-way ANOVA with only the main effects was performed. When interaction was significant, genetic groups were compared within feed, or feeds were compared within genetic groups, with a one-way ANOVA. During the feeding trial, individual data (BW, K, TGC, fillet fat and processing yields) were analysed with a mixed model:

$$Y_{ijkl} = \mu + G_i + F_j + GF_{ij} + c_{k(ij)} + \varepsilon_{ijkl}$$

With Y_{ijkl} the phenotype of fish l, μ the intercept, G_i the fixed effect of genotype i, F_j the fixed effect of feed j, GF_{ij} the genotype x feed interaction, $c_{k(ij)}$ the random effect of cage k nested within interaction, and ε_{ijkl} the random residual. Post-hoc multiple comparisons of means or least square means were performed with Tukey adjustment, and degrees of freedom for statistical tests for unbalanced data in mixed models were estimated with Satterthwaite's approximation. An effect was considered significant at $P < 0.05$, except for fatty acids content where 50 variables were studied and significance was thus fixed at $P < 0.001$, following Bonferroni correction.

Weight data were not reliable for head weight and viscera weight, showing unusual values and high variability, in two sequences of 61 and 167 successive records during the 374 dph sampling. The reason for this has not been identified. Those data were removed from the analysis, leading to missing data for Head yield, Viscera yield and Carcass yield (which is the addition of fillet yield, half carcass yield and head yield). For these traits, this led to lack of data from one cage for Selected fish fed the Standard feed and for Control fish fed the Standard diet, and for all Control fish fed the Future feed. For these traits, data were thus analysed either within the Standard feed for comparing the two genetic groups, or within the Selected group for comparing feeds.

Data analysis was performed using base R software (R Core Team, 2021) with packages *lme4* (Bates et al., 2015) and *emmeans* (Lenth, 2021).

The Selected fish in the experiment were from a G10 sires x G10 dams cross, thus representative of the G10 line. The Control fish were from a G0 sires x G10 dams cross, and thus their mean phenotype $\overline{P}_{Con}$ is halfway between that of the G10 ($\overline{P}_{Sel}$) and that of the G0 line. The G0 phenotype estimate $\widehat{P}_{G0}$ was estimated by $\overline{P}_{Sel} - \widehat{P}_{G0} = 2(\overline{P}_{Sel} - \overline{P}_{Con})$ and thus $\widehat{P}_{G0} = 2\overline{P}_{Con} - \overline{P}_{Sel}$.

The ten generation genetic gain in percent of G0 performance was expressed as:

$$\Delta_G\% = \frac{2(\overline{P}_{Sel} - \overline{P}_{Con})}{2\overline{P}_{Con} - \overline{P}_{Sel}} * 100$$

These calculations were conducted for fish fed the Standard feed (Le Gouessant or Aqualia depending on stage), for which reliable data were available at all stages, while some processing traits were missing for Control fish fed the Future feed (see before) and FCR was not considered reliable for the Future feed (see § 4.1.4).

3. Results

3.1. Growth and survival

All estimates of means or least square means are expressed as mean ± standard error. The Selected fish were heavier than the Control fish at the end of the initial growth period at 250 dph (607 ± 7 g vs. 521 ± 7 g, $F_{1,4}$ =73.2, P = 0.001). The difference between genotypes was not significant at 83 dph (1.95 ± 0.06 g vs. 1.80 ± 0.06 g, $F_{1,4}$ =2.76, P = 0.17) and became significant only at 192 dph (Fig. 1).

During the feeding trial, there was no genotype x feed interaction for body weight at any time (P > 0.05). An effect of feed was seen at 311 dph (Fig. 1), with a higher weight with the Future feed (Future feed: 989 ± 13 g, Standard feed: 939 ± 13 g, F_{1592} =7.6, P = 0.006), however this effect was not significant anymore at 374 dph (Fig. 1). Selected fish were larger than Control fish at 374 dph (Selected: 1688 ± 24 g, Control: 1375 ± 20 g, $F_{1,6.4}$ =100.6, P = 0.00004). In line with observations for body weight, growth rate measured as TGC was higher with the Future feed from 264 to 311 dph (Future feed: 2.58 ± 0.06, Standard feed: 2.32 ± 0.06, $F_{1,9.4}$ =7.6, P = 0.04) but not on the whole feeding trial (Future feed: 2.56 ± 0.05, Standard feed: 2.51 ± 0.05, $F_{1,8}$ =0.69, P = 0.43). Selected fish grew faster than Control fish during all phases of the feeding trial, especially on the whole period (Selected 2.66 ± 0.05 vs. Control 2.41 ± 0.04, $F_{1,7.5}$ =14.8, P = 0.0056). Line x feed interaction for TGC was not significant at any time (P > 0.20).

Survival did not differ between the two genotypes during the 83–250 dpf period (Selected: 76.0 ± 3.2%, Control: 67.2 ± 3.2%, $F_{1,4}$ =3.80, P = 0.12). During the 264–374 dpf period, survival differed among feeds (Standard: 99.3 ± 1.6%, Future: 94.1 ± 1.6%, $F_{1,8}$ =6.13, P = 0.038) but not among genotypes (Selected: 96.3 ± 1.6%n, Control: 97.2 ± 1.6%, $F_{1,8}$ =0.002, P = 0.96). Genotype x feed interaction on survival was not significant (P > 0.8).

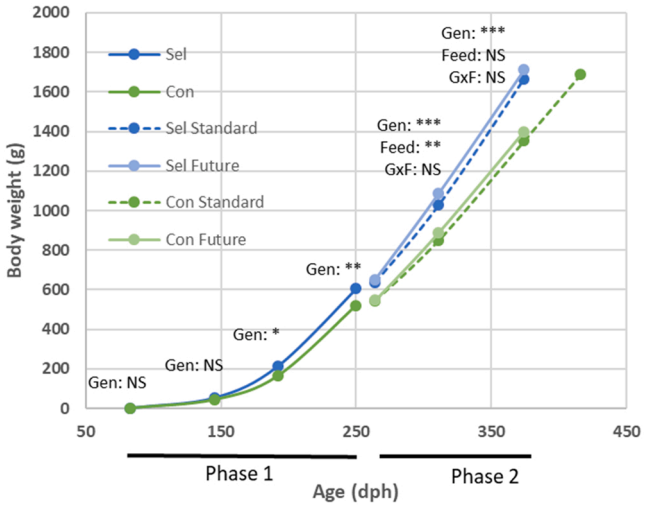

Fig. 1. Growth performance of the Selected (Sel) and Control (Con) genotypes of rainbow trout, with the same feed until 250 dph and a Standard or Future feed from 264 to 374 dph. NS:non significant, *P < 0.05, **P < 0.01, ***P < 0.001.

3.2. Body shape and processing traits

Fulton's condition coefficient varied over time but was consistently higher in the Control fish than in the Selected fish throughout the experiment, and neither feed nor genotype x feed interactions were significant during the feeding trial (Fig. 2).

Muscle fat percent was only marginally higher in the Selected fish at 250 dph (Selected: 7.95 ± 0.37, Control: 6.56 ± 0.37, $F_{1,4}$ =6.93, P = 0.058), but the difference became clear at 374 dph (Selected: 10.62 ± 0.17, Control: 8.92 ± 0.16, F_{1427} =54.5, P = 10^{-12}), where feed had a marginal effect, with fish fed the Future feed being fatter than those fed the Standard feed (Future: 9.99 ± 0.17, Standard: 9.54 ± 0.16, F_{1427} =3.84, P = 0.051).

For processing traits, at the end of the feeding trial, Selected fish had significantly higher headless carcass yield, fillet yield, vertebral axis yield and lower viscero-somatic index than Control fish (Table 2).

Carcass yield was also higher in Selected fish, to an amount similar to that observed for headless carcass yield (+1.3% vs. +1.5%, respectively) but this difference was not significant, probably due to the absence of carcass yield data for Control fish fed the Standard feed (see Section 2.6). Fish fed the Standard feed had higher headless carcass yield, fillet yield and liver yield and marginally lower viscero-somatic index. Genotype x feed interaction was never significant for processing traits (Table 2).

When Selected fish were compared to Control fish at the same weight (i.e. when we compared 374 dph Selected fish with 416 dph Control fish), body weight, as expected, was similar (Table 3) and selected fish still had a lower condition factor, although not significantly different (P = 0.082).

Muscle fat content at the same weight was still higher in Selected fish. For processing yields assessed at the same weight, Selected fish had a similar carcass yield compared to Control fish and had a higher headless carcass yield. Fillet yield was similar as well as head yield or liver yield. However, Viscero-somatic index was still lower in Selected fish, while vertebral axis yield remained higher.

3.3. Body composition

Whole body composition data for both genotypes are provided in Table 4. Dry matter content and energy relative to wet weight (WW) increased over the course of the experiment due to an increase in lipid content, while protein content, also relative to wet weight, remained stable. No difference between genotypes was found at any time (P > 0.05).

At the end of the feeding trial (374 dpf), while genotypes were still not different, a significant difference in dry matter content was found between the Future and Standard feed groups (Standard feed: 35.7

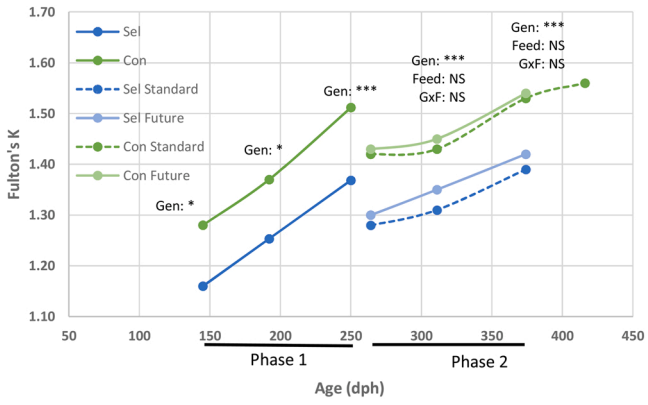

Fig. 2. Fulton's condition coefficient of the Selected (Sel) and Control (Con) genotypes of rainbow trout, with the same feed until 250 dph and a Standard or a Future feed from 264 to 374 dph. NS:non significant, *P < 0.05, **P < 0.01, ***P < 0.001.

Table 2
Processing traits at the end of the feeding trial (374 dph), comparing a Selected (Sel) and a Control (Con) genotype of rainbow trout fed a Standard or Future diet. Different letters denote significant differences ($p < 0.05$). Genotype x feed interaction (GxF) could not be estimated for carcass yield, head yield and viscero-somatic index due to the absence of data for head and viscera weight in the Control genotype x Future feed combination. In this case, Genotype effects were estimated within the Standard feed, and Feed effects within the Selected genotype. Results are presented as least square means ± standard error. Ls means with different superscripts are significantly different ($P < 0.05$).

Processing yield	Line	Feed	Statistical tests
Carcass yield	Sel: 89.9 ± 0.5% Con: 88.1 ± 0.5%	Standard: 89.9 ± 0.4% Future: 89.1 ± 0.4%	Gen: $F_{1,2} = 7.26$ P = 0.11 Feed: $F_{1,3.1} = 3.05$ P = 0.22 GxF: N/A
Headless carcass yield	Sel: 78.6 ± 0.2%[a] Con: 77.1 ± 0.2%[b]	Standard: 78.3 ± 0.2%[a] Future: 77.4 ± 0.2%[b]	Gen: $F_{1,8.1} = 42.1$ P = 0.0002 Feed: $F_{1,8.1} = 17.4$ P = 0.003 GxF: $F_{1,8.1} = 0.28$ P = 0.61
Fillet yield	Sel: 68.9 ± 0.2%[a] Con: 67.9 ± 0.2%[b]	Standard: 68.8 ± 0.2%[a] Future: 68.0 ± 0.2%[b]	Gen: $F_{1,8.5} = 17.6$ P = 0.003 Feed: $F_{1,8.1} = 11.3$ P = 0.009 GxF: $F_{1,8.5} = 1.33$ P = 0.28
Head yield	Sel: 10.7 ± 0.2% Con: 10.7 ± 0.2%	Standard: 10.7 ± 0.2% Future: 10.7 ± 0.2%	Gen: $F_{1,1.8} = 0.08$ P = 0.81 Feed: $F_{1,2.5} = 0.02$ P = 0.91 GxF: N/A
Viscero-somatic index	Sel: 7.7 ± 0.3%[b] Con: 9.6 ± 0.3%[a]	Standard: 7.7 ± 0.2% Future: 8.5 ± 0.2%	Gen: $F_{1,1.9} = 21.5$ P = 0.046 Feed: $F_{1,2.8} = 9.87$ P = 0.058 GxF: N/A
Vertebral axis yield	Sel: 9.7 ± 0.1%[a] Con: 9.2 ± 0.1%[b]	Standard: 9.5 ± 0.1% Future: 9.4 ± 0.1%	Gen: $F_{1,8} = 12.1$ P = 0.008 Feed: $F_{1,8.1} = 11.3$ P = 0.009 GxF: $F_{1,8.5} = 1.33$ P = 0.28
Liver yield	Sel: 1.27 ± 0.02% Con: 1.30 ± 0.02%	Standard: 1.33 ± 0.02%[a] Future: 1.24 ± 0.02%[b]	Gen: $F_{1,8.1} = 0.89$ P = 0.37 Feed: $F_{1,8.1} = 7.7$ P = 0.02 GxF: $F_{1,8.5} = 0.77$ P = 0.41

Table 3
Comparison of a Selected genotype of rainbow trout at 374 dph with a Control genotype at 416 dph, at the same mean body weight. Three cages of 30 selected fish fed a Standard diet were considered at 374 dph, and were compared to two cages of 45 Control fish fed a Standard diet from 375 to 416 dph. Results are presented as least square means ± standard error. Ls means with different superscripts are significantly different ($P < 0.05$).

Trait	Selected 374 dph	Control 416 dph	Statistical test
Body weight	1661 ± 34 g	1631 ± 55 g	$F_{1,5} = 0.36$, P > 0.58
Fulton's K	1.39 ± 0.02	1.51 ± 0.03	$F_{1,3} = 6.54$, P = 0.082
Muscle fat	10.5 ± 0.2[a]	9.3 ± 0.03[b]	$F_{1,194} = 10.7$, P = 0.003
Carcass yield	89.9 ± 0.4%	88.1 ± 0.4%	$F_{1,1.9} = 8.44$, P = 0.11
Headless carcass yield	79.0 ± 0.3%[a]	77.5 ± 0.4%[b]	$F_{1,2.8} = 13.2$, P = 0.04
Fillet yield	69.1 ± 0.2%	68.9 ± 0.2%	$F_{1,194} = 0.94$, P = 0.33
Head yield	10.7 ± 0.2%	10.6 ± 0.1%,	$F_{1,1.8} = 0.17$, P = 0.72
Viscero-somatic index	7.73 ± 0.20%[b]	9.22 ± 0.29%[a]	$F_{1,149} = 37.7$, $P = 10^{-8}$
Vertebral axis yield	9.90 ± 0.18%[a]	8.62 ± 0.20%[b]	$F_{1,2.8} = 21.0$, P = 0.02
Liver yield	1.33 ± 0.04%	1.15 ± 0.05%	$F_{1,2.9} = 7.68$, P = 0.07

Table 4
Whole body proximal composition of trout genotypes from145 to 374 dpf. DM: Dry matter; WW: Wet weight. Data at 374 dph are the least-square means of genotypes across the Standard and the Future diet. Diet differences are discussed in the text.

Age (dph)	Genotype	% DM	Protein (% WW)	Lipid (% WW)	Energy (KJ/gWW)
145	Selected	29.0 ± 0.5	15.8 ± 0.3	11.6 ± 0.3	7.9 ± 0.2
	Control	30.3 ± 0.5	16.0 ± 0.3	12.3 ± 0.3	8.3 ± 0.2
192	Selected	33.1 ± 0.3	16.5 ± 0.2	15.7 ± 0.4	9.7 ± 0.2
	Control	32.8 ± 0.3	16.6 ± 0.2	15.4 ± 0.4	9.5 ± 0.2
250	Selected	35.4 ± 0.4	15.9 ± 0.1	20.1 ± 0.3	10.8 ± 0.2
	Control	35.9 ± 0.4	16.1 ± 0.1	19.7 ± 0.3	10.8 ± 0.2
374	Selected	36.3 ± 0.4	16.9 ± 0.2	19.3 ± 0.5	11.1 ± 0.2
	Control	36.9 ± 0.4	16.8 ± 0.2	19.9 ± 0.5	11.3 ± 0.2

± 0.4%, Future feed: 37.5 ± 0.4%, $F_{1,8}$ =11.3, P = 0.01). There was also a positive effect of the Future feed on lipid content (Standard: 18.6 ± 0.5%, Future: 20.6 ± 0.5%, $F_{1,8}$ =7.51, P = 0.025) and energy content (Standard: 10.8 ± 0.2 KJ/g WW, Future: 11.5 ± 0.2 KJ/g WW, $F_{1,8}$ =9.57, P = 0.015) but not on protein content (Standard: 16.7 ± 0.2%, Future: 16.9 ± 0.2%, $F_{1,8}$ =0.83, P = 0.39). The genotype x feed interaction was not significant for any body composition trait ($P > 0.60$).

There was no difference between genotypes in fatty acids profile at any sampling time. At the end of the feeding trial (374 dpf), there were many differences between fish fed the Standard or the Future diet (Table S2), with more saturated fatty acids in the Standard diet fed fish (Standard: 19.0 ± 0.1%, Future: 17.8 ± 0.1%, $P < 0.05$), as observed for 14:0, 15:0 and 17:0 fatty acids. There were also more monounsaturated fatty acids in Standard diet fed fish (Standard: 48.52 ± 0.09%, Future: 44.50 ± 0.09%, $P < 0.05$), this being linked to a higher proportion in 18:1, 20:1 and 22:1. The proportion of n-6 polyunsaturated fatty acids in Future diet fed fish was higher (Future: 20.8 ± 0.1%, Standard: 16.9 ± 0.1%, $P < 0.05$) with more 18:2n-6 and 22:5n-6. Future diet fed fish also had a higher percentage of total n-3 PUFA (Future: 15.8 ± 0.1%, Standard: 13.7 ± 0.1%, $P < 0.05$) mainly due to more 18:3n-3 (ALA) whereas the proportion of long chain n-3 PUFA was higher in Standard diet fed fish (Standard: 9.32 ± 0.05%, Future: 7.68 ± 0.05%, $P < 0.05$), with more 20:5n-3 (EPA), 21:5n-3, 22:5n-3 and 22:6n-3 (DHA). There was no significant genotype x feed interaction for any fatty acid trait.

3.4. FCR and nutrient gain

Feed conversion efficiency, measured as FCR, was better in Selected fish on the 145–250 dph period, although this was only close to significance (Sel: 1.03 ± 0.007 vs. Con: 1.05 ± 0.007, $F_{1,4}$ =7.42, P = 0.053). During the feeding trial, there was a significant genotype x feed interaction ($P < 0.05$), thus the main effects could not be compared in the general model, but only within the other main effect. Within genotype, the effect of feed was significant ($P < 0.01$), and the Standard feed always gave a better FCR (Fig. 3).

Within feed, both genotypes had the same FCR with the Future feed (Selected: 1.24 ± 0.03, Control: 1.24 ± 0.03, $F_{1,4}$ =0.014, P = 0.91),

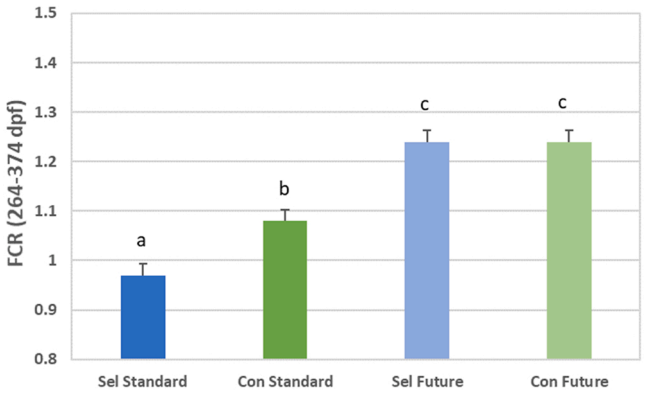

Fig. 3. Food Conversion ratio (FCR) during the feeding trial (264–374 dph), comparing a Selected (Sel) and a Control (Con) genotype of rainbow trout fed a Standard or a Future feed. Different letters denote significant differences ($p < 0.05$). Error bars represent the standard error of the mean.

while the Selected fish were more efficient than the Control fish when fed the Standard feed (Selected: 0.97 ± 0.02, Control: 1.08 ± 0.02, $F_{1,4}$ =16.0, P = 0.016).

Nutrient gain was evaluated during the feeding trial, from 264 to 374 dph (Table 5). There was a feed effect on lipids, with the Standard feed providing lower gain than the Future feed. There was no genotype effect and the genotype x feed interaction was never significant.

The gain in selected fatty acids showed no effect of genotype nor genotype x feed interaction for any fatty acid. No effect of feed was seen on DHA gain. In contrast, there was a major effect of feed on EPA, for which the gain with the Standard feed was 3.05 g/kg BWG, while it was only 1.19 g/kg BWG with the Future Feed. Conversely, the gain in ALA was much higher with the Future feed (20.8 g/kg BWG) than with the Standard feed (7.8 g/kg BWG).

3.5. Genetic gain between G0 and G10

When doubling the difference between Control and Selected fish to account for the fact that the control group was a G0xG10 hybrid, we could evaluate the expected performance of G0 fish relative to G10 fish, either at the same age (374 dph) or at the same body weight (~1650 g, 374 dph for G10 fish, 416 dph for G0xG10 fish). These data are shown in Table 6.

The G10 line was estimated to be 61% heavier than the G0 line at 374 dph, and the estimated time to reach commercial weight (here 1650 g) was reduced by 18%. The G10 line was consistently slimmer (as estimated by Fulton's K) by 15–17%, irrespective of whether the comparison was at the same age or at the same body weight. The G10 line had considerably more (+53%) muscle fat at 374 dph, but this difference was lower (+28%) when compared with the G0 line at 1650 g. Conversely, viscera yield was much reduced both at the same age

Table 6
Estimation of genetic gains from G0 to G10 rainbow trout from Aqualande, expressed as Δ_G%, in percentage change from the estimated performance of the G0 line. On the left part of the table, the performance of the G0 line is estimated at the same age (374 dph) using the difference between the performance of the G10 and that of the G0xG10 cross, while on the right part of the table, the performance of the G0 line is estimated using the difference between the performance of the G10 and that of the G0xG10 cross at the same body weight (1650 g, corresponding to 374 dph for the G1à and 416 dph for the G0xG10). Data concern only fish fed the Standard diet.

	Same age (374 dph)			Same body weight (~1650 g)	
Trait	G0 estimate	Δ_G%	G10 estimate	Δ_G%	G0 estimate
Body weight (g)	1038	61%	1666	–	–
Age at 1650 g (dpf)	–	–	374	-18%	458
Fulton's K	1.67	-17%	1.39	-15%	1.63
FCR (50 g-slaughter)	1.19	-17%	0.99	-20%	1.23
Fillet fat	6.8	53%	10.5	28%	8.2
Viscera yield	11.5	-33%	7.71	-28%	10.73
Carcass yield	86.3	4.2%	89.9	4.2%	86.3
Headless carcass yield	76.2	3.7%	79.0	3.9%	76.0
Fillet yield	67.7	2.1%	69.1	0.6%	68.7
Head yield	10.7	0.0%	10.7	2%	10.5
Vertebral axis yield	8.4	18%	9.9	35%	7.3

(−33%) and at the same weight (−28%). Generally, changes in processing yields were small. Carcass and headless carcass yield were 3.7–4.2% higher in the G10, both at the same age and at the same weight. Fillet yield was increased by 2.1% in G10 at the same age, but this disappeared at the same weight, where the gain was only 0.6% in G10 compared to G0. This was linked to a concurrent large increase of vertebral axis yield, which was 18% larger in G10 than in G0 at the same age, and 35% increased at the same body weight.

4. Discussion

The present study is the first one to evaluate selection response in rainbow trout on a ten generations scale. The longest previous evaluation of selection response in this species was conducted by Kause et al. (2005) and Janhunen et al. (2012) over three and four generations of the Finnish national breeding programme, respectively. It was performed with a different method, the evaluation of genetic trends on traits measured in a pedigreed population. While the genetic trends methods is considered optimal in terms of precision if all selection candidates are pedigreed and phenotyped (Hill, 2011), it is limited by the fact that selection response can be estimated only for the traits for which animals are measured along the selection process, which, in the cited studies, includes growth, maturation, viscera yield, flesh colour, deformities, and survival. The main advantage of using the control line approach is

Table 5
Gains (g/kg BWG) in protein, energy, lipids and specific fatty acids (ALA, EPA, DHA) in the rainbow trout feed trial from 264 to 374 dph. Results are presented as Least square means ± S.E. Different superscripts among levels of the main effects denote a significant difference ($P < 0.05$).

		Protein gain (g/kg BWG)	Lipid gain (g/kg BWG)	EPA gain (g/kg BWG)	DHA gain (g/kg BWG)	ALA gain (g/kg BWG)
Group	Standard feed					
Means	Selected	172 ± 4	177 ± 12	2.94 ± 0.16	10.1 ± 0.6	7.7 ± 0.6
	Control	168 ± 4	186 ± 12	3.17 ± 0.16	11.5 ± 0.6	7.9 ± 0.6
	Future feed					
	Selected	174 ± 4	214 ± 12	1.20 ± 0.16	10.4 ± 0.6	20.0 ± 0.6
	Control	174 ± 4	214 ± 12	1.18 ± 0.16	10.8 ± 0.6	21.6 ± 0.6
Main	Standard feed	170 ± 3	181 ± 8^{b}	3.05 ± 0.11^{a}	10.8 ± 0.4	7.8 ± 0.4^{b}
Effects	Future feed	174 ± 3	214 ± 8^{a}	1.19 ± 0.11^{b}	10.6 ± 0.4	20.8 ± 0.4^{a}
	Selected	173 ± 3	195 ± 8	2.07 ± 0.11	10.2 ± 0.4	13.8 ± 0.4
	Control	171 ± 3	200 ± 8	2.17 ± 0.11	11.1 ± 0.4	14.8 ± 0.4
Interaction	GenotypexFeed	NS (P = 0.60)	NS (P = 0.72)	NS (P = 0.47)	NS (P = 0.42)	NS (P = 0.29)

that selection response can also be estimated for traits which are not recorded in the breeding programme (in our case head yield, vertebral axis yield, fillet yield, body composition – including fatty acids), or even traits that cannot be recorded on an individual basis (FCR, nutrient gain), which have a key importance for production sustainability of the. It has to be noted that although pedigree selection was used in the present breeding programme, it was combined with individual pre-selection for growth and externally recorded quality traits (muscle fat-meter value, morphological index, ultrasound estimates of gutted yield) (Haffray et al., 2018) for which the performance and pedigree of culled animals was not known, thus precluding a straightforward use of genetic trends to evaluate selection gains. Finally, comparing a selected and a control line also enabled us to evaluate their relative performance both at the same age (374 dph) and at the same body weight (1650 g). Evaluation at the same age is generally applied, as it is easier to obtain, but arguably, as commercial weight is defined by the market, evaluation at the same body weight is probably even more important (Kristjánsson et al., 2020).

4.1. Selection response

4.1.1. Selection response on growth

The Selected fish grew faster than the Control fish. This was established at 192 dph, and became more and more significant over time. At the end of the experiment, the G10 had a 61% higher weight than the estimate for G0, corresponding to an average 6.1% improvement per generation. This is in the lower range of previously published gains on the same species, which ranged from 6% to 13% per generation (Gjerde, 1986; Janhunen et al., 2012; Kause et al., 2005; Kincaid et al., 1977). This is likely at least partly due to the multi-trait nature of the Aqualande breeding programme, which proportionally lowers selection intensity on growth. Indeed in the literature, gains of 6–7% per generation were obtained in the (multi-trait) Finnish national breeding programme (Janhunen et al., 2012; Kause et al., 2005), while higher figures (10–13% per generation) were obtained in single trait selection experiments (Gjerde, 1986; Kincaid et al., 1977). We could also see that the Selected fish took 42 days less than the Control fish (374 days vs. 416 days) to reach 1650 g, which represents a 10% reduction in the production cycle (or 18% if we extrapolate the performance of the G0). This reduction of 1.8% of the production cycle per generation is lower than the final gain in weight (+6.1%), due to the exponential nature of the growth curve. However, in practice, as harvest size is decided by the market, the real premium of fast growth often lies in the reduction of the duration of the production cycle (Kankainen et al., 2012). Survival did not significantly differ between genotypes, although it was slightly higher in the Selected fish (73.2% vs. 65.3% in Control fish for the 83–374 dph period). That survival was in the same range as that recorded in the Finnish programme on the second year of growth (72% from 53 to 964 g, Vehviläinen et al., 2012) and showed no negative effect of selection for growth on fish robustness. A positive effect could even be postulated, similar to the Finnish breeding programme where there was a 0.17 positive genetic correlation between growth and survival (Vehviläinen et al., 2012).

4.1.2. Selection response on morphology and processing traits

The second category of traits for which selection was applied was morphology and processing traits. Selection for growth was performed mainly using body length as a criterion, and in addition the fish selected for growth were further selected for an elongated “salmon-like” body shape as salmon is known to exhibit a higher carcass yield than rainbow trout. Selection on this trait was successful, as we could see that Selected fish had a lower Fulton’s condition coefficient at all stages (Fig. 3). This was expected as it has already been shown that using length as a selection criterion tends to favour an elongated shape (Chevassus et al., 2004). Moreover, the heritability of K or of the height/length ratio is often moderate to high in fish (Kause et al., 2011; Prchal et al., 2018), and successful selection for H/L ratio has already been demonstrated in common carp (Ankorion et al., 1992). In this specific population, the heritability of K had previously been estimated to be 0.54 (Haffray et al., 2013).

While shape may be important for consumer acceptance when fish is sold whole, the reason to select for it when the main target is the production of fillet is different. In that case, what was expected from an appropriate shape was an increase in carcass and fillet yields. In this population, selection for shape started at the 3rd generation. Since this time candidates were also indirectly mass-selected for carcass yield using ultrasound according to Haffray et al. (2013). From the 4th generation, selection for carcass yield was further improved by sib selection on slaughtered sibs of the candidates. The direct response in carcass yield was in the right direction with 4.2% more carcass in the G10 than in the G0, irrespective of the fact that it was estimated at the same age or at the same body weight. This represents a gain of 0.7% per generation (considering 6 generations of selection for this trait). However, it was only close to significance ($P = 0.11$). As carcass yield = 1 – viscera yield, we can change focus and examine viscera, which is the body part for which reduction was sought. In this case, reduction was spectacular (−33% at the same age, - 28% at the same body weight, thus some 5% per generation) and significant ($P < 0.05$). If now we consider the final target trait, fillet yield, we observed a significant response at the same age of 374 dph (2.1%, Table 6) but a much more limited one at the same weight (0.6%). The response of 2.1% corresponds to 0.35% per generation, lower than the ≈ 0.6% per generation obtained experimentally by Vandeputte et al. (2019) in rainbow trout, by combined selection for ultrasound ratios and sib-selection for fillet yield. Selection response on fillet yield has also been evaluated on Nile Tilapia in a multi-trait breeding programme (Gjerde et al., 2012; Thodesen et al., 2012). In those two studies, the gains in fillet yield were 0.14% and 0.20% fillet units gain per generation, respectively. With an approximate average fillet yield of 42% and 44%, respectively, the relative increase in those two programmes was 0.33% and 0.45%, in the same range as what we observed here at the same age, also in a multi-trait selection programme. However, in our case, the picture was quite different at the same weight, as then the relative gain in fillet yield was only 0.1% per generation. Surprisingly, when looking at headless carcass yield, which is generally considered a good surrogate for fillet yield (Haffray et al., 2012), the picture was quite different, as the improvement between G0 and G10 was 3.7% at the same age and 3.9% at the same body weight (Table 6). The difference lied in the vertebral axis yield, for which there was already a significant selection response at the same age (+18% in G10 relative to G0) but a very high increase (+35%) at the same body weight. The increase in vertebral axis yield could be somehow expected, as it has a positive genetic correlation (+0.20) with both body weight in this population (Haffray et al., 2012). As selection for growth was done on body length, resulting in a slimmer body, it is also logical that the proportion of vertebral axis was even more increased, even if we do not have an estimate of the genetic correlation of axis yield with body length. As selection for processing was performed on carcass yield, we must also note a positive genetic correlation of carcass yield with axis yield (0.45, Haffray et al., 2012). Thus, at least two traits in the breeding goal were positively correlated with axis yield, leading to a significant increase over generations.

The last compartment of interest is the head. It had been predicted previously that selection for fillet yield would cause a decrease in head yield, due to a rather high negative genetic correlation between both traits (−0.53, Haffray et al., 2012), which is found also in other species such as Nile tilapia, common carp or European sea bass (Kocour et al., 2007; Prchal et al., 2018; Rutten et al., 2005; Saillant et al., 2009). This could be problematic, as the head of the fish contains the respiratory organs (gills) and the heart, and negative trade-offs between the functionality of such organs and production traits have already caused significant health and welfare issues in poultry production (Emmans and Kyriazakis, 2000; Hartcher and Lum, 2020; Rauw et al., 1998). In the

present population, selection for carcass yield was preferred, as it had no genetic correlation with head yield ($r_G = 0.03 \pm 0.11$, Haffray et al., 2012) while still having a large positive correlation with fillet yield ($r_G = 0.79 \pm 0.05$, Haffray et al., 2012), but also a positive correlation with vertebral axis yield ($r_G = 0.45 \pm 0.26$, Haffray et al., 2012). This approach was successful for keeping head yield stable (0% difference between G0 and G10 at the same age, 2% in favour of G10 at the same weight). It also caused the expectable increase in axis yield, but was less effective to increase fillet yield. It has been shown recently that fillet yield could be improved in rainbow trout either by evaluating headless carcass yield on sibs of the candidates or by using correlated ultrasound measurements on the candidates themselves (Vandeputte et al., 2019). This may provide a 0.5% increase per generation, while still keeping head size constant, which is a good precautionary approach to ensure welfare of the selected fish, and should be considered for the future of the breeding programme, to obtain more tangible results on fillet yield.

Another way to express these results is to examine how mass (in body weight units) has been transferred from one compartment to another. At the same age, viscera were reduced from 11.5% of BW in G0 to 7.7% in G10, a − 3.8% units difference (Table 6). This reduction was compensated by an increase of fillet from 67.7% of BW in G0 to 69.1% in G10 (+1.4% units), while head weight did not change and vertebral axis weight was increased by 1.5% units (8.4% in G0 to 9.9% in G10). However, the increase in fillet yield at the same age is likely due to a positive allometry of fillet weight relative to body weight, as G10 fish were larger than G0 fish. At the same body weight, the decrease in viscera yield was comparable, from 10.7% in G0 to 7.7% in G10 (−3.0% units), but this time the increase in fillet was much smaller (68.7% in G0 to 69.1% in G10, thus +0.4%) while there was an larger increase both in vertebral axis yield (7.3% in G0 to 9.9% in G10, thus +2.6%) while head yield hardly increased (10.5% in G0 to 10.7% in G10, thus +0.2%).

4.1.3. Selection response for body composition

Body composition is also an important trait, because it has implications on the nutritional value of the fish, but also on its taste and on its processing ability (Mørkøre et al., 2001). The breeding programme aimed at increasing fillet fat in order to improve smoking yield, and this was very successful, with 53% increase in G0 relative to G10 at the same age (374 dph). However, there is a known positive phenotypic correlation of percent fillet fat with body weight (Haffray et al., 2013; Kause et al., 2002), such that part of this increase at the same age is expected to be linked to the larger size of G10 fish. When evaluated at the same body weight, there was still a large (though reduced) difference between G10 and G0, which amounted to 28%. Thus, for this trait also, the breeding programme was successful.

However, when evaluating whole body composition, no difference between genotypes was seen at any time of the experiment for dry matter, lipid, protein and energy content (Table 4). For lipids, this has to be put in perspective with the strong reduction in viscera yield. In fish, variation in viscera yield is mostly due to variation in visceral fat, and thus it is likely that the additional fat in the fillet of the G10 line was compensated by lower visceral fat, so that the total amount of fat in the fish did not vary. This trade-off between fillet fat and visceral fat has already been observed in pan-size rainbow trout divergently selected for fillet fat (Quillet et al., 2007a, 2007b), and is also expected in larger trout for which negative genetic correlations between fillet fat and visceral fat ($r_G = -0.43 \pm 0.23$, Kause et al., 2002) have been estimated.

Both selected and control genotypes had similar fatty acid profiles (in percent of total fatty acids) at all times. Thus, the breeding programme did not select for any differential capacity to store or metabolise specific fatty acids, and the fatty acids profile was mostly affected by the feed given. This was not completely expected as, in salmon, there are quite strong genetic correlations between muscle fat, visceral fat and fatty acid composition in the muscle (Horn et al., 2018). In rainbow trout, there are also strong genetic correlations between growth, processing yields and fatty acids profiles in visceral fat (Blay et al., 2021b). However, in our case, we did not examine muscle fatty acids nor visceral fat fatty acids but whole body fatty acids, which may explain part of the difference.

4.1.4. Indirect response on FCR and nutrient gains

One of the most striking results of the present study is the large decrease in FCR found in the G10 line, relative to the G0 line, when fed Standard feed (−17% at the same age, −20% at the same body weight), which represents a 1.7–2% improvement per generation. Previous similar experiments of correlated response to selection for growth showed no improvement of FCR in brown trout after four generations (Sanchez et al., 2001). No improvement of FCR was reported at the same age in Japanese flounder after two generations (Ogata et al., 2002), although in this study an adjustment for body weight by ANCOVA yielded a 5% improvement of FCR per generation. In another study in Atlantic salmon, Thodesen et al. (1999) showed a 4.6% improvement of FCR per generation after 5 generations of selection for growth. Finally, the last available study on the matter showed a 11.7% improvement in FCR after one generation of selection for fast growth in amago salmon (Yamamoto et al., 2015). Of these four published studies, two utilised wild parents rather than an unselected control from the same base population to produce the control line (Ogata et al., 2002; Thodesen et al., 1999). Thus, it was possible in those cases that 1) the wild stock had a different performance relative to the base population of the selected line and 2) selection response may have been to some extent confounded with a domestication effect. This is not the case here, as both the G0 and the G10 broodstocks derived from the same base population, the G0 being randomly bred while the G10 was selected towards the breeding goal. In addition, all previous experiments involved fish lines selected exclusively for growth, while in our case, the breeding goal included higher growth, “salmon-like” shape, high fillet lipid and high carcass yield. While higher growth is generally supposed to improve FCR in fish (Knap and Kause, 2018), it is not the case of lipid content, as muscle lipid was shown to be positively correlated with FCR in rainbow trout ($r_G = 0.68 \pm 0.24$, Kause et al., 2016), meaning that increasing fillet lipid would increase (and thus degrade) FCR. Even more, percent viscera has a genetic correlation of -0.39 ± 0.23 with FCR (Kause et al., 2016), which is again unfavourable in our case as percent viscera was decreased by selection, and thus would cause an increase in FCR – although this last genetic correlation estimate was not significantly different from zero. However, the main theoretical reason why body lipid would be positively correlated with FCR is the fact that depositing 1 g of lipids generates 4–5 times less wet weight gain than depositing 1 g of protein (Jobling, 1994). Thus, as the total lipid content of the fish was not changed by selection, it may be reasonable to think that the combined effects of selection for muscle lipid and against percent viscera had altogether no effect on FCR. Direct selection for FCR is extremely difficult in fish, although new methods have been recently tested, such as individual rearing in European sea bass (Besson et al., 2019), video-recording of meals in Nile tilapia (de Verdal et al., 2018b) and stable isotopes ratios in Atlantic salmon (Dvergedal et al., 2019). Selection for FCR using video-recording of meals in Nile tilapia has been proven successful, with a 0.6–0.7% reduction in FCR at each generation (de Verdal et al., 2022). However, the high level of the correlated response observed here questions the necessity to try to more directly select for FCR in rainbow trout, as we could obtain a 1.7–2% gain in FCR per generation without any complicated phenotyping for individual FCR.

It has to be noted that the gain in FCR in the Selected line was only visible (and significant) with the Standard feed. However, feedback from the fish farmers indicated that the Future feed was sinking, while the Standard feed was floating, and thus feeding to near satiation was much easier with the Standard feed. It is thus quite sure that a significant amount of the Future feed distributed was not consumed by the fish, leading to weed wastage and to an over estimation of feed intake and thus of FCR, possibly masking differences between fish lines. Indeed,

while each fish line had a similar growth with both feeds, the amount of Future feed distributed exceeded that of Standard feed by 16.6% for the Control line and by 29.7% for the Selected line.

Globally, there was no significant difference in nutrient gain (protein, lipids and the main polyunsaturated fatty acids) among genotypes, meaning that the composition of the gains in the whole fish was the same for both genotypes (when accounted for per kg body weight gain). However, this does not necessarily mean that there were no differential gains in specific body compartments (such as muscle and viscera, as highlighted before for fat content). Additionally, with only 6 fish per line sampled at 274 dph, the power to detect differences between lines for nutrient gains was indeed rather low.

4.2. Diet effects

Globally, both diets gave similar results in terms of growth rate, although the body weight of Future diet fed fish was transiently higher at 311 dph. This is an excellent result, as the Future diet is rather extreme, as both fishmeal and fish oil were fully replaced by alternative raw materials. To our knowledge, this is the first report showing similar growth in rainbow trout when comparing a commercial feed with a feed completely devoid of fishmeal and fish oil. In general, total replacement is tested either for fishmeal or for fish oil, but complete replacement of both was seldom tested and generally led to decreased growth, as seen in rainbow trout (Callet et al., 2017; Lazzarotto et al., 2018; Le Boucher et al., 2012), Californian yellowtail *Seriola dorsalis* (Stuart et al., 2021) and European seabass *Dicentrarchus labrax* (Le Boucher et al., 2013, 2011). However, similar and even better growth has already been obtained in Nile tilapia with a feed based on microalgae protein and oil compared to a commercial feed (Sarker et al., 2020). It has to be noted that the two studies showing good performance of fish-free diets (the present one and Sarker et al., 2020) both use microalgae to provide DHA in the diet, as DHA cannot be provided by terrestrial plant oils (Gladyshev et al., 2013), except some genetically-engineered plants (Napier et al., 2020; Ruiz-Lopez et al., 2014). Thus, the use of microalgae-based DHA (or of DHA from other sources) could be key in achieving full replacement of fishmeal and fish oil in fish feeds. However, in the present case, although both fish meal and fish oil were used in the Standard diet, the quantity used was not disclosed (trade secret) by the feed company, which may complicate the interpretation of the data. Still, the EPA/DHA content of the Standard feed is comparable with that of grow out feeds from another provider (Le Gouessant LG19–4 and LG19–5, see Supplementary table S1), showing they are rather representative of an industry standard.

The Future diet also led to a higher FCR than that observed with the Standard diet, especially with the Selected genotype. However, as explained before, due to differences in floatability between both feeds, some of the Future feed distributed was not ingested by the fish, leading to an over estimation of FCR. Thus, the comparison of FCR with both diets may not be conclusive.

The composition of the fish was maybe the category of traits that was most impacted by the diet. First, while protein content was not affected by the diet, there were more lipids, dry matter and energy in the Future diet fed fish, but this feed also had a slightly higher lipid content than the Standard feed (21.8% vs. 19.4%) Fish fed the Standard diet were richer in saturated and monounsaturated fatty acids, while those fed the Future diet had more PUFA, either n-3 or n-6. This somehow mirrored the composition of the feeds, but with variations. Indeed, we could see that the fish gained a significant amount of EPA (20:5 n-3) when fed the Future feed (1.19 g/kg BWG), which was 39% of what they gained with the Standard feed (3.05 g/kg BWG), even though the EPA content of the Future feed was minimal with 0.29 g/kg, which was only 5.7% of the amount in the Standard Feed (5.06 g/kg); This is indicative of a significant endogenous synthesis of EPA in the Future diet fed fish. For DHA, the Future feed contained 9.51 g/kg, the Standard feed 7.13 g/kg, and the gain in the fish was similar with both diets (10.6 and 10.8 g/kg BWG, respectively).

Previous studies have shown that the expression of desaturases *FADS2a(Δ5)*, *FADS2a(Δ6)* and elongases *ELOVL5* and *ELOVL2*, which are needed to convert ALA to EPA and DHA, was highly stimulated in rainbow trout fed diets rich in ALA but devoid of EPA and DHA (Gregory et al., 2016). Indeed, the Future feed contained 15.3% of ALA in its fatty acids, and was almost devoid of EPA (0.14%). However DHA was shown to be the one that down regulated the most effectively the four enzymes (Gregory et al., 2016), but the amount present in our feeds (4.62% of the FAs in the Future feed, 3.85% in the Standard feed) was probably not enough to significantly down-regulate *FADS2a(Δ5)* (needed to produce EPA from ALA), as 15% of DHA were necessary to achieve significant down regulation in Gregory et al. (2016).

In the end, both feeds permitted to produce fish with an EPA+DHA content of 1.84 g/130 g fish (Standard Feed) or 1.68 g/130 g fish (Future feed), that can cover the weekly adequate intake of 1.75 g recommended by the European Food Safety Authority (EFSA, 2010). In our case, the amount calculated is on whole fish and not on the edible part (fillet), but in rainbow trout there tends to be slightly more EPA and DHA in the fillet than in the whole body (Codabaccus et al., 2013), thus 130 g of fillet with any of the tested feeds would be more than covering the weekly adequate intake. Lowering of health benefits of farmed fish because of lower EPA+DHA content, due to the restricted use of fishmeal and fish oil, is a growing concern (Napier et al., 2020). In this study, we were thus able to produce a fish with excellent health benefits for the consumer with zero use of fish meal, fish oil and soybean products, paving the way for sustainable production of healthy farmed fish products.

4.3. Genotype by diet interactions

During the feeding trial, we could see very little genotype by diet interactions. The only clear one was for FCR. Even for that one, doubts remain as it may be linked to inadequate estimates of the feed intake with the Future diet, which was sinking and made the identification of satiation more difficult. This absence of genotype by diet interaction is reassuring for breeding programmes, as this implies that selection performed using one feed will likely produce selection response even if another feed is used in the next generations. Indeed, previous work in several species had shown significant re-ranking of families when fed on contrasted diets, especially in rainbow trout (Callet et al., 2017; Kause et al., 2007; Le Boucher et al., 2012; Overturf et al., in press; Pierce et al., 2008), European sea bass (Le Boucher et al., 2013, 2011) and European whitefish (Quinton et al., 2007). They used contrasted feeds, generally using more or less fishmeal and/or fish oil, to a level causing sub-optimal performance in one of the feeds tested. In our case, although the Future feed contained zero fishmeal, zero fish oil, zero soy-based products, it was iso-energetic, iso-lipidic and iso proteic with the Standard diet, and contained a microalgal source of DHA. Though the raw materials differed a lot, growth performance was similar with both diets, showing that the Future feed did not really challenge the fish. In this context, it is less surprising to see no genotype by feed interaction, as fish that were not much challenged by the feed did not need to express specific adaptation strategies. Maybe another reason is that fish in the breeding programme were selected using commercial feed, which every year contains less and less fishmeal and fish oil (Aas et al., 2019). Thus, they had the opportunity to become progressively adapted to feeds with low level of fish products. As the G0 was propagated by random breeding along years, it also experienced this progressive decrease in fish products in the diet, and may also have become adapted to it by unintentional selection.

5. Conclusion

This experiment showed the important medium-term effects of a breeding programme for the production of large trout in fresh water,

crossed with a comparison of a Standard commercial feed and a Future fish-free and soy-free feed, where DHA is provided by micro-algal biomass. Selection largely improved growth and feed conversion ratio, thus making the fish culture both more economically and environmentally efficient (Besson et al., 2020). As expected, fillet fat was also increased, with expected benefits for the smoking ability and texture of the fillets produced. The only result that was well below expectation was the gain in fillet yield, which was negligible at the same size. The strategy chosen was still efficient to reduce visceral mass while maintaining head yield unchanged. We could see very little if any genotype by feed interaction, but as such interactions are known to exist, a good precautionary approach would also be to select fish on feeds that are likely to be close to production feeds in the next years, to pre-adapt fish to their future feed environment. Finally, the Future feed we formulated showed excellent zootechnical performance, similar to that of commercial feed, and importantly was able to provide a fish with relatively high levels of EPA+DHA, while not using any of the most criticised raw materials in terms of sustainability, namely fishmeal, fish oil and soy-based products.

CRediT authorship contribution statement

Marc Vandeputte: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Geneviève Corraze**: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition. **Jérôme Doerflinger**: Investigation, Resources, Supervision, Writing – review & editing. **Florian Enez**: Investigation, Resources, Writing – review & editing. **Frédéric Clota**: Investigation, Writing – review & editing. **Frédéric Terrier**: Methodology, Resources. **Mathilde Horat**: Investigation. **Laurence Larroquet**: Investigation. **Vincent Petit**: Investigation, Methodology, Resources, Supervision, Project administration, Funding acquisition. **Pierrick Haffray**: Conceptualization, Methodology, Investigation, Supervision, Project administration, Funding acquisition, Writing – review & editing. **Sandrine Skiba-Cassy**: Conceptualization, Methodology, Investigation, Resources, Supervision, Project administration, Funding acquisition, Writing – review & editing. **Mathilde Dupont-Nivet**: Conceptualization, Methodology, Investigation, Supervision, Project administration, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

Jérôme Doerflinger, Mathilde Horat and Vincent Petit are running the commercial breeding programme which provided fish for the present experiment. Pierrick Haffray and Florian Enez are advising them for the design and operation of this breeding programme. The other 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.

Data availability

The data supporting this article are available from Recherche Data Gouv: https://doi.org/10.15454/EDIKCU.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2022.101363.

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